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Effects of Stocked Trout, Native Small-bodied Fish, and Winter Surface Aeration on Zooplankton in Small Boreal Foothills Lakes

by

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Abstract

Trout are commonly stocked into Alberta lakes to enhance angling opportunities. Many of these lakes contain native fish and require aeration to prevent trout winterkill. I assessed effects of trout and native fish on zooplankton abundance, biomass, size, community composition, and vertical distribution among six stocked, five unstocked, and three fishless lakes in the boreal foothills; I also investigated the impact of aeration in a Before-After-Control-Impact study. Stocked trout had limited affects on zooplankton communities and populations in lakes containing native fish, with greater microcrustacean richness and greater abundance of one rotifer species. Fish-bearing lakes (stocked and unstocked), however, differed greatly from fishless systems, with higher abundances of most taxa but smaller cladoceran and calanoid sizes. In fish-bearing lakes, conspicuous zooplankton also demonstrated selection for deeper water. No effect of aeration was detected. Thus, impacts of trout and aeration on zooplankton in boreal foothills lakes containing native fishes appear limited.

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Chapter 1. General Introduction

The History of Sport Fish Stocking in North America

Repeated glaciations during the Pleistocene epoch left many existing lakes throughout the continent relatively species poor and without large gamefish (Schmidt 1986; Underhilll 1986; Halliwell *et al.* 1999) and also created many landlocked lakes across the landscape and at high elevations in the Cordillera that were totally barren of fish (Bahls 1992; Donald 1987). Thousands of lakes were historically isolated from nearby fish populations by a lack of inlets/outlets or geographic barriers such as steep drainages and falls that prevented colonisation. Given this historical pattern of fish distribution, sport fish stocking in North American began in the late nineteenth century to increase the attractiveness of aquatic systems for tourism and recreation (Whittier and Kincaid 1999; Wiley 2003).

In North America, most fish introductions to lakes and streams that had historically lacked the introduced species occurred during the first half of the twentieth century when management was focused almost exclusively on fish harvest and consumption (Wiley 2003). The first introductions were done without management plans by cattlemen and miners, but they were followed by activities of government agencies with the construction of the first government hatchery in the late 1800s (Pister 2001). Despite the adoption of freshwater fisheries management by governments, unregulated introductions by sportsmen's clubs and private citizens continued till the mid twentieth century (Pister 2001). Often non-native species were considered more valuable than native fish that resided within the region, resulting in the spread of exotic gamefish taxa.

By the 1960s, concerns over the unintended effects of sport fish stocking began to emerge. At this time, the utilitarian ethic in fisheries management was slowly being replaced by one that acknowledged the value of biological integrity and the existence of diverse ecosystems (Pister 2001). Many scientists were concerned with a regional or global "homogenization" of assemblages, reducing among-lake diversity (Radomski and Goeman 1995; Vitousek *et al.* 1996). Concerns were also expressed over the extirpation of native populations of fish and other taxa.

As a result of historical practices, an estimated 95% of the nearly 16,000 originally fishless, high elevation lakes in the western USA contain non-native stocked fish, and approximately 60% of all lakes in western USA, including sites with or without native fish, have been stocked with exotic species (Bahls 1992). In northeastern USA, where the presence of native fishes is more prevalent, an estimated 74% of the region's 10,608 lakes contain at least one introduced sport fish species (Whittier and Kincaid 1999). Within western Canada's seven national parks (Banff, Jasper, Waterton Lakes, Yoho, Kootenay, Glacier, and Mount Revelstoke), at least 95% of the 1,464 lakes were devoid of fish prior to the twentieth century. Over the next eight decades, 305 of these "protected" lakes were stocked with non-native fish (Donald 1987).

Sport fish stocking was discontinued in Canada's national parks in 1988. Although a system-wide ban on non-native fish stocking has not been implemented across national parks in the USA, many American parks ceased the practice by the early 1990s. Some stocked lakes do not contain suitable spawning habitat for non-native species, resulting in the eventual extirpation of exotic fish following cessation of stocking while others maintain self-sustaining populations in the absence of stocking. Despite current concerns, sport fish stocking remains a widespread management technique outside national parks in North America and is mostly used to improve the quality and diversity of recreational fisheries, with a minority conducted for the conservation of threatened species (Cowx 1994; Cowx 1998; Young and Harig 2001). The popularity of many “created” fisheries and the difficulty in eradicating well established, introduced populations will likely result in the presence of non-native fish in many aquatic ecosystems far into the foreseeable future.

Effects of Stocked Sport Fish on Receiving Systems

As top predators in aquatic food webs, sport fish have the potential to alter populations of prey. Negative effects of stocking on native fauna have been well documented, though the severity of impacts appears to depend on characteristics of the receiving system, such as habitat structure and food web complexity (Dunham *et al.* 2004). Negative impacts have been documented for native gamefish (Schindler 2000), minnows (Whittier and Kincaid 1999), macroinvertebrates (Herbst *et al.* 2009), amphibians (Bradford *et al.* 1998), and certain zooplankton taxa (Donald *et al.* 2001). The majority of past research has focused on naturally fishless, headwater lakes and streams in high altitude areas where introduced fish have consistent (albeit selective) detrimental effects on native fauna (Knapp *et al.* 2001; Dunham *et al.* 2004). More recent research on relatively productive lakes in a variety of low elevation habitats, however, have shown that stocking can produce a successful fishery with little to no detectable impact on receiving systems (e.g., Hickley and Chare 2004).

In the absence of fish, headwater lakes, such as those in the North American Cordillera, often evolved distinctive aquatic communities containing taxa unable to coexist with fish (Schindler 2000). Typically these fishless systems have the predatory macroinvertebrate *Chaoborus* or a large calanoid copepod as the top predator (Anderson 1974; Donald *et al.* 2001). These invertebrates feed on small microcrustacean and rotifer prey (Elser *et al.* 1987; Paul and Schindler 1994). As a result of this size-limited predation, large microcrustaceans such as *Daphnia* and often other large invertebrates such as *Gammarus* flourish as these taxa can reach a size refuge where they are safe from the top predator (Anderson 1974; McNaught *et al.* 1999; Wilhelm 1999; Donald *et al.* 2001). The introduction of fish to naturally fishless lakes can eliminate or decrease the abundance of large conspicuous zooplankton and macroinvertebrate species (Blumenshine *et al.* 2000; Schindler 2000; Schabetsberger *et al.* 2009), resulting in a dominance of small rotifers (Schabetsberger *et al.* 2009). Subsequently, reduced grazing can alter algal biomass and species composition causing large or toxic taxa of phytoplankton to flourish (McNaught *et al.* 1999; Schindler 2000), which, in turn, can decrease water clarity and quality.

In addition to the direct effects of trout predation on native fauna, stocking with non-native gamefish can also have indirect effects on taxa within receiving systems. Native small-bodied fish and zooplankton may alter their habitat use in the presence of trout, spending more time in areas that provide refuge from these large visual predators. Native fish will often allocate more time to littoral versus pelagic habitats in the presence of trout, where dense macrophyte beds provide shelter from these picivorous predators (Dupuch *et al.* 2009). Vertical migration to deeper and darker waters during the day has also been observed in large conspicuous zooplankton that are favored prey of small-bodied trout (Hembre and Megard 2003). At night, these zooplankton taxa return to epilimnetic waters, where conditions (e.g., food, temperature) are more favorable to growth and reproduction (Johnsen and Jakobsen 1987; Leibold 1990; Dini and Carpenter 1992).

Unlike the naturally fishless, headwater systems that experience particularly severe effects from sport fish stocking, many lakes within Alberta's boreal foothills are relative productive (mesotrophic) and contain natural populations of small-bodied fish. Numerous lakes in this area are stocked annually with non-native trout. Previous studies on these systems have found little direct impact of stocked trout on native taxa including small-bodied fish (Nasmith *et al.* 2010), macroinvertebrates (Nasmith *et al.* 2012), and amphibians (Schank *et al.* 2011), although the indirect effect of altered habitat use has been observed for native fish (Hanisch *et al.* 2012). The direct and indirect impacts of stocking on zooplankton in lakes in this area is not known.

As zooplankton have coexisted with native fish in these lakes prior to trout stocking, zooplankton communities may be well adapted to the presence of a fish predator. Native fish may have structured zooplankton communities through predation preceding trout introductions since native small-bodied fish and non-native trout show similar size selectivity for large zooplankton prey. In addition, boreal foothills lakes have moderate productivity, which could contribute resilience of native populations, as well as decreased water clarity and thus decreased ability of fish to detect invertebrate prey (Liljendahl-Nurminen *et al.* 2008)

Sport Fish Stocking in Alberta

Of the 62 species of fish found within Alberta, 52 are native and 10 are introduced (Zwickel 2012). Recreational, commercial, and domestic fisheries rely on 19 of these species while the remaining 43 are mostly small-bodied and of little economic interest despite their ecological importance as predators of aquatic invertebrates and prey for large fish and fish-eating birds and mammals (Zwickel 2012). Compared to other prairie provinces, Alberta has more anglers, but a smaller number of lakes, resulting in relatively high angling pressure. Angling pressure combined with habitat alterations due to human use of land and water has, in recent decades, resulted in the decline of many fish populations (Post *et al.* 2002). Currently several species of native gamefish are listed as "at risk" or "threatened" within the province including Bull Trout (*Salvelinus confluentus*), Lake Sturgeon (*Acipenser fluvescens*), Athabasca Rainbow Trout (*Oncorhynchus* *mykiss athabascae*), Western Cutthroat Trout (*O. clarkii lewisi*) and Arctic Grayling (*Thymallus articus*). In addition, 21 of 27 Walleye (*Stizostedion vitreum*) populations have shown signs of collapse due to overfishing, with strong evidence also available for the overexploitation of many populations of Northern Pike (*Esox lucius*, Post *et al.* 2002).

Recently, changes to sport fish regulations and management actions have led to the recovery or re-establishment of some populations in the province such as Walleye and a few Bull Trout populations in protected parks (Zwickel 2012). Stocking fishless lakes and lakes that lack sport fish has also alleviated some angling pressure from native gamefish populations, while dealing with high demands for fishing opportunities. Of the 20.8 million sport fish stocked in Alberta's freshwater ecosystems in 2010, 18 million were Walleye that were often native to the lakes where they were stocked, while an additional 2.6 million were non-native trout (ASRD 2010 Stocking Report).

The high demand for recreational fishing within Alberta is evident from the 252,000 anglers that bought sport fish licences in the province in 2010 (Zwickel 2012). This does not include unlicensed youth (<16) and seniors (>64) that brought the total to an estimated 336,000 anglers that year (Zwickel 2012). These anglers caught an estimated 17.3 million fish during 2010 (Zwickel 2012), with an uneven distribution of fishing efforts within the province. Of those fish caught, 2.4 million fish were harvested, while the remainder were released. Since most of Alberta anglers reside in central and southern Alberta along the Edmonton-Red Deer-Calgary-Lethbridge corridor, it should come as no surprise that 65% of fishing effort was in the southern one third of the province (the area south of Edmonton, Zwickel 2012).

Despite high angling pressure on native sport fish populations and the potential impact of non-native sport fish on aquatic systems, recreational fisheries not only provide enjoyment to residents and visitors within the province but also hold economic value. An estimated 488 million dollars in expenditures and investments was attributed directly to sport fishing within Alberta in 2010 (Zwickel 2012). Managers in the province are now faced with the potentially difficult balance of recreational fishery promotion and the conservation of natural ecosystems and resources.

The Alberta Conservation Association, along with Alberta Sustainable Resource Development, manages the stocking and aeration program within Alberta that is used to enhance angling opportunities. Besides the 800 lakes in the province with natural sport fish producing capabilities, another 300 lakes and ponds that lack appropriate spawning habitat are stocked annually or biennially with hatchery-raised fish (Zwickel 2012). This includes a series of lakes and ponds in the boreal foothills along the east slopes of the Rocky Mountains about 200 km from the two largest cities in the province (Edmonton and Calgary). These lakes are stocked with one or more salmonid species, including Brown Trout (*Salmo trutta*) native to Europe, Brook Trout (*Salvelinus frontinalis*) native to eastern North America, and non-native strains of Rainbow Trout (*Oncorhynchus mykiss*) originally from several western North American regions. Unlike many other gamefish species, these trout are generalist predators as adults that feed on a variety of vertebrate and invertebrate prey (Beauchamp 1990; Nelson and Paetz 1992; Lynott *et al.* 1995) and thus have the potential to directly impact a diversity of taxa.

Due to the relatively high productivity and shallow depth of many Alberta lakes, such as those in the boreal foothills, dissolved oxygen can be a major limiting factor in the survival of sport fish populations. As a result, many lakes require winter aeration to prevent winterkills of fish and maintain oxygen levels suited to introduced sport fish. When lakes are at high risk of winterkill, surface aeration is often implemented in fisheries management due to high oxygen input rates and low power and maintenance requirements of surface versus subsurface aeration. Over-winter survival of gamefish allows these introduced species to achieve larger sizes, which results in superior fishing opportunities within aerated systems (Ashley and Nordin 1999).

In addition to non-native trout stocking, winter surface aeration could also impact native fauna in a number of ways, including changes to the abiotic characteristics of lakes (McCord *et al.* 2000, Miller *et al.* 2001) or predator-prey interactions due to increased winter survival of target and non-target predators (Miller and Mackay 2003; Nasmith *et al.* 2010). The limited research on the effects of artificial aeration has focused on year-round aeration and subsurface aeration systems leaving uncertain the impact of winter surface aeration on zooplankton communities.

Objectives

The impact of stocking programs on productive, fish-bearing lakes is poorly studied, raising questions regarding the effects of food web complexity on the impact of an introduced predator. Despite the widespread practice of stocking trout in boreal lakes, my study will be the first to determine if native small-bodied fish can structure zooplankton assemblages to the presence of fish predators prior to trout stocking, while investigating the additional effect of artificial aeration. An understanding of the influence of native fish and aeration on the effects of trout could allow lakes to be ranked in terms of suitability for stocking and could also allow for the identification of species with heightened sensitivities.

The primary objectives of my study are to document impacts of the non-native trout stocking program (both trout introduction and winter surface aeration) on native zooplankton communities in Alberta’s boreal foothills lakes that contain native small-bodied fish and to assess the ability of native fish to structure zooplankton communities to fish predation prior to trout stocking. More specifically, in Chapter 2, I examine the effects of trout and native fish on microcrustacean communities. In Chapter 3, I investigate the effects of trout and native fish on rotifer communities. In Chapter 4, I consider the impact of trout and native fish on the vertical distribution of both microcrustaceans and rotifers. In Chapter 5, I investigate short-term effects of winter aeration, aimed at preventing trout mortality due to hypoxia, on both microcrustacean and rotifer communities. Finally, in Chapter 6, I summarize my findings and make recommendations to resource managers based on my results.

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Chapter 2. Effects of stocked trout and native small-bodied fish on pelagic microcrustacean communities in small boreal foothills lakes

Introduction

Sport fish stocking is a management practice employed throughout North America to enhance angling opportunities. Such stocking creates and enhances populations of gamefish where they were previously absent. Many species used for this purpose belong to the family Salmonidae, such as Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*), and Brook Trout (*Salvelinus fontinalis*). In Alberta, stocking supports recreational fisheries in 345 lakes, with over 2,000,000 trout released into the province's freshwater ecosystems in 2010 (Zwickel 2012). Though trout stocking in Alberta supports a popular recreational fishery of over 250,000 anglers (Zwickel 2012), the introduction of non-native trout into surface waters could alter populations of native taxa, as sport fish typically act as top predators in aquatic food webs.

Unlike many gamefish that are specialist predators, trout feed on a variety of fish species as well as terrestrial, benthic, and pelagic invertebrates, with diet depending on both size and maturity (Beauchamp 1990; Nelson and Paetz 1992; Lynott *et al.* 1995). Similar to other gamefish, trout are gape-limited predators (Montori *et al.* 2006), as well as size selective feeders, choosing large-bodied prey over small individuals (Budy *et al.* 2005). Since trout feed on an assortment of taxa, stocking these fish could impact a number of species and alter aquatic communities through selective feeding on large conspicuous prey.

Negative effects of trout stocking on a variety of native prey communities have been documented throughout the world, including native small-bodied fish (e.g., Townsend 1996; Jellyman and McIntosh 2010), macroinvertebrates (e.g., Bradford *et al.* 1998; Herbst *et al.* 2009; Martinez-Sanz *et al.* 2010), and amphibians (e.g., Bradford *et al.* 1998; Mathews *et al.* 2001; Welsh *et al.* 2006). In addition to these larger prey organisms, trout can also have strong selective effects on microcrustacean communities (Bradford *et al.* 1998). Stocking mountain lakes in North America with Rainbow, Brown, and Brook Trout has decreased the abundance and mean body size of microcrustacean taxa (Carlisle and Hawkins 1998; Schindler 2000; Parker *et al.* 2001). In many cases, common large-bodied species become rare or absent in stocked lakes (Bradford *et al.* 1998). Outside North America, the introduction of Rainbow and Brown Trout has also impacted the structure of microcrustacean communities in mountain lakes through decreased size and biomass of microcrustaceans in Denmark and New Zealand (reviewed by Jeppesen *et al.* 1997; Jeppesen *et al.* 2000).

Indeed, the most pronounced effects of trout stocking have been documented in unproductive and naturally fishless mountain lakes and streams, where native communities evolved in the absence of fish (reviewed by Dunham *et al.* 2004). Effects in other environments, however, can be difficult to predict due to the varying responses of different taxa and differences in native community-structure and habitat characteristics across lake ecosystems (Dunham *et al.* 2004). Although research on this topic has focused on headwater lakes in the North

American Cordillera, the majority of stocked lakes in Alberta are located in the Boreal Plains and Prairies ecoregions and remain relatively understudied. These lowland areas contain freshwater systems that differ from mountain systems by having higher productivity, greater species diversity, and often, dense populations of invertebrates and native small-bodied fishes.

Studies outside mountain systems have shown that the effects of trout stocking are not universal. No or reduced effects of salmonids on native fish abundance and macroinvertebrate communities have been detected globally in lowland lakes compared to adjacent, high-elevation alpine systems (Wissinger *et al.* 2006; Pink *et al.* 2007; Schilling *et al.* 2009a). Similarly, limited effects of trout stocking have been observed for microcrustacean communities beyond high-altitude, headwater lakes (Hembre and Megard 2005; Aguilera *et al.* 2006; Drouin *et al.* 2009).

In the boreal foothills of west-central Alberta, previous studies have similarly detected only weak effects of trout. Trout stocking in lakes did not affect the density and recruitment of native fish (Nasmith *et al.* 2010), community composition and size structure of macroinvertebrates (Nasmith *et al.* 2012), or amphibian abundance (Schank *et al.* 2011), but did alter habitat use by native fish, which spent increased time in littoral versus pelagic areas in the presence of trout (Hanisch *et al.* 2012). To extend the investigation of trout effects in these systems, I examined the impact of trout on microcrustacean communities within the pelagic zone of these lakes. Unlike most studies on trout and microcrustaceans, the stocked lakes here contained both non-native trout and native small-bodied fish. Since trout prey upon both plankton and planktivorous fish, they could affect microcrustacean communities both directly as predators and indirectly through a trophic cascade (Elser *et al.* 1995), including altered habitat use and foraging of mid-level predators. If sufficient native fish move to littoral areas in the presence of trout, then overall vertebrate planktivore density in the pelagic zone of lakes could remain constant or even decrease after trout stocking.

Planktivory by native fish prior to trout introduction could also reduce the impact of stocking since, like trout, native fish prefer large-bodied prey (Naud and Magnan 1988; Laurich *et al.* 2003). The presence of native small-bodied fish could thus "structure" prey assemblages prior to the arrival of trout. If non-native trout and native small-bodied fish exhibit similar predation pressure on pelagic microcrustacean communities, then one would expect no additional effects after trout stocking if pelagic planktivore densities do not drastically change. Rather than stocked vs. unstocked, I suggest that the significant ecological contrast exists between lakes with and without planktivorous fish (fish-bearing versus fishless lakes).

To examine the independent effects of introduced trout and native small-bodied fish on pelagic microcrustacean communities, I collected samples from stocked, unstocked (but with native fish), and fishless lakes in the boreal foothills of Alberta throughout most of the ice-free season (May through August). All stocked lakes contained non-native trout (mostly Rainbow Trout), while both stocked and unstocked lakes contained native small-bodied fish. Lakes chosen for stocking are generally those with native fish, as those lakes tend to have more suitable habitat for trout (e.g., greater depth, less productive) than fishless lakes. Overlap in physical and chemical characteristics among the three lake types, however, does exist.

I examined microcrustacean abundance, biomass, mean individual body length, mean taxon body length, size structure, and community composition on a monthly basis to determine how native fish and trout affect microcrustacean communities and their seasonal succession. Due to greater vulnerability of large taxa to predation by fish, I expected smaller mean body lengths within and among taxa, and a smaller proportion of large individuals for all major taxa (Cladocera, Calanoida, and Cyclopoida) in stocked and unstocked (fish-bearing) lakes compared to fishless systems. In the absence of fish, macroinvertebrate predators, such as *Chaoborus,* can occur in high densities (Von Ende 1979). These macroinvertebrate predators selectively feed on small microcrustaceans compared to planktivorous fishes (Elser *et al.* 1987), which could also contribute to a difference in mean body lengths between fish-bearing and fishless lakes.

I expected a greater abundance of each of the three major microcrustacean groups in fish-bearing compared to fishless lakes. In fish-bearing lakes, smaller species and individuals should flourish since fish will not select for these small individuals, while in fishless lakes, effective feeding by macroinvertebrate predators on small individuals and strong competition with (and within) large individuals should keep the microcrustacean abundance low. A smaller mean body length, but greater abundance in fish-bearing compared to fishless lakes should then result in a comparable biomass between lake types.

Due to differences in predation pressures, I expected fish-bearing and fishless systems to harbor distinct communities. I expected this difference to increase as the summer progressed as predation by fish in fish-bearing lakes should increase after spring stocking and young-of-year native fish hatching and since predation by pelagic macroinvertebrates in fishless systems should increase as larval abundance, activity, and consumption increase along with warming temperatures. Since, large-bodied taxa are capable of excluding small, competitively inferior species, and planktivorous fish can mediate the coexistence of species, I also expected a greater richness, diversity, and evenness in fish-bearing compared to fishless lakes. As study lakes are broadly comparable in physical, chemical, and biological properties (other than fish presence), I did not expect environmental variables to play a major role in structuring microcrustacean communities compared to the presence of trout and native fish, and expected fish presence to explain more of the variation in the community data sets then environmental variables.

Methods

Study Area

Microcrustaceans were sampled from 14 lakes in the boreal foothills near the towns of Rocky Mountain House (52°22’39’’N and 144°54’37’’W) and Caroline (52° 5’36’’N and 114°45’28’’W), Alberta. Samples were collected from May through August 2009 from lakes that were either stocked with trout (n=6), unstocked but containing native fish (n=5), or fishless (n=3). Four of the stocked lakes supported trout populations for 10-60 years. Ironside Lake was stocked for the first time in 18 years four years prior to this study, and Fiesta Lake, was initially stocked two years prior. Rainbow Trout were the main gamefish stocked in the study lakes with the exception of Mitchell Lake, which contained both Rainbow and Brown Trout, and Birch Lake, which had only Brook Trout. Depending on lake size and the management strategy, between 250 and 20,300 trout/lake were stocked between May-June 2009 (Table 2-1). Stocking strategies included low density stocking of larger trout for catch-and-release fisheries (e.g., Ironside), and higher density stocking that allowed fish removal but resulted in a smaller mean fish size (e.g., Strubel). In addition to being stocked, four of six stocked lakes received aeration to prevent fish-kills. These lakes had been aerated for 2-10 years using one to three floating aerators with ½ to 1 hp motors. Beaver Lake was aerated throughout the year, while the other three lakes received aeration from mid-October to early April.

Stocked and unstocked lakes supported native fish populations including Fathead Minnow (*Pimephales promelas*), Brook Stickleback (*Culaea inconstans*), Pearl Dace (*Margariscus nachtriebi*), and a dace species complex consisting of Northern Redbelly Dace (*Chrosomus eos*), Finescale Dace (*Chrosomus neogaeus*), and their parthenogenic hybrid (Appendix A). Native small-bodied fish densities were monitored between 2005-2009 and were found to vary between years and lakes but usually ranged from 2000 to 10,000 fish/ha (Nasmith *et al.* 2010; J. Hanisch, University of Alberta, unpublished).

Lakes were relatively small and shallow, typically surrounded by forest. Two lakes (Strubel and Teal) had a small amount of shoreline development in the form of cottages, whereas several other lakes (Dog Leg, Picard, Dog Paw, and Conundrum) had a mix of cattle pastures and forest stands. Many shorelines supported thick patches of *Typha latifolia*. The dominant macrophytes within lakes were *Potamogeton* spp., *Sparganium angustifolium*, and *Nuphar variegatum* (Nasmith *et al.* 2010).

Water Chemistry

I monitored study lakes monthly (May- August 2009) for chemical, physical and biological factors. Epilimnetic water samples were collected just below the waters surface at the deepest location within each lake. I filtered water samples (200 mL) through GFF filters onsite; filters were then frozen for chlorophyll-a (Chl-a) analysis. Other water samples (500 mL) were refrigerated until analysed for total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorous (TP), and total dissolved phosphorous (TDP). Samples were processed within 7 days of collection by the Biogeochemical Analytical Laboratory at the University of Alberta. Procedures followed the guidelines of the Canadian Association for Environmental Analytical Laboratories (M. Ma, Biogeochemical Analytical Laboratory, personal communication).

I took temperature and dissolved oxygen (DO) profiles at the end of each month, using an OxyGuard International Handy Mark II meter, with readings taken from the deepest known location in lakes every meter from just below the waters surface to about 1 m above the lake bottom. Readings were recorded for both up- and down-casts, with the average of the two used for vertical profiles. I used a pH/conductivity meter to take single readings just below the waters surface and measured Secchi transparency monthly (May-August).

Microcrustacean Collection and Laboratory Processing

All 14 study lakes were sampled monthly (May- August 2009) during the last week of each month. Pelagic microcrustaceans were collected as discrete samples at 1-m intervals at the deepest location in each lake using a 30-L Schindler-Patalas trap with a 63 μm mesh dolphin-cup. Samples were stored in jars and preserved in 80% ethanol until laboratory processing. For May, June, and August, samples from each metre were combined to produce a single composite sample for each lake while the samples from each depth were processed separately for July to examine depth distribution (see Chapter 4).

Individuals were counted and identified down to the lowest feasible taxonomic level (LFTL; generally species, however family was used for Chydoridae) using a dissecting microscope with a PVC Ward counting-wheel. Identifications were made based on Ward and Whipple 1966. In the case of damaged individuals, only fragments with a head were counted to avoid counting an individual twice. Samples were sub-sampled until at least 250 individuals were detected, consisting of a maximum of 50 individual from each LFTL group. All individuals in a sub-sample were counted but sub-sampling did not halt until the 250 criterion was met for that sample. This method results in final counts greater than 250 individuals, but provides greater detection of rare taxa. Sub-samples were taken using a 1 mL Hensen-Stempel pipette.

A subset of each taxon (n=15 per sample if possible) was measured using a calibrated ocular micrometer. Individuals chosen for measurements were initially intact. Measurements were dorsal lengths excluding appendages/projections such as spines, setae and caudal rami with individuals straightened before measurements were taken. These measurements were used to determine the mean length of each taxon, which was used along with taxon abundance data to determine biomass. Biomass calculations were conducted as described by McCauley (1984) and Culver *et al.* (1985).

Chaoborus collected in plankton samples were counted and identified to species. *Chaoborus* are known predators of small pelagic microcrustaceans and were the only macroinvertebrate caught consistently in the plankton trap during the study (the occasional Acari or *Gammarus* was also found). For May, June, and August only the first 20 *Chaoborus* were counted and identified down to species, while in July only the first 20 were identified while all individuals in a sample were counted.

Statistical Analyses

Univariate analyses were conducted using SPSS Statistics 19.0 (SPSS for Mac OS X, Rel. 19.0.0 2010). A nonparametric K-S test assessed normality for each data set and Levene’s test of Equality of Variances assessed the homogeneity of variance. Data that were not normally distributed were $\log_{10}$ (x+1) transformed. For all Linear Mixed Models, if the interaction term was not significant ($p>.05$), it was removed from the analysis so the remaining explanatory variables could explain the variance in the data that was potentially being explained by the non-significant interaction. Results were considered significant if $p<0.05$, and marginally significant if $0.05<p<0.1$.

Lake area and maximum depth data from the 14 lakes were analyzed using one-way ANOVAs to determine if lake types differed. TN, TDN, TP, TDP, Chl-a, pH, conductivity, Secchi depth, surface temperature, maximum DO and minimum DO were analyzed using Linear Mixed Models with lake type, month, and their interaction as fixed variables and lake as a random variable.

I determined abundance, biomass, mean individual body length, and mean taxon body length (at the LFTL) for Calanoida, Cyclopoida, and Cladocera across all 14 lakes in each monthly sampling period (May-August 2009). Juvenile cladocerans and copepod copepodites were grouped with adults due to the low abundance of adults in some months. Taxonomic groups were chosen based on the presence of individuals in all three lake types (stocked, unstocked, and fishless) in each month investigated and similarities in life-history (e.g. feeding behavior and development) among taxa in each order.

Mean individual body length was calculated by taking the average length of each taxon within an order and then calculating weighted mean individual length based on the proportions of taxa present. Mean taxon body length was calculated using the average length of each taxon within an order and then taking the average of those average lengths.

Linear Mixed Models assessed differences in abundance, biomass, mean individual length, and mean taxon length among the three lake types and the four sampling periods using lake type, month, and their interaction as fixed variables and lake as a random variable. Due to insufficient sample sizes (<15 lengths/lake/sample periods), May was excluded from cladoceran length analysis, whereas May and June were excluded from calanoid and cyclopoid analyses. I also assessed differences in *Chaoborus* abundance among lake types in July using a one-way ANOVA.

For orders and sampling periods that had sufficient sample sizes (>15 lengths/lake/sample period), I analyzed proportions of large individuals in a lake. "Large" was defined as lengths in the 4th quartile of the distribution for each taxon across all lakes and months. Comparisons among lake types were made using the same Linear Mixed Model described above.

To examine if fish predation was size-selective, I analyzed quantile-quantile (QQ; *sensu* Post and Evans 1989) plots of the mean length distribution in stocked versus fishless lakes, unstocked versus fishless lakes, and stocked versus unstocked lakes for orders and sampling periods with sufficient sample sizes (>15 lengths/lake/sample period). QQ plots were used to transform length-frequency-distributions into linear functions by plotting the length at each quantile. This allowed distributions to be compared between lake types. Distributions for each taxon were compared at the following quantiles: 1, 5, 10, 25, 35, 50, 65, 75, 90, 95, and 99. A one-sample t-test was used to determine if the mean slope (from the sampling periods) for each taxon differed from 1. In QQ plots, a slope of 1.0 indicates no difference in the distribution of two lake types. A slope < or > 1, however, indicates potential size-selective predation in one or the other lake type.

Community composition and structure were analyzed using several different procedures. To assess differences in Shannon-Weiner diversity, richness, and evenness (% of maximum diversity; Legendre and Legendre 1998), I applied Linear Mixed Models with lake type, month, and their interaction as fixed variables, and lake as a random variable. Juvenile cladocerans, copepod copepodites and nauplii could not be identified down to species and were removed from the analyses. When significant lake-type effects were identified for diversity and richness, these measures were regressed against lake area and depth using linear regression analysis since these physical attributes can provide increased heterogeneity within lake ecosystems and thus additional habitats for taxa (Tessier and Welser 1991).

To compare patterns of microcrustacean community composition between the three lake types, I used Nonmetric Multidimensional Scaling (NMS) ordinations on species presence/absence data. NMS lacks assumptions that are rarely met with community data (McCune and Grace 2002). Ordinations were conducted separately for each sampling period, and for all lake-months combined; for the latter analysis, lake type-month centroids were plotted to illustrate the succession of microcrustacean communities through time. Ordinations were performed using the "slow and thorough" method of PC-ORD version 6.0 (McCune and Mefford 2011). Data sets were checked for rare taxa (occurring in < 3 lakes), which were deleted or merged with a larger taxonomic group. NMS ordinations were performed using Sorensen (Bray-Curtis) distance measure. When three or more axes were recommended, the two axes that represented the most variation were plotted for visual assessment. Biplots of taxa ($r^2 > 0.5$) and environmental variables ($r^2 > 0.3$) were also plotted.

To represent the relationship among microcrustacean communities in study lakes, cluster analyses were performed separately for each month on species presence/absence data. Analyses used Sorensen (Bray-Curtis) distance measure and group average as the linkage method.

To test for compositional differences among the three lake types, I performed Multiple Response Permutation Procedures (MRPP; McCune and Grace 2002) on species presence/absence data. MRPPs were also performed on environmental data. Preliminary analyses revealed significant or marginally significant effects of area and maximum depth; to see if the lake types differed using the remaining environmental variables (TN, TDN, TP, TDP, Chl-a, pH, conductivity, surface temperature, Secchi depth, and maximum and minimum DO), area and depth were removed from the final analyses. All MRPPs were done separately for each month.

Mantel Tests were performed on microcrustacean and fish species presence/absence data to compare similarities between the two matrices. Fish taxa included were trout, Fathead Minnow, Brook Stickleback, dace species complex, and a "fishless" category. Mantel Tests were also performed on microcrustacean and environmental data. Again, area and maximum depth were recognized as important contributors to similarities between microcrustacean and environmental matrices in preliminary analyses and were again removed from the analysis to assess relationships with the remaining environmental variables. All Mantel Tests were done separately for each sampling period.

A two-way Variance Partitioning Analysis (VPA; Borcard *et al.* 1992; Hall *et al.* 1999) was used to assess the proportion of variance in the microcrustacean community composition that could be explained by the environmental variables and the fish assemblage type (stocked, unstocked, and fishless). Analyses were conducted using CANOCO for windows, version 4.5 (ter Braak and Smilauer 2006). Based on the length of the dominant axis from a preliminary detrended correspondence analysis (DCA), I determined that a linear model (using redundancy analysis – RDA) was appropriate for the VPA (ter Braak and Smilauer 2006). Environmental variables entered the analysis based on forward stepwise selection ($p<0.09$; ter Braak and Smilauer 2006). VPA was conducted for June, July, and August.

Results

Across the 14 study lakes and four sampling periods I collected and identified 13 cladoceran, 3 cyclopoid and 3 calanoid species (Table 2-2). In total, 143,194 microcrustaceans were counted, while 13,709 microcrustaceans were measured from the 130 samples collected. As expected, stocked lakes had a greater area compared to unstocked and fishless lakes, and were deeper compared to fishless lakes (one-way ANOVAs, Table 2-3).

Water Chemistry

All lakes showed varying degrees of stratification by the end of July with the most pronounced temperature drops at the thermocline occurring in the deeper lakes. Thermal stratification often prevented oxygen mixing into the lower half of the water column (regardless of lake depth) with a metalimnetic DO peak detected in at least one month (May, June, and/or July) for most lakes (Appendix A).

Nutrients, Chl-a, and surface temperature were all lower in the stocked compared to unstocked and fishless lakes, whereas Secchi depth was greater in stocked compared to unstocked and fishless lakes (Linear Mixed Models, Table 2-3). These parameters indicated that stocked lakes were mesotrophic, while unstocked and fishless lakes were meso-eutrophic (Carlson 1977). No difference among lake types was found for pH, conductivity, and minimum DO (Table 2-3). A significant effect of month was seen for most environmental variables. TN, TDN, surface temperature, and Secchi depth increased significantly from May-July and then dropped in August. TP, Chl-a, and conductivity were all significantly higher in May (and June for conductivity), compared to other months.

Microcrustacean Abundance, Biomass, and Length

Overall, cladoceran abundance differed marginally with respect to lake type ($p=0.061$) and significantly with respect to month ($p<0.001$, Linear Mixed

Model). Cladoceran abundance was greater in stocked compared to fishless lakes (p=0.022), with unstocked lakes intermediate (Table 2-4). Abundance was lowest in May (p<0.001) and highest in July (p<0.001).

Calanoid abundance differed among lake types (p=0.029) and months (p<0.001), with a significant interaction (p= 0.042). Abundance was lowest in fishless lakes (p<0.03), but similar between stocked and unstocked lakes (p=0.904). Abundance was lowest in May and June (p≤0.012), but similar in July and August (p=0.246). The abundance in stocked and unstocked lakes increased dramatically in the summer (June-August) compared to spring (May), while fishless lakes experiences a relatively minimal increase during summer months (Table 2-4).

Cyclopoid abundance differed among lake types (p=0.012) but not among months (p=0.334). Cyclopoid abundance was lowest in fishless lakes (p≤0.032) but did not differ between stocked and unstocked lakes (p=0.213, Table 2-4).

Cladoceran and calanoid biomass differed among months (p<0.001) but not lake types (p≥0.159). Cladoceran biomass was lowest in May (p<0.001) and highest in July (p≤0.089; Table 2-4). Calanoid biomass was also lowest in May (p<0.001) and highest in July and August, which did not differ from each other (p=0.976, Table 2-4).

In contrast, cyclopoid biomass differed among lake types (p=0.002) but not among months (p=0.296). Cyclopoid biomass was lowest in fishless lakes (p≤0.015) and marginally lower in unstocked than in stocked lakes (p=0.066, Table 2-4).

No differences in mean individual cladoceran length were detected for lake type (p=0.558) or month (p=0.909, Table 2-5). However, cladoceran taxa were largest in fishless lakes (p≤0.006), but mean taxon length did not differ between stocked and unstocked lakes (p= 0.230, Table 2-5).

Calanoid mean individual length differed marginally among lake types (p=0.088) but not among months (p=0.240). Overall, individual calanoids in fishless lakes were larger and marginally larger than in stocked and unstocked lakes, respectively; no difference was detected between unstocked and stocked lakes (p=0.621, Table 2-5). Calanoid mean taxon length also differed among lake types (p= 0.034) but not months (p= 0.116). Fishless lakes supported larger (p= 0.011) and marginally larger (p= 0.056) calanoid taxa than stocked and unstocked lakes, respectively; no difference was detected between the latter lake types (p= 0.343, Table 2-5).

The mean length of individual cyclopoids did not differ among lake types (p=0.333) or months (p=0.425, Table 2-5). Similarly, no difference in mean lengths of cyclopoid taxa existed among lake types (p= 0.162) or months (p= 0.393, Table 2-5).

Microcrustacean Size Structure

The proportion of large individual cladocerans was marginally significant among lake types (p= 0.095; Linear Mixed Model), but months did not differ (p= 0.914). Proportionately fewer large individuals occurred in unstocked compared to fishless lakes (p= 0.034), with stocked lakes having intermediate levels ($p \geq 0.174$, Figure 2-1).

A significant effect of lake type (p= 0.043), month (p= 0.044), and their interaction (p= 0.044) was found for the proportion of large calanoids. Pairwise comparisons of lake types found a significantly lower proportion of large individuals in stocked compared to fishless lakes (p= 0.020) and a marginally lower proportion in stocked compared to unstocked lakes (p= 0.066). No difference was detected between unstocked and fishless lakes (p= 0.370). Pairwise comparison of months found a significantly lower proportion of larger calanoids in July compared to August (p= 0.044). The proportion of large calanoid individuals increased substantially from July to August in fishless lakes but not in the two fish-bearing lakes types (Figure 2-1). For cyclopoids the proportion of large individuals was not related to either lake type (p= 0.188) or month (p= 0.551, Figure 2-1).

To examine if fish predation was size-selective, I analyzed quantile-quantile (QQ) plots of the mean length distributions of microrustacean orders in the different lake types. In the comparison of stocked versus unstocked lakes (Appendix B), the average slope for cladocerans (*t*-test, t_2=0.728, p=0.542) and cyclopoids (*t*-test, t_2=-0.081, p=0.943) did not differ from 1, while calanoids (*t*-test, t_2=-5.058, p=0.037) had an average slope <1, indicating size selectivity for large calanoids in stocked compared to unstocked lakes. For stocked versus fishless lakes (Appendix B), the average slope for cyclopoids did not differ from 1 (*t*-test, t_1=2.256, p=0.266). In contrast, the average slope for cladocerans was <1 (*t*-test, t_2=-18.393, p=0.003), and average slope was marginally <1 for calanoids (*t*-test, t_1=-6.491, p=0.097), indicating size selectivity for large cladocerans and calanoids in stocked compared to fishless lakes. For unstocked versus fishless lakes (Appendix B), the average slope for calanoids (*t*-test, t_1=-5.079, p=0.124) and cyclopoids (*t*-test, t_1=5.820, p=0.108) did not differ from 1, whereas the average slope for cladocerans (*t*-test, t_2=-4.404, p=0.048) was <1, indicating size selectivity for large cladocerans in unstocked compared to fishless lakes.

Microcrustacean Community Composition

Crustacean richness differed among lake types (p=0.002) and months (p<0.001, Linear Mixed Model). Species richness was greater in stocked compared to unstocked (p=0.004) and fishless lakes (p=0.002); unstocked and fishless lakes did not differ (p=0.376). For all three lake types, species richness increased from May through July and then dropped in August (Table 2-6).

Shannon diversity also differed among lake types (p=0.011) and months (p=0.011). Diversity was highest in stocked lakes (p=0.010), whereas unstocked and fishless lakes did not differ (p=0.693). For all three lake types, diversity increased from May through July and then dropped in August (Table 2-6). Correlation analyses indicated that lake area potentially contributed to differences in diversity and richness among lake types at certain points during the spring/summer, but depth was not likely a contributing factor (Table 2-7).

Evenness differed among months (p=0.043) but not among lake types (p=0.309), and the interaction was significant (p=0.021). Evenness in stocked lakes increased throughout the summer, whereas in unstocked and fishless lakes evenness was higher at the beginning and end of summer with low evenness in June and July (Table 2-6).

No useful ordination of microcrustacean communities were created for May, most likely due to the absence of many crustacean taxa as identifiable adults. For May, three major groups emerged from the cluster analysis, but these groups did not reflect fish community types, suggesting little effect of fish in structuring microcrustacean communities during the spring (Figure 2-6). Indeed, MRPP indicated no significant difference in microcrustacean community composition among lake types in May (p=0.461), nor were the crustacean and fish community matrices related (Mantel Test; p=0.121). MRPP also indicated that there was no difference in environmental factors (area and maximum depth removed) among the three lake types in May (p=0.179), and the crustacean and environmental matrices (area and maximum depth removed) were not related (Mantel Test; p=0.183).

The ordination for June (Figure 2-2) represented 81% of variance in the data set (15 taxa), at a stress level of 12.7 (Monte Carlo test, p= 0.043). Crustacean taxa that were strongly correlated with the two axes (r^2>0.5) included *Diaptomus leptopus*, *Skistodiaptomus oregonensis*, *Mesocyclops edax*, *Daphnia pulex* and *Diaphanosoma*. Environmental variables that were strongly correlated with the two axes (r^2>0.3) were TP, TDP, surface temperature, and area. The three major groups that emerged from cluster analysis strongly reflected the fish community types (Figure 2-6). The first, most distinct, group comprised all three fishless lakes, a single unstocked lake formed the second group, and the remaining fish-bearing lakes (stocked and unstocked), made up the third group. MRPP identified a significant difference in community composition among lake types in June (p=0.001). Composition differed for both stocked vs. fishless lakes (p=0.002) and unstocked vs. fishless lakes (p=0.019); composition in stocked and unstocked lakes were marginally different (p=0.054). In June, the crustacean and fish community matrices were related (Mantel Test; p=0.003), whereas the crustacean and environmental matrices (area and maximum depth removed) were not related (Mantel Test; p=0.459).

The ordination from July (Figure 2-3) represented 47% of variance in the data set (16 taxa), at a stress level of 9.5 (Monte Carlo test, p= 0.003). Microcrustacean taxa that were strongly correlated with the 2 axes (r^2>0.5) included *Diaptomus leptopus*, *Mesocyclops edax*, *Bosmina longirostris*, *Daphnia middendorffiana*, *Daphnia pulex*, and *Daphnia schodleri*. Environmental variables that were strongly correlated with the 2 axes (r^2>0.3) include TP, TDP, surface temperature, Chl-a, maximum DO, and area. In July, the three major groups that emerged from cluster analysis reflected the fish community types: the fishless lakes dominated the first and second groups, whereas most fish-bearing (unstocked and stocked) lakes created a third group (Figure 2-6). Community composition differed among lake types in July (MRPP; p=0.002); communities in fishless lakes differed from those in stocked (p=0.002) and marginally from unstocked lakes (p=0.075), whereas composition in stocked and unstocked lakes also differed (p=0.016). Environmental conditions differed among lake types in

July (MRPP; p=0.022), due to a significant difference between stocked and unstocked lakes (p=0.003). In July, the microcrustacean community matrix was related to both the fish (p=0.009) and environmental (p=0.044) matrices (Mantel Test).

The ordination from August (Figure 2-4) represented 92% of variance in the data set (17 taxa), at a stress level of 8.4 (Monte Carlo test, p= 0.003). Microcrustacean taxa that were strongly correlated with the two axes ($r^2>0.5$) included *Diaptomus leptopus*, *Skistodiaptomus oregonensis, Mesocyclops edax*, *Daphnia middendorffiana*, *Daphnia schodleri*, and *Diaphanosoma*. No environmental variables were strongly correlated with the two axes ($r^2>0.3$). In August, two of the three major groups that emerged from cluster analysis reflected the fish community. The most distinct group (Group 1; Figure 2-6) consisted of two fishless lakes, while Group 3 consisted of the remaining unstocked and stocked lakes. Community composition differed among lake types in August (MRPP; p=0.004), with fishless lake communities differing from both stocked (p=0.003) and unstocked lakes (p=0.008). Composition in the latter two lake types were marginally different (p=0.078). In contrast, there was no difference in environmental factors (area and maximum depth removed) among the three lake types in August (MRPP; p=0.140). Microcrustacean and fish communities showed correspondence (Mantel Test; p=0.002), whereas the microcrustacean and environmental matrices (area and maximum depth removed) were not related (Mantel Test; p=0.365).

The ordination of all lake-months (Figure 2-5) represented 84% of variance in the data set (18 taxa), at a stress level of 13.6 (Monte Carlo, p= 0.003). Successional vectors following lake type-month centroids move in a similar upward direction in stocked and unstocked lakes from May through August suggesting increasing densities of *Skistodiaptomus oregonensis* and *Diaphanosoma*, while fishless vectors follow a perpendicular leftward trajectory through time, suggesting increases in *Diaptomus leptopus and Daphnia middendorffiana*. No environmental variables were strongly correlated with the axes ($r^2>0.3$).

The environmental variables that were chosen for Variance Partitioning Analysis through forward stepwise selection were surface temperature for June; depth and TDP for July; and depth, area, and maximum DO for August. These environmental variables explained between 11- 21% of the variance in microcrustacean communities, compared to 16- 21% explained by the fish assemblage (Figure 2-7). The variance explained by the interaction of environment and/or fish assemblage was 15-16%.

Chaoborus Abundance and Community Composition

Four species of *Chaoborus* were identified in the study lakes (Appendix A): *C. americana* was exclusive to fishless lakes, *C. punctipennis* was exclusive to fish-bearing lakes (stocked and unstocked), *C. trivitatus* was found only in unstocked and fishless lakes, whereas *C. flavicans* was common to all lake types. All species were found to coexist with the exception of *C. americana* and *C. punctipennis*. *Chaoborus* were detected in most unstocked lakes and all fishless lakes during each month (May-August), but did not appear in the stocked lake type until July and August. *Chaoborus* abundance differed significantly among lake types with three to 14 times the number of individuals/L in fishless compared to unstocked and stocked lakes, respectively (Table 2-3).

Discussion

Non-native trout had little impact on microcrustacean abundance, biomass, body size, and community composition in boreal foothills lakes containing native small bodied fish. A fish effect, however, was detected as stocked and unstocked lakes significantly differed from fishless systems in most respects. Stocked lakes were associated with higher levels of microcrustacean richness and diversity, however, suggesting a potential impact of non-native trout on coexistence among microcrustacean taxa.

Microcrustacean Abundance, Biomass, and Length

Few differences existed in the abundance, biomass, and size structure of the major crustacean groups between stocked lakes and unstocked lakes. However, cladocerans and calanoids in the presence of trout and native fish had greater abundances but smaller mean individual and/or taxon lengths compared to fishless lakes, resulting in comparable biomass between lake types. The proportion of large individuals was greater in fishless compared to fish-bearing lakes for both orders, with QQ plots suggesting size-selective predation on large cladoceran and calanoid prey in fish-bearing lakes. These results are consistent with Carlisle and Hawkins (1998) where trout introduction into previously fishless mountain lakes in northeastern Utah increased the abundance of cladocerans but reduced cladoceran and calanoid lengths by ~25%. Indeed, since Brooks and Dodson (1965), many other studies have also found small microcrustaceans dominating the pelagic region of fish-bearing lakes, whereas large microcrustaceans, such as certain *Daphnia* species, and various invertebrate predators dominate fishless systems. My study, however, suggests that trout do not have an additive effect on the abundance, biomass, and size of major microcrustacean taxa in the presence of native fish.

Trout and native fish appear to have similar prey selectivity on large microcrustacean individuals, which comprise an important part of the diets of both groups (Naud and Magnan 1988; Beauchamp 1990; Lynott *et al*. 1995; Laurich *et al*. 2003). As a result, small-bodied individuals should have an advantage in fish-bearing lakes. Both trout and native small-bodied fish also feed on large invertebrate predators (Cochran *et al.* 1988; Lynott *et al.* 1995), potentially reducing predation on smaller cladocerans and calanoids (Dodson 1974; Ha and Hanazato 2009) and contributing to their greater abundance in fish-bearing lakes (Carlisle and Hawkins 1998; Schilling *et al.* 2009a). In addition, large grazing microcrustaceans in fishless systems can outcompete smaller species and exclude these taxa (Brooks and Dodson 1965; Gliwicz *et al.* 2010).

In contrast to cladocerans and calanoid copepods, stocked lakes and lakes with native fish had greater mean cyclopoid abundances and biomasses compared to fishless lakes, with no difference in mean individual and taxon lengths. There was also no difference in the proportion of large individual cyclopoids between treatments and no evidence of size-selective mortality based on QQ plots. Carlisle and Hawkins (1998) reported similar patterns for cyclopoid populations in response to the introduction of trout to fishless lakes.

Unlike the cladoceran and calanoid species found in my study lakes, the cyclopoids present (*Mesocyclops edax/leukarti* and *Cyclops bicuspidatus thomasi*) are relatively small as adults (Kerfoot 1980; Ha and Hanazato 2009). Their size should reduce predation from fish compared to other microcrustaceans. In addition, cyclopoids are strong swimmers compared to cladocerans and calanoids (Thorp and Covich 1991) and thus more efficient at evading fish predation.

The presence of fish (native or stocked) could also benefit cyclopoids through two key mechanisms. First, fish predation on large invertebrate predators could reduce predation on small cyclopoids, while decreasing competition between cyclopoids and macroinvertebrate predators due to overlap in diets (Liljendahl-Nurminen *et al.* 2003). Second, fish often shift the size structure in cladoceran communities to a dominance of small instead of large taxa. Small cladocerans (e.g., *Bosmina*), which often dominate fish-bearing systems (as seen in the current study), are common prey of cyclopoids (Kerfoot 1980; Ha and Hanazato 2009). Adult cyclopoid survival and reproduction increase with greater ingestion of zooplankton versus algae, giving cyclopoids an advantage in fish-bearing lakes (Williamson and Butler 1986; Hansen and Santer 1995; Hopp *et al.* 1997). In addition, herbivorous cyclopoid nauplii and copepodites could also experience improved feeding condition in stocked and unstocked lakes due to reduced competition with large cladoceran grazers, increasing their developmental rates and survival (Hopp and Maier 2005).

Microcrustacean Community Diversity and Composition

Stocked lakes had a greater richness and diversity of microcrustacean species compared to unstocked and fishless lakes. These results could indicate a trout effect, or could be a product of lake morphology, as greater lake size and depth can provide increased habit heterogeneity within lake ecosystems (Tessier and Welser 1991). Stocked lakes are somewhat larger and deeper compared to unstocked and fishless lakes; they were selected for stocking due to their greater ability to support gamefish populations in the face of potential hypoxic conditions in winter and warm water temperatures in summer. Differences in lake morphology, although statistically significant, were not large and mainly involved stocked vs. fishless lakes. Richness and diversity, in fact, were unrelated to lake depth. At least a marginal correlation in some months between area and richness (or diversity) suggests that lake area may contribute to the observed differences among lake types but because area was not consistently significant and overlap in lake area exists among lake types, I suggest that the presence of trout likely plays an important role.

The presence of fish could lead to greater species richness and diversity through predator-mediated coexistence of species (Hairston *et al.* 1960). Fish are expected to feed selectively on large, often competitively superior zooplankton, which could increase resource availability for competitively inferior taxa, allowing such taxa to coexist with larger species. In addition, fish can impact the composition and density of invertebrate predators that are capable of excluding small zooplankton (Dodson 1974). Despite strong evidence for a more general "fish effect" (versus a "trout effect"), including similar community compositions in stocked and unstocked lakes (discussed below), greater microcrustacean richness and diversity in stocked lakes compared to unstocked and fishless systems indicates a potential effect of trout on the coexistence of plankton species. Similar to this study, Donald *et al.* (2001) found evidence for fish-induced changes in zooplankton assemblages between lakes with and without fish in the Canadian Rocky Mountains, but also documented greater microcrustacean richness and diversity in lakes with complex fish communities (both stocked trout and indigenous fish) compared to lakes with simple fish communities (stocked trout only) and fishless lakes. Donald *et al.* (2001) suggested that predation on zooplankton by numerous fish species of various sizes and feeding strategies, rather than a single fish species, reduced niche breadth and dominance by particular zooplankton taxa, allowing the establishment of rare plankton species in communities.

In addition to the potential impact of trout planktivory resulting in greater microcrustacean richness and diversity, an indirect impact of trout predation on macroinvertebrates could also contribute to the observed pattern. *Chaoborus* abundance was 14 and four times greater in fishless and unstocked lakes relative to stocked systems, with fewer *Chaoborus* species present in stocked lakes. *Chaoborus* feed selectively on small zooplankton and could potentially eliminate susceptible microcrustacean taxa from a system when predator densities are high. *Daphnia galeata mendotae* and *Daphnia parvula*, two relatively small cladoceran species, were found mostly in stocked lakes, but were often excluded from the other lake types. An additional small cladoceran species (*Ceriodaphnia lacustris*) was also restricted to a single stocked lake, similar to findings of Schabetsberger and Luger (2009).

Overall, microcrustacean community matrices and fish community matrices were significantly related during the summer months. Both the cluster analyses and ordinations of microcrustacean communities suggested the existence of a gradient among the three fish-community types, with fishless and stocked lakes each harboring relatively distinctive microcrustacean communities. Although communities in unstocked lakes were intermediate, the analyses did indicate a closer affinity to stocked lakes. Both stocked and unstocked lakes differed significantly from communities in fishless lakes during most months, but stocked and unstocked lakes only differed from each other during a single month (July). This suggests a strong fish effect but only a mild trout effect.

Consistent with a more general fish effect (Sosnovsky and Quiros 2009; Schabetsberger and Luger 2009), the two largest cladoceran species (*Daphnia middendorffiana* and *Daphnia pulex*) showed a strong affinity for fishless lakes in NMS ordinations. In contrast, two of the smallest cladoceran species (*Bosmina longirostris* and *Diaphanosoma brachyurum/leuchtenbergianum*) were strongly associated with fish-bearing lakes. Unlike reports from alpine lakes in Alberta (e.g. Schindler 2000), there was no evidence that large cladocerans were completely extirpated after trout were introduced, suggesting reduced effects of stocking in Alberta's boreal foothills relative to lakes at higher elevations.

Similar to alpine lakes (Donald *et al.* 2001), the largest calanoid species (*Diaptomus leptopus*) was exclusive to fishless lakes, while the smallest calanoid species (*Skistodiaptomus oregonensis*) showed a strong affinity for fish-bearing lakes. Conversely, invertebrate predators exclusive to fishless lakes (e.g., *Chaoborus americana*) can decrease the abundance of *S. oregonensis* (Mackay *et al.* 1990), potentially contributing to its strong association with fish-bearing lakes in my study.

Both cyclopoid species were relatively small and present in all lake types. *Mesocyclops edax/leukarti,* the larger of the two taxa, showed a strong association with fish-bearing lakes, consistent with reports of increased cyclopoid abundance following initial stocking of previously fishless systems (Carlisle and Hawkins 1998; Crutchfield *et al.* 2003). Adult *Mesocyclops* have more diverse diets than *Cyclops bicuspidatus thomasi* (Brandl 2005) and eat proportionately more zooplankton versus phytoplankton (Hansen and Santer 1995). This could provide an advantage for *Mesocyclops* in fish-bearing lakes with abundant small cladocerans and rotifers, while *Cyclops* could experience heightened competition with cladocerans for algal resources.

Seasonal Effects on Microcrustaceans

A common seasonal pattern (Yoshida *et al.* 2001) of increased abundance and biomass of cladocerans and calanoids from May through August was consistent in all three lake types, indicating little effect of trout and native fish on overall microcrustacean population dynamics. The proportion of large Calanoida, however, did increase in fishless lakes from July to August but remained at similar levels in stocked and unstocked lakes. This indicates a potential impact of fish (trout and native fish as a whole) on the proportion of large calanoids from July-August. Numbers of large calanoid individuals in stocked and unstocked lakes may have been incapable of increasing, despite greater densities of food (Santer 1994), due to the selective predation of trout and native fish on large-bodied individuals.

A useful ordination (NMS) of microcrustacean communities could not be made for May nor could a meaningful dendrogram based on fish community type. The NMS ordination of lake-months revealed similar communities among lake types in May, but an increasing difference between fish-bearing and fishless lakes as community succession progressed through the summer. Indeed, differences in microcrustacean community composition (MRPP) among lake types and a relationship between fish and microcrustacean community matrices (Mantel test) were not detected in May, in contrast to June-August, and the percentage of variance explained by fish increased throughout the summer from June-August (VPA). These results suggest that the pressures resulting in divergence among microcrustacean communities in the different lake types were weak or absent in spring but strong throughout the summer.

Changes in predation pressures from top predators within lakes could be responsible for the difference seen between May and the three summer months. Trout are stocked in the spring and early summer (May and June), and the native fishes all reproduce in the spring, with young hatching by the end of June, ready to begin feeding on zooplankton (Abrahams 1996). Increased fish planktivory in June-August may have increased fish effects on microcrustaceans and contributed to the strong community differences between fish-bearing and fishless lakes seen during the summer.

Fish Community versus Environmental Differences

In contrast to the microcrustacean communities, environmental variables (maximum depth and area excluded) rarely differed among lake types during the four sampling periods. Environment and microcrustacean community matrices were similar only in July (Mantel tests), whereas fish and microcrustacean community matrices were similar throughout June-August. Fish also accounted for a slightly larger portion of explained variance compared to the environment in the majority of months investigated (VPA). As a whole, these results suggest that fish are more important in structuring microcrustacean communities than environmental variables. Carlisle and Hawkins (1998) also found that although microcrustacean communities varied according to habitat type, differences in environmental variables did not mediate the overriding effects of trout presence.

Microcrustaceans can be the primary food source for Rainbow Trout under 250-330 mm (Beauchamp 1990, Lynott *et al.* 1995). In my study lakes, trout are stocked at 90-260 mm, and reach average lengths < 330 mm in the majority of stocked lakes due to removal by anglers (J. Hanisch, University of Alberta, unpublished data). Cladocerans (such as large *Daphnia*) are known to be slow, conspicuous prey relative to most copepods (Ward and Whipple 1966): data from several stocked lakes, indicate that cladocerans are important food for trout comprising approximately 75% (numerically) of trout prey items (J. Hanisch unpublished). Among the small-bodied native fish in my lakes, dace (Naud and Magnan 1988) and Brook Sticklebacks (Laurich *et al.* 2003) have also been found to select for large cladocerans. Hambright and Hall (1992) found Fathead Minnows selecting for large *Daphnia* and against small cladocerans and fast swimming copepods, whereas Fisher *et al.* (1998) found Fathead Minnows preferred large calanoids.

Fish, Chaoborus, and Microcrustacean Communities

Chaoborus species were present in all fishless lakes but were absent from a majority of fish-bearing lakes. *Chaoborus* abundance in July was also three times and 14 times greater in fishless compared to unstocked and stocked lakes, respectively. These results are similar to those of Pope *et al.* (1973) and Schilling *et al.* (2009b).

Species composition of *Chaoborus* also differed between fishless and fish-bearing lakes, with *C. americana* exclusive to the former and *C. punctipennis* exclusive to the latter. *C. americana* is the largest *Chaoborus* found in my study systems and the only species incapable of diel vertical migration to minimize predation by fish. Consequently, *C. americana* is particularly susceptible to predation by fish and does not co-exist with fish (e.g., Schilling *et al.* 2009b). In contrast, *C. punctipennis* is small, transparent, and capable of retreating to deep waters during the day, but is vulnerable to predation by and competition with *C. americana* (Roth 1968; Von Ende 1979, 1982). Indeed, the presence and abundance of *C. punctipennis* has been positively associated with the presence of fish (Yan *et al.* 1985; Wissel *et al.* 2003; Schilling *et al.* 2009b).

Chaoborus can affect zooplankton communities through selective feeding, with a strong preference for small microcrustaceans such as *Bosmina* (Liljendahl-Nurminen *et al.* 2003). Other cladoceran taxa, including *Daphnia*, can also be impacted by *Chaoborus* predation (Elser *et al.* 1987; Mackay *et al.* 1990; Liljendahl-Nurminen *et al.* 2003). The strong affinity that several small cladocerans, including *Bosmina longirostris, Diaphanosoma,* and even small *Daphnia* species, had to fish-bearing lakes is consistent with a decreased abundance of *Chaoborus* due to predation by trout and native fish.

In general, *Chaoborus* do not feed selectively on copepods, however, slower taxa such as *Skistodiaptomus* can be susceptible (Luecke and Litt 1987). Indeed, *C. americana*, can significantly decrease *Skistodiaptomus oregonensis* abundance (Mackay *et al.* 1990) and like the small cladocerans, *S. oregonensis* showed a strong association with fish-bearing lakes that lacked *C. americana* in my study.

Stocking in the Boreal Foothills versus Headwater Regions

Effects of trout stocking on microcrustacean communities in the current study were relatively weak compared to impacts documented in headwater regions. Lakes within Alberta's boreal foothills may be buffered against trout impacts due to greater lake productivity, extensive macrophyte cover, and more complex communities shaped by coexistence with native fish. Higher primary production provides greater quantities of phytoplankton food, whereas macrophyte beds have been shown to provide effective refugia for invertebrate prey, including zooplankton (Crowder and Cooper 1982; Carlisle and Hawkins 1998; Kuczynska-Kippen and Nagengast 2006). Previous studies of other native taxa in my study area have also documented weak effects of trout including no impact on native fish abundance (Nasmith *et al.* 2010), macroinvertebrate communities (Nasmith *et al.* 2012), and amphibian populations (Schank *et al.* 2011), although habitat preference for littoral versus pelagic areas was documented for native fish in the presence of trout (Hanisch *et al.* 2012).

Unlike headwater lakes that are often naturally fishless with simple and sparse macroinvertebrate and microcrustacean communities, boreal foothills lakes contain native small-bodied fish and complex macroinvertebrate and microcrustacean communities composed of numerous taxa. Native fish likely shape the ecology and life history of invertebrate prey prior to trout introduction, resulting in communities that are not naïve to predation by fish. Previous studies have found that fish presence is the primary factor influencing both macroinvertebrate (Schilling *et al.* 2009b) and zooplankton communities (Jeppesen *et al.* 2000), not the identity of fish species, resulting in no negative associations between non-native trout and zooplankton communities in the presence of native fish (Aguilera *et al.* 2006). Behavioral adaptations, such as diel vertical migration to deeper and darker waters in the presence of fish, have been well documented (e.g. Semyalo and Nattabi 2009) and could aid coexistence between microcrustaceans and their fish predators in boreal foothills lakes. In addition, boreal lakes often stratify, creating near hypoxic hypolimnia that can provide refugia from fish predation (Klumb *et al.* 2004). Complex invertebrate and microcrustacean communities may also weaken the impact of trout as trout are generalist predators as adults feeding on a wide variety of prey (Beauchamp 1990; Nelson and Paetz 1992; Lynott *et al.* 1995). The availability of numerous prey types should reduce the impact of trout on any one taxa as the effects of predation would be spread over many species.

Conclusions

Trout stocking did not significantly affect microcrustacean abundance, biomass, and body size, as well as community composition, though a general fish effect was detected with stocked and unstocked lakes differing from fishless systems. Selective predation, combined with the competitive advantage of large grazers, are likely the mechanisms responsible for the observed patterns in microcrustacean communities. Fish predation on large invertebrate predators (e.g., *Chaoborus*) could also contribute indirectly to the observed pattern. The minimal impacts of trout stocking on microcrustaceans in these boreal foothills lakes appears to result from similar effects of trout and native fish on microcrustacean and predatory invertebrate communities (Nasmith *et al.* 2012), making fish identity irrelevant in terms of impact on prey.

Stocked lakes, however, had higher richness and diversity than unstocked and fishless lakes. The mechanism behind this phenomenon appears to be, at least in part, the effects of trout stocking on biotic interactions, such as the direct impact of predation on zooplankton and the indirect impact of trout on *Chaoborus* species, which could help mediate coexistence of plankton species. Though stocked lakes were on average slightly larger and deeper then unstocked and fishless lakes, relationships between richness and diversity with lake area were limited, whereas lake depth was never correlated with these two community variables.

Understanding how stocking non-native trout influences lake ecosystems is essential for the conservation of native communities. Due to the position of microcrustaceans as primary consumers within lake ecosystems, they have the potential to control lake productivity and water quality, and thus usage by humans. In my study, the presence of native fish appears to structure zooplankton communities to fish predation prior to trout stocking. High productivity may also buffer taxa against fish predation as I did not observe the extirpation of large cladoceran species in lakes with fish, as seen in alpine systems. Based on my results, lakes in Alberta's boreal foothills with native small-bodied fish are good candidates for trout stocking.

Table 2-1 Stocking and aeration regimes for the six trout-bearing study lakes. Stocking numbers and sizes are from 2009 (Alberta Sustainable Resource Development 2012), whereas resident sizes are from fish caught by hook and line angling (2009, Hanisch, unpublished data) and multimesh gillnets (Birch Lake; R. Konynenbelt, Alberta Sustainable Resource Development, personal communication). All lakes are stocked annually in May or June (Mitchell was stocked in both months since Rainbow Trout were stocked in May and Brown Trout were stocked in June). All aerated lakes receive winter surface aeration, except Beaver Lake, which is aerated year round.

Lake	Year of Initial Stocking	Trout Species	Number Stocked	Stocking Size (cm)	Resident Size Mean ±SE (n)(cm)	Regulations	Year of Initial Aeration
Beaver	1999	Rainbow	3,500	26	326 ± 6 (85)	Apr 1- Nov 30; Trout limit 2	1999
Birch	1938	Brook	15,800	9	314 ± 9 (64)	Open all year; Trout limit 5	2009
Ironside	1977[1]	Rainbow	250	22	452 ± 7 (62)	Apr 16- Oct 31; Trout limit 0	2005
Strubel	1950	Rainbow	20,300	12	248 ± 6 (79)	Open all year; Trout limit 5	None
Fiesta	2007	Rainbow	550	26	380 ± 6 (88)	Apr 16- Oct 31; Trout limit 0	2007
Mitchell	1950	Rainbow	4,000	17	269 ± 5 (85)	Open all year; Trout limit 5	2003
	2003	Brown	500	25	327 ± 20 (15)		

[1] Ironside was stocked for the first time in 18 years in 2005.

Table 2-2 Taxa of pelagic microcrustaceans identified in the study lakes in 2009. Species listed together could not always be differentiated. Mean lengths ±SE (n) are from all individuals measured across all lakes and months. The % present in each lake type is based on all lake-months (May-August, except one fishless lake that was not sampled in May). S: stocked (n=24), U: unstocked (n=20), F: fishless (n=11).

Order	**Family**	**Genus**	**Species**	**Mean Length ±SE (n)**	**% Present**		
					S	**U**	**F**
Cladocera	*Bosminidae*	*Bosmina*	*longirostris*	0.27 ± 0.00 (786)	92	70	36
	Chydoridae	unknown	unknown	0.26 ± 0.00 (220)	42	55	27
	Daphniidae	*Ceriodaphnia*	*lacustris*	0.73 ± 0.05 (7)	8	0	0
		Daphnia	*catawba*	1.20 ± 0.01 (377)	42	35	18
			galeata mendotae	1.33 ± 0.01 (666)	79	5	9
			middendorffiana	2.36 ± 0.05 (121)	4	15	45
			parvula	0.96 ± 0.01 (118)	33	15	0
			pulex	1.69 ± 0.02 (604)	42	40	64
			rosea	1.46 ± 0.01 (317)	38	10	45
			schodleri	1.23 ± 0.01 (212)	4	10	45
	Sididae	*Diaphanosoma*	*brachyurum/ leuchtenbergianum*	0.63 ± 0.01 (1077)	67	65	18
Calanoida	*Diaptomidae*	*Acanthodiaptomus*	*denticornis*	1.68 ± 0.01 (283)	13	30	18
		Diaptomus	*leptopus*	1.95 ± 0.03 (134)	0	0	82
		Skistodiaptomus	*oregonensis*	1.25 ± 0.00 (981)	92	65	9
Cyclopoida	*Cyclopidae*	*Cyclops*	*bicuspidatus thomasi*	0.98 ± 0.00 (565)	79	35	18
		Mesocyclops	*edax/leukarti*	1.16 ± 0.01 (877)	83	85	55

Table 2-3 Physical, chemical, and biological properties of the study lakes, 2009. All values are the means ±SE of the lakes within each lake type (with the exception of area, maximum depth, and *Chaoborus* abundance, values for each lake are May-August means except for one fishless lake, which is July-August). *Chaoborus* abundance is the mean from July. Again, with the exception of area, maximum depth, and *Chaoborus* abundance, results are from Linear Mixed Models with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. Results for area, maximum depth, and *Chaoborus* abundance are from one-way ANOVAs. TN: total nitrogen; TDN: total dissolved nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; Chl-a: specrophometric chlorophyll-a; DO: dissolved oxygen; S: stocked; U: unstocked; F: fishless; n/s: not significant; n/a: not applicable or not available. *0.1>p>0.05, **p<0.05

Lake Type (n)	**TN (µg/L)**	**TDN (µg/L)**	**TP (µg/L)**	**TDP (µg/L)**	**Chl-a (µg/L)**	**Conductivity (µS/cm)**	**Secchi Depth (m)**
Stocked (6)	660 ± 53	581 ± 46	17 ± 4	9 ± 3	1.5 ± 0.3	156.7 ± 32.4	4.0 ± 0.4
Unstocked (5)	910 ± 55	773 ± 54	26 ± 4	11 ± 2	3.7 ± 0.8	151.5 ± 32.0	2.6 ± 0.3
Fishless (3)	887 ± 159	770 ± 127	37 ± 12	18 ± 5	4.1 ± 2.1	123.7 ± 74.7	2.4 ± 0.8
Results							
Lake Type	$F_{2,11}$=4.1**	$F_{2,11}$=3.2*	$F_{2,11}$=3.9*	$F_{2,11}$=3.8*	$F_{2,10}$=3.0*	$F_{2,11}$=0.5	$F_{2,11}$=4.5**
Month	$F_{3,37}$=6.7**	$F_{3,37}$=7.3**	$F_{3,37}$=6.8**	$F_{3,37}$=1.2	$F_{3,36}$=5.0**	$F_{3,37}$=3.0**	$F_{3,37}$=2.8*
Interaction	Removed	Removed	Removed	Removed	Removed	Removed	Removed
Comparisons of Lake Types							
S vs. U	**	**	*	n/s	*	n/s	**
S vs. F	*	*	**	**	*	n/s	**
U vs. F	n/s	n/s	n/s	n/s	n/s	n/s	n/s

Table 2-3 continued

Lake Type (n)	Area (ha)	Max. Depth (m)	*Chaoborus* Abundance	pH	Surface Temp (°C)	Max. DO (mg/L)	Min. DO (mg/L)
Stocked (6)	17.1 ± 4.4	9.7 ± 1.1	1.7 ± 1.4	7.6 ± 0.2	17.8 ± 0.3	10.24 ± 0.55	3.60 ± 0.95
Unstocked (5)	11.1 ± 2.5	7.1 ± 1.8	7.3 ± 4.2	7.6 ± 0.1	18.6 ± 0.2	9.52 ± 0.39	2.61 ± 0.81
Fishless (3)	4.7 ± 2.7	4.8 ± 1.2	24.5 ± 4.6	7.8 ± 0.3	19.9 ± 0.1	8.02 ± 0.85	2.94 ± 0.81
Results							
Lake Type	$F_{2,11}$=5.0*	$F_{2,11}$=3.0*	$F_{2,11}$=10.9**	$F_{2,10}$=0.6	$F_{2,11}$=6.0**	$F_{2,11}$=3.3*	$F_{2,11}$=0.5
Month	n/a	n/a	n/a	$F_{3,31}$=0.3	$F_{3,31}$=239.7**	$F_{3,37}$=4.1**	$F_{3,37}$=1.6
Interaction	n/a	n/a	n/a	$F_{6,30}$=3.8**	$F_{6,31}$=2.6**	Removed	Removed
Comparisons of Lake Types							
S vs. U	n/s	n/s	n/s	n/s	*	n/s	n/s
S vs. F	**	**	**	n/s	**	**	n/s
U vs. F	*	n/s	**	n/s	n/s	*	n/s

Table 2-4 Mean (±SE) abundance and biomass of major taxa in each month in 2009 for each lake type: stocked lakes (S; n= 6), unstocked lakes (U; n=5), and fishless lakes (F; n= 3). Also presented are results from Linear Mixed Models for each taxa with lake type (LT), month (M), and their interaction (I) as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. *0.1>p>0.05, **p<0.05

	Taxa	**Lake Type**	**May**	**June**	**July**	**August**	**Mean of Months**	**Main Effect**	**F-Statistic**
Mean Abundance (individuals/L)	Cladocera	S	3.7±1.8	25.3±10.7	63.1±10.3	49.0±8.0	35.3±6.2	LT	$F_{2,11}$=3.6*
		U	4.8±3.0	22.2±5.7	35.9±13.7	22.2±12.9	21.3±5.2	M	$F_{3,38}$=23.7**
		F	0.4±0.3	6.7±2.2	22.6±2.2	9.1±3.0	10.5±2.7	I	Removed
	Calanoida	S	1.4±0.8	10.5±3.1	29.4±6.2	22.6±6.0	16.0±3.1	LT	$F_{2,11}$=4.9**
		U	0.4±0.2	18.8±8.0	18.7±4.7	35.5±13.7	18.3±4.8	M	$F_{3,32}$=33.0**
		F	0.1±0.0	1.5±1.3	9.7±4.4	1.9±0.5	3.6±1.6	I	$F_{6,32}$=2.5**
	Cyclopoida	S	20.7±9.2	16.9±5.6	27.5±7.1	20.5±2.5	21.4±3.2	LT	$F_{2,11}$= 6.6**
		U	41.0±17.6	14.4±9.0	13.0±5.5	10.3±3.3	19.7±5.6	M	$F_{3,38}$=1.2
		F	3.7±3.6	0.3±0.2	3.9±1.6	2.4±1.4	2.5±0.8	I	Removed
Mean Biomass (mg/L)	Cladocera	S	12.8±7.4	96.2±47.9	359.5±67.7	286.0±51.8	188.6±37.0	LT	$F_{2,11}$=1.5
		U	19.4±11.6	121.8±42.1	200.4±111.2	80.5±45.3	105.5±33.0	M	$F_{3,38}$=28.7**
		F	0.7±0.5	45.9±20.6	132.0±49.6	78.6±7.9	70.1±19.3	I	Removed
	Calanoida	S	9.4±4.4	47.9±15.9	151.1±34.5	120.9±36.0	82.3±17.0	LT	$F_{2,11}$=2.2
		U	0.6±0.3	73.0±31.5	97.3±18.7	197.7±79.9	92.1±25.8	M	$F_{3,38}$=47.4**
		F	0.2±0.1	25.3±22.1	107.4±81.1	32.0±7.1	45.0±23.4	I	Removed
	Cyclopoida	S	46.8±21.4	33.8±8.6	86.7±24.2	69.5±14.6	59.2±9.5	LT	$F_{2,11}$=11.1**
		U	42.3±17.6	35.7±18.7	34.9±20.4	28.8±16.4	35.4±8.5	M	$F_{3,38}$=1.3
		F	3.7±3.1	0.4±0.2	3.3±1.6	3.4±1.6	2.6±0.8	I	Removed

Table 2-5 Mean (±SE) individual and taxon length (see text for definitions) of major taxa in each month in 2009 for each lake type: stocked lakes (S; n= 6), unstocked lakes (U; n=5), and fishless lakes (F; n= 3). Also presented are results from Linear Mixed Models for each taxa with lake type (LT), month (M), and their interaction (I) as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. n/a: not applicable or not available. *0.1>p>0.05, **p<0.05

	Taxa	**Lake Type**	**May**	**June**	**July**	**August**	**Mean of Months**	**Main Effect**	**F- Statistic**
Mean Individual Length (mm)	Cladocera	S	n/a	0.73±0.08	0.88±0.08	0.94±0.05	0.85±0.04	LT	$F_{2,11}=0.6$
		U	n/a	0.85±0.22	0.81±0.17	0.65±0.18	0.77±0.10	M	$F_{2,26}=0.1$
		F	n/a	0.99±0.23	0.84±0.08	1.07±0.11	0.97±0.08	I	Removed
	Calanoida	S	n/a	n/a	0.93±0.06	0.92±0.06	0.92±0.04	LT	$F_{2,11}=3.0$*
		U	n/a	n/a	0.96±0.11	1.00±0.06	0.98±0.06	M	$F_{1,13}=1.5$
		F	n/a	n/a	1.07±0.26	1.43±0.16	1.25±0.16	I	Removed
	Cyclopoida	S	n/a	n/a	0.74±0.03	0.74±0.04	0.74±0.03	LT	$F_{2,11}=1.2$
		U	n/a	n/a	0.64±0.09	0.62±0.07	0.63±0.05	M	$F_{1,13}=0.7$
		F	n/a	n/a	0.45±0.02	0.74±0.28	0.59±0.14	I	Removed
Mean Species Length (mm)	Cladocera	S	n/a	0.82±0.05	0.87±0.03	0.88±0.06	0.85±0.03	LT	$F_{2,11}=9.5$**
		U	n/a	0.76±0.17	0.77±0.14	0.68±0.11	0.74±0.08	M	$F_{2,26}=0.0$
		F	n/a	1.25±0.04	1.16±0.18	1.24±0.14	1.22±0.07	I	Removed
	Calanoida	S	n/a	n/a	1.05±0.05	1.05±0.02	1.05±0.02	LT	$F_{2,11}=4.7$**
		U	n/a	n/a	1.09±0.08	1.14±0.06	1.12±0.05	M	$F_{1,13}=2.8$
		F	n/a	n/a	1.24±0.06	1.34±0.02	1.29±0.04	I	Removed
	Cyclopoida	S	n/a	n/a	0.88±0.03	0.83±0.01	0.85±0.01	LT	$F_{2,11}=2.2$
		U	n/a	n/a	0.74±0.09	0.80±0.04	0.77±0.05	M	$F_{1,13}=0.8$
		F	n/a	n/a	0.53±0.11	0.81±0.26	0.67±0.14	I	Removed

Table 2-6 Mean (±SE) lowest feasible taxonomic level (often species) richness, Shannon-Weiner diversity, and evenness (%) for each sampling period and lake type: stocked (S; n=6), unstocked (U; n=5), fishless (F; n=3). Also presented are results from Linear Mixed Models with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the Linear Mixed Model. *0.1>p>0.05, **p<0.05

Metric Lake Type	May	June	July	August	Mean of Months	Main Effect	F-Statistic	Comparisons of Lake Types
Richness								
Stocked	6.0±0.3	7.2±0.5	9.0±0.9	6.3±0.6	7.1±0.4	Lake Type	$F_{2,11}=10.8$**	S vs. U**
Unstocked	4.8±0.4	6.2±1.0	5.8±0.4	4.4±0.2	5.3±0.3	Month	$F_{3,38}=8.1$**	S vs. F**
Fishless	3.5±0.5	4.3±0.3	5.7±0.3	5.0±1.0	4.7±0.4	Interaction	Removed	U vs. F
Diversity								
Stocked	1.15±0.08	1.47±0.03	1.70±0.07	1.50±0.06	1.46±0.05	Lake Type	$F_{2,11}=7.0$**	S vs. U**
Unstocked	1.09±0.13	1.11±0.20	1.33±0.07	0.97±0.21	1.13±0.08	Month	$F_{3,38}=4.3$**	S vs. F**
Fishless	1.20±0.10	0.85±0.10	1.07±0.15	1.27±0.11	1.09±0.07	Interaction	Removed	U vs. F
Evenness								
Stocked	64.3±3.7	75.8±1.9	78.5±1.7	82.8±2.8	75.4±1.9	Lake Type	$F_{2,11}=1.3$	S vs. U
Unstocked	70.2±8.5	61.2±8.7	76.6±5.2	65.0±13.5	68.3±4.5	Month	$F_{3,33}=3.0$**	S vs. F
Fishless	96.5±3.5	59.3±8.8	62.3±8.4	83.0±6.6	73.4±5.6	Interaction	$F_{6,33}=2.9$**	U vs. F

Table 2-7 Results from linear regression analysis of lowest feasible taxonomic richness and Shannon-Weiner diversity, May-August 2009, versus lake area and depth. Degrees of freedom were 1 and 12 for all months except May, when they were 1 and 11. *0.1>p>0.05, **p<0.05

Analysis & Results	**May**	**June**	**July**	**August**
Richness vs. Area				
r^2 -value	0.706	0.114	0.579	0.391
F -value	10.938**	0.159	6.064**	2.169
Richness vs. Depth				
r^2 -value	0.272	0.056	0.384	0.181
F -value	0.878	0.038	2.081	0.408
Diversity vs. Area				
r^2 -value	0.343	0.029	0.294	0.516
F -value	1.471	0.010	1.132	4.349*
Diversity vs. Depth				
r^2 -value	0.397	0.353	0.427	0.123
F -value	2.053	1.707	2.683	0.186

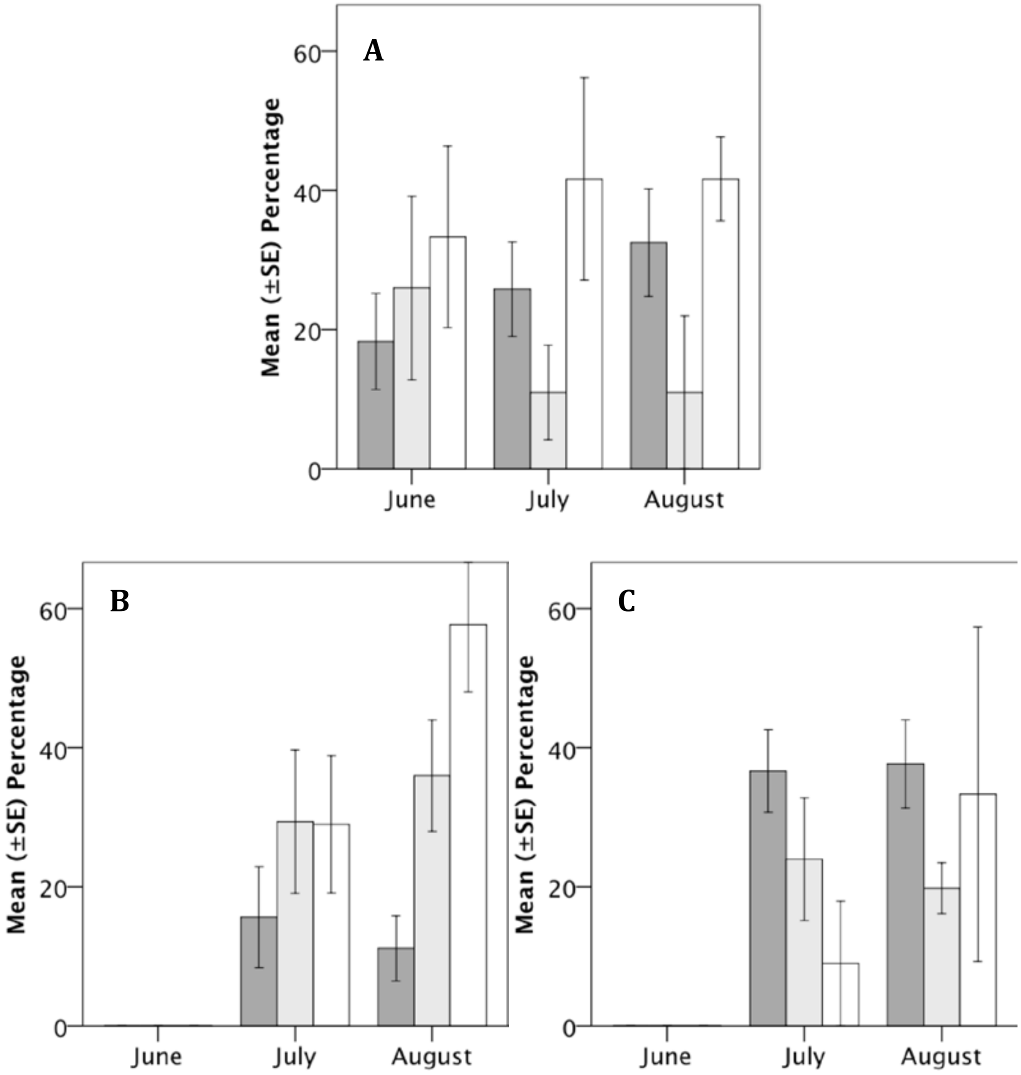


Figure 2-1 Mean percentage (±SE) of large individuals in stocked, unstocked, and fishless lakes over three sample periods in 2009 for (A) Cladocera >1.26mm; (B) Calanoida >1.33mm; and (C) Cyclopoida >0.95mm. June could not be included for calanoids and cyclopoids due to inadequate sample sizes. Dark grey bars: stocked lakes (n=6), light grey bars: unstocked lakes (n=5), white bars: fishless lakes (n=3).

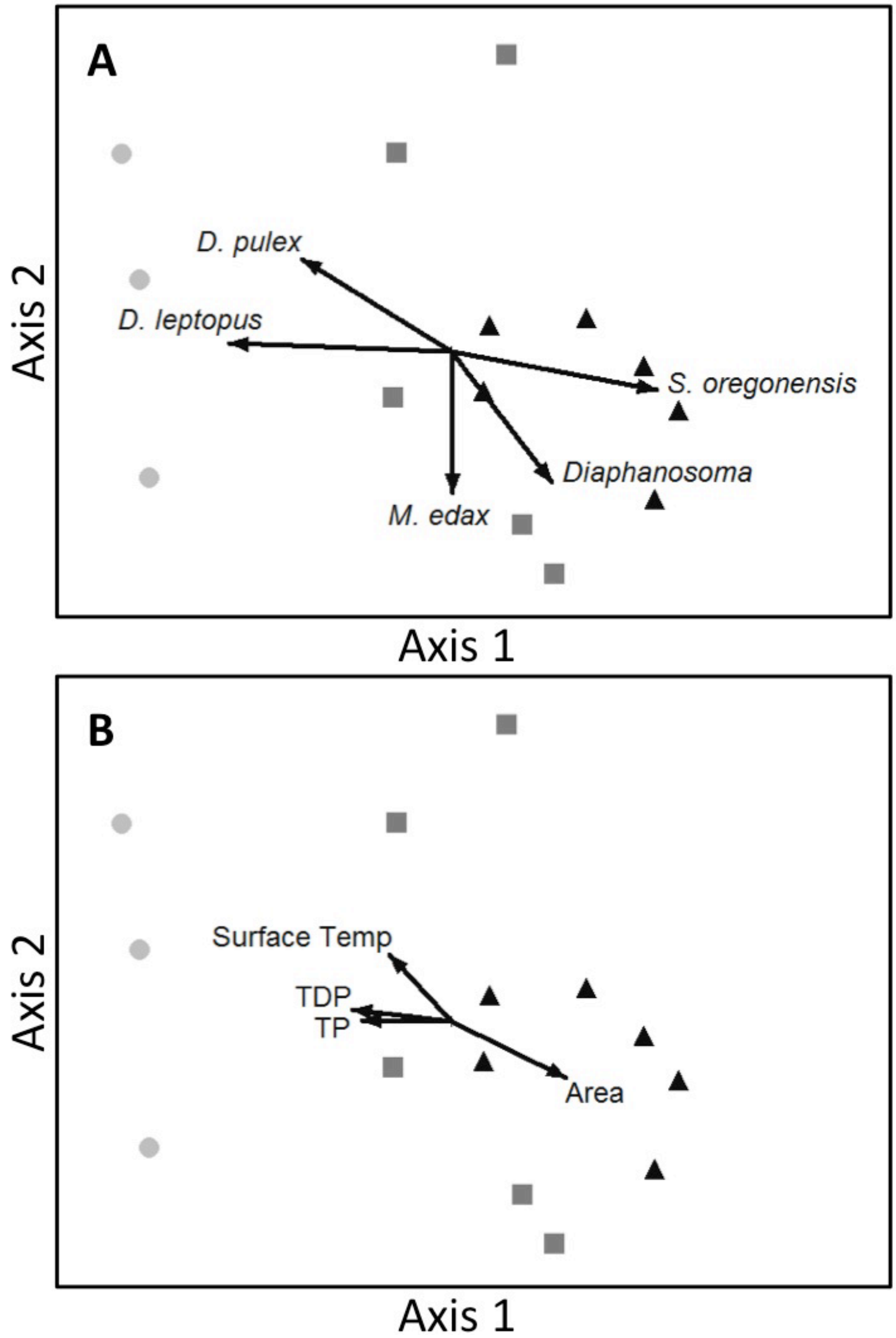


Figure 2-2 Non-metric multidimensional scaling (NMS) joint plots of pelagic microcrustacean communities in study lakes in June 2009. Vectors point in the direction of increased (A) presence of microcrustacea taxa (r^2>0.5) and (B) levels of environmental variables (r^2>0.3), and the length of vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

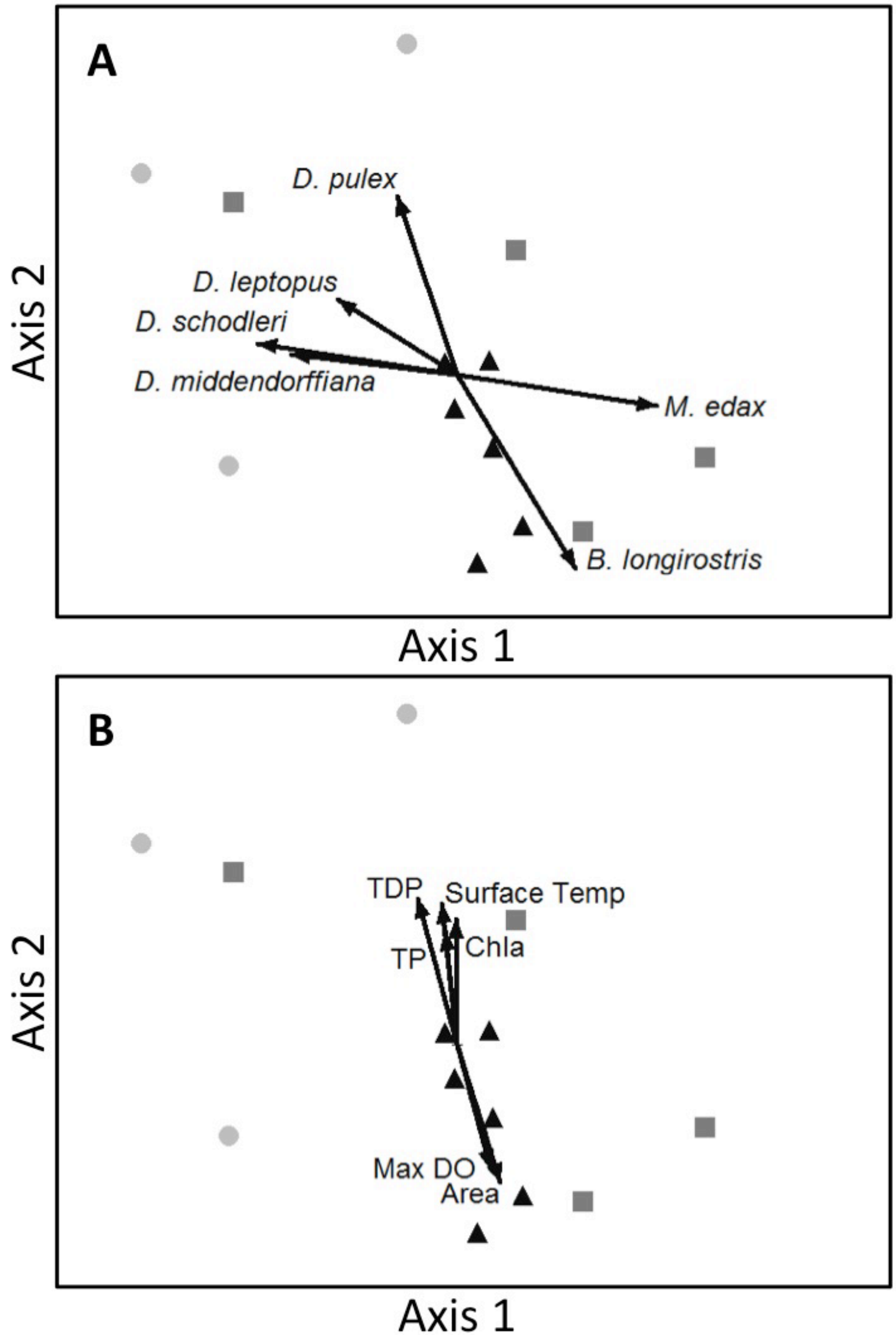


Figure 2-3 Non-metric multidimensional scaling (NMS) joint plots of pelagic microcrustacean communities in study lakes in July 2009. Vectors point in the direction of increased (A) presence of microcrustacea taxa (r^2>0.5) and (B) levels of environmental variables (r^2>0.3), and the length of vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

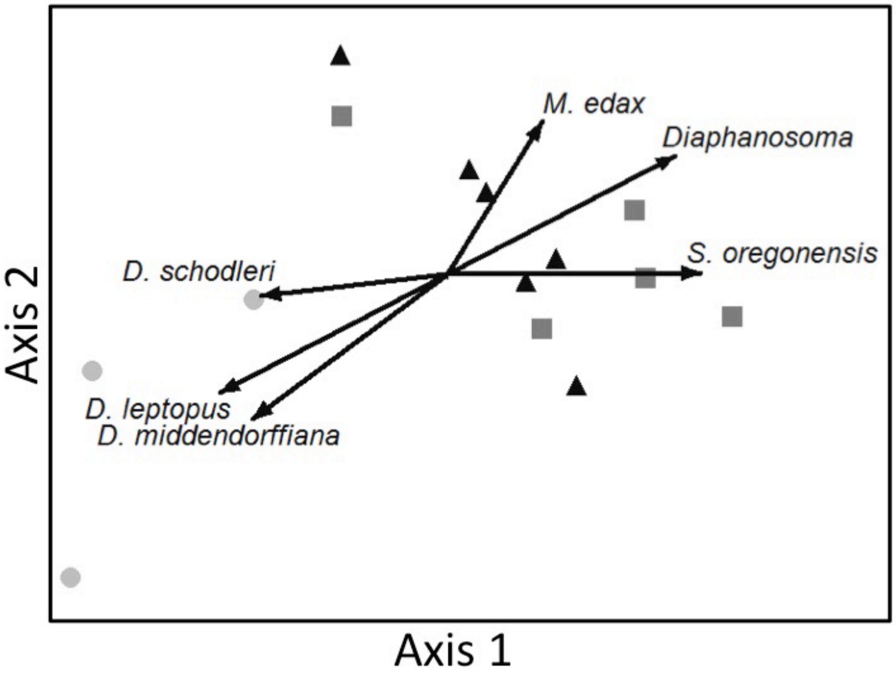


Figure 2-4 Non-metric multidimensional scaling (NMS) joint plot of pelagic microcrustacean communities in study lakes in August 2009. Vectors point in the direction of increased presence of microcrustacea taxa (r^2>0.5) and the length of vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3). None of the environmental variables were strongly correlated with the axes (r^2>0.3).

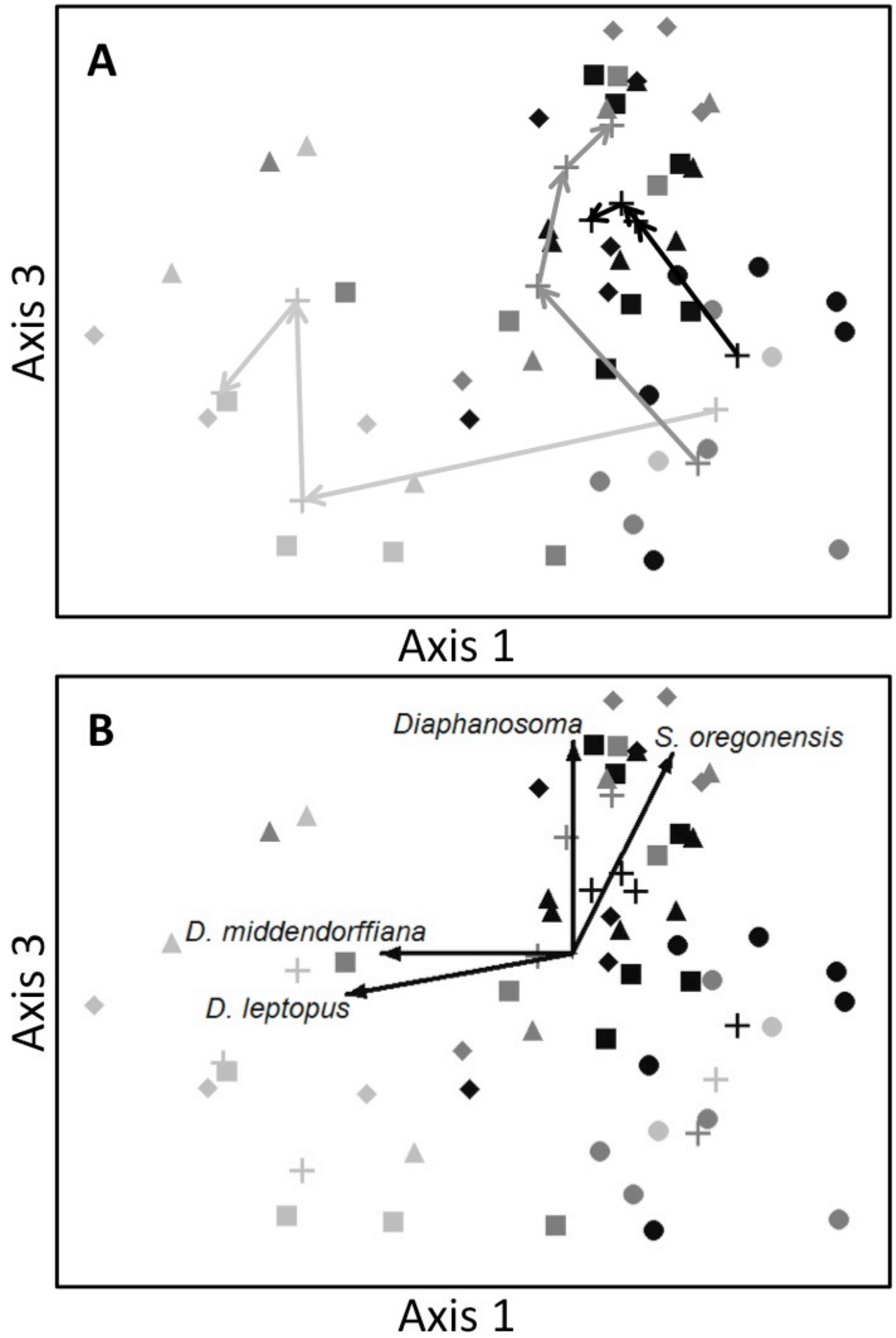
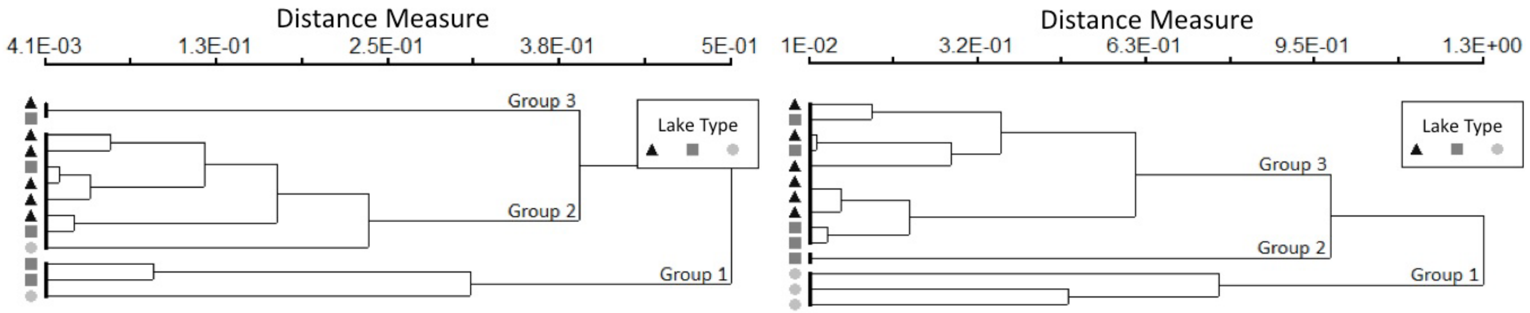
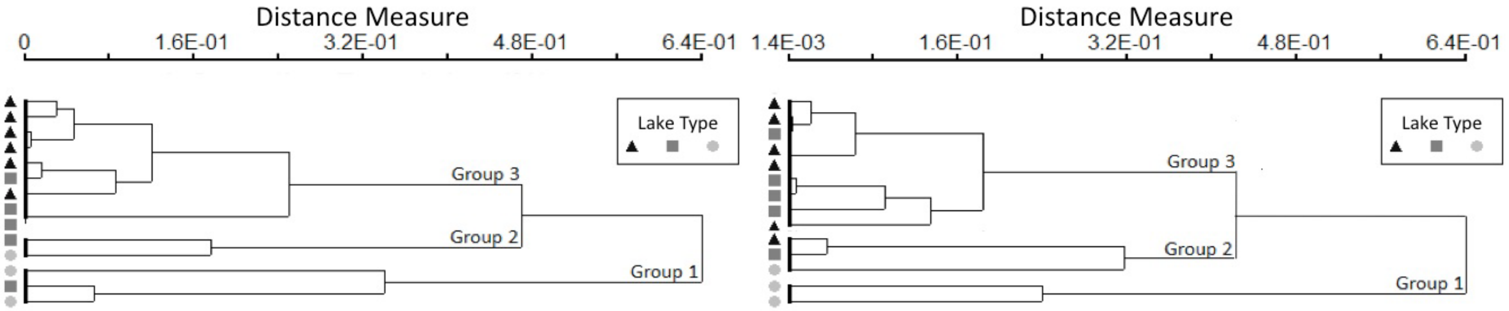


Figure 2-5 Non-metric multidimensional scaling (NMS) ordinations of pelagic microcrustacean communities in study lakes during the four monthly sampling periods (May-August) in 2009. (A) successional vectors follow lake type monthly centroids through time and (B) joint plot vectors point in the direction of increased presence of microcrustacea taxa ($r^2>0.5$) and the length of joint plot vectors indicate the strength of the relationship. Black symbols: stocked lake-months (n=18), dark grey symbols: unstocked lake-months (n=15), light grey symbols: fishless lake-months (n=8), circles: May, squares: June, triangles: July, diamonds: August. None of the environmental variables were strongly correlated with the axes ($r^2>0.3$).



May

June



July

August

Figure 2-6 Dendrograms of cluster analysis of study lakes for each of the 4 sampling periods (May, June, July, and August 2009). Lakes were grouped by their similarity in microcrustacean composition based on presence/absence data. Three major groups are identified for each month. The smaller the distance between pairs of lakes, the more similar they are in species composition. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

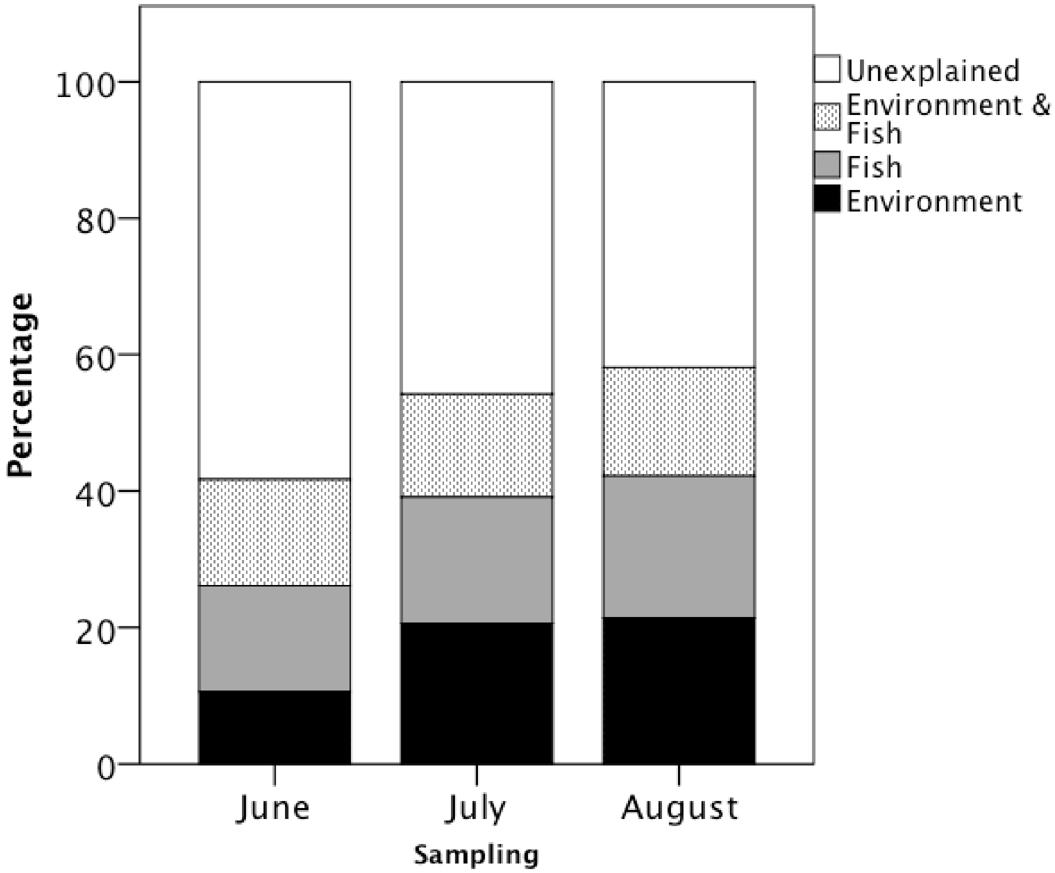


Figure 2-7 Results from a two-way variance partitioning analyses for three sampling periods in 2009. Values represent the percentage of variance in the composition of microcrustacean communities explained independently by environmental variables and fish taxa, the percentage shared by environment and fish, and the variation left unexplained.

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Chapter 3. Effects of stocked trout and native small-bodied fish on pelagic rotifer communities in small boreal foothills lakes

Introduction

Stocking gamefish in freshwater lakes occurs commonly throughout North America to maintain or enhance recreational fisheries. Common species introduced to these aquatic systems include Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*), and Brook Trout (*Salvelinus fontinalis*). Although these sport fish are generalist predators as adults feeding on a variety of prey (Beauchamp 1990; Nelson and Paetz 1992; Lynott *et al.* 1995), they often become the top predator in systems into which they are introduced. The impact of stocking these predators on native fauna has received considerable attention, with differing effects dependent on the receiving habitat and native community (Dunham *et al.* 2004). Trout stocking can negatively impact many forms of native taxa including small-bodied fish (Townsend 1996), amphibians (Tyler *et al.* 1998), macroinvertebrates (Martinez-Sanz *et al.* 2010), and microcrustaceans (Carlisle and Hawkins 1998). Few studies to date have investigated the impact of trout stocking on native rotifer communities, as stocked trout do not select rotifers as prey. Trout stocking, however, could impact rotifers indirectly since trout feed upon both competitors and predators of rotifers within freshwater systems.

The few studies investigating impacts of non-native trout on rotifer communities have found mixed results. Equal or greater abundances of rotifers in trout-bearing compared to fishless lakes occur in alpine temperate lakes (Knapp *et al.* 2001) and high-altitude tropical lakes (Anguilera *et al.* 2006). In contrast, a lower abundance of rotifers occurred in lakes with Brook Trout compared to fishless lakes on Quebec's Boreal Shield (Drouin *et al.* 2009), primarily due to an atypical impact of *Chaoborus* on daphniids in the fishless lakes. More often, however, both *Chaoborus* and large *Daphnia* dominate fishless lakes (e.g. Donald *et al.* 2001), resulting in low rotifer abundance due to strong competition with *Daphnia*.

More generally, fish tend to have a positive impact on rotifer communities. Increased abundance of many rotifer taxa and greater species richness have been found in the presence of fish ranging from the small-bodied planktivirous fish, Brook Stickleback, *Culaea inconstans* (Beisner and Peres-Neto 2009) to Alpine Charr, *Salvelinus umbla* (Schabetsberger *et al*. 2009).

The present study lakes are located in Alberta's boreal foothills, where a trout-stocking program is managed to enhance angling opportunities. Few impacts of this stocking program have been observed on native fish (Nasmith *et al.* 2010), amphibians (Schank *et al*. 2011), and macroinvertebrate assemblages (Nasmith *et al.* 2012). I also detected only minor impacts of trout on microcrustaceans (Chapter 2). Distinct differences, however, were detected between fish-bearing lakes (unstocked lakes with native fish and stocked lakes with trout and native fish) and fishless systems, suggesting a general fish effect but little additive effect of trout in lakes with native fish. Fish-bearing lakes contained greater abundances of Cladocera, Calanoida, and Cyclopoida, with size distributions shifted to smaller taxa and/or individuals for both cladocerans and calanoids, compared to fishless lakes.

Numerous studies have suggested that competition with large cladocerans and selective predation by cyclopoid predators are the primary factors influencing rotifer communities (e.g. Stemberger and Evans 1984; Devetter and Seda 2006, 2008; Ha and Hanazato 2009). The parallel impacts of trout and native fish on microcrustacean communities in my study lakes suggests that the main ecological contrast in rotifer communities also exists between fish-bearing and fishless lake types.

To examine the independent effects of introduced trout and native small-bodied fish on pelagic rotifer communities, I collected samples from stocked, unstocked, and fishless lakes throughout most of the ice-free season (May through August). All stocked lakes contained non-native trout (mostly Rainbow Trout), whereas all stocked and unstocked lakes contained native small-bodied fish. Lakes with native fish were chosen for stocking over fishless lakes due to accessibility, habitat suitability (e.g. greater depth, less productive), and availability of fish prey.

Rotifer abundance, mean individual body length, mean taxon body length, size structure, and community composition were examined on a monthly basis to determine how stocked trout and native fish affect rotifer communities and their seasonal succession. Overall, I did not expect a distinct effect of trout due to parallel impacts of trout and native fish on the microcrustacean predators and competitors of rotifers in stocked and unstocked lakes. Differences in microcrustaceans between fish-bearing and fishless systems, however, should result in dissimilar rotifer communities.

With the exception of Brachionidae, which posses adaptations for defense against cyclopoid predation, I expected larger mean individual and mean taxon body lengths in stocked and unstocked (fish-bearing) lakes compared to fishless systems, due to greater cyclopoid abundance and their selection for small-bodied taxa (Brandl 1998). Correspondingly, I also expected a greater abundance of rotifer taxa possessing adaptations for defense from predatory cyclopoids (e.g. *Keratella cochlearis* and *Ascomorpha*) in fish-bearing compared to fishless lakes.

Due to differences in cyclopoid predation and cladoceran competition, I expected fish-bearing and fishless systems to harbor distinct communities and that differences would increase over the summer as predation by trout and native fish increased. I also expected greater species richness, diversity, and evenness in fish-bearing lakes because of greater predator-mediated coexistence. Since study lakes are broadly comparable in terms of physical, chemical, and other biological properties, I expected fish presence to explain more variation in the community data sets than environmental variables.

Methods

Study Area & Water Chemistry

See study area and water chemistry methods in Chapter 2.

Rotifer Collection and Laboratory Processing

All 14 study lakes were sampled during the last week of each month (May- August 2009). Pelagic rotifers were collected as discrete samples at 1-m intervals at the deepest location in each lake using a 30-L Schindler-Patalas Trap with a 63 μm mesh dolphin-cup. Samples were preserved in 80% ethanol until laboratory processing. For May, June, and August, samples from each metre were combined to produce a single composite sample for each lake while the samples from each depth were processed separately for July to examine depth distribution (see Chapter 4).

Individuals were counted and identified down to the lowest feasible taxonomic level (LFTL; generally species, sometimes genus). Identifications were made based on Ward and Whipple 1966. Individuals of the large rotifer, *Asplanchna* sp., were counted first using a dissecting microscope with a PVC Ward counting-wheel and then separated from smaller rotifers using a 250 μm mesh sieve. The remaining rotifers were counted using a compound scope with a Sedwick Rafter Counting Cell. Samples were sub-sampled until at least 250 individuals were detected, consisting of a maximum of 50 individual from each LFTL group. All individuals in a sub-sample were counted but sub-sampling did not halt until the detection criteria were met for that sample. This method results in final counts greater then 250 individuals, but provides greater detection of rare taxa. Sub-samples were taken using a 1 mL Hensen-Stempel pipette.

A subset of each taxon (n=15 per sample if possible) was measured (dorsal lengths excluding appendages/projections) using a calibrated ocular micrometer. These measurements were used to determine the mean length of each taxon, which was used along with abundance data to determine biomass. Biomass calculations were conducted as described by McCauley (1984) and Culver *et al.* (1985).

Statistical Analysis

Univariate analyses were conducted using SPSS Statistics 19.0 (SPSS for Mac OS X, Rel. 19.0.0 2010). A nonparametric K-S test assessed normality for each data set and Levene's test of Equality of Variances assessed the homogeneity of variance. Data that were not normally distributed were $\log_{10}(x+1)$ transformed (or square root transformed as a second attempt at normality). Transformation of rotifer length data sets did not successfully normalize data (with the exception of Synchaetidae species length) due to low variation but were still presented when the model residuals were found to be normal. For all Linear Mixed Models, if the interaction was not significant ($p>.05$), it was removed from the analysis so the remaining explanatory variables could explain the variance in the data that was potentially being explained by the non-significant interaction. Results were considered significant if $p< 0.05$, whereas $0.05 <p< 0.1$ was considered marginally significant. For methods on water chemistry analysis see Chapter 2.

I determined rotifer abundance, mean individual body length, and mean taxon body length (at the LFTL) for all rotifers combined and at the family, genus, and species levels across all 14 lakes in each monthly sampling period (May-August 2009). Taxonomic groups included were Rotifera (all from Order

Ploima) the families Brachionidae, Gastropidae, Lecanidae, and Synchaetidae, the genera *Ascomorpha*, *Kellicottia*, *Keratella*, and *Polyarthra*, and the species *Kellicottia longispina*, *Keratella cochlearis*, *Keratella crassa*, and *Keratella earlinae*; other taxa were excluded due to infrequent occurrence, low sample size, or non-normal data. Mean individual body length was calculated by taking the average length of each taxon within an order or family and then calculating a weighted individual length based on the proportions of taxa present. Mean taxon body length was also calculated using the average length of each taxon within an order or family and then taking the average of those average taxon lengths.

Linear Mixed Models assessed differences in abundance, mean individual length, and mean taxon length among the three lake types and the four sampling periods using lake type, month, and their interaction as fixed variables and lake as a random variable. Taxon length was only analyzed for groups with sufficient sample sizes (>15 lengths/lake/sample period).

To assess whether predation was size-selective, I analyzed quantile-quantile (QQ; *sensu* Post and Evans 1989) plots of the mean length distribution for each pairwise comparison of the three lake types during the four sampling periods. QQ plots were used to transform length-frequency-distributions into linear functions by plotting the length at the following quantiles: 1, 5, 10, 25, 35, 50, 65, 75, 90, 95, and 99. In QQ plots, a slope of 1.0 indicates that no difference exists between two distributions. A slope < or > 1 indicates a difference between size distributions and the potential size-selective predation for large or small prey. Mean slopes from the four sampling periods were compared to 1.0 using one-sample t-tests.

I used Linear Mixed Models to assess differences among lake types and sampling periods in Shannon-Weiner diversity, richness, and evenness (% of maximum diversity; Legendre and Legendre 1998), calculated using LFTL abundance data. Lake type, month, and their interaction were included as fixed variables, whereas lake was included as a random variable. When lake type was significant for diversity or richness, relationships with lake area and depth were assessed using linear regression since these physical attributes can provide increased heterogeneity within lake ecosystems and thus additional habitats supporting additional taxa (Tessier and Welser 1991).

To compare patterns of rotifer community composition between the three lake types, I used Principle Component Analysis (PCA) on rotifer genera abundance data. PCA was chosen based on the results from a preliminary detrended correspondence analysis (DCA) of the rotifer matrix that calculated the length of the dominant axis. PCA analyses were done separately for each sampling period, and for all lake-months combined. The latter allowed the succession of rotifer communities in each lake type to be followed through time. Ordinations were performed using PC-ORD version 6.0 (McCune and Mefford 2011). Data sets were checked for rare (in < 3 lakes) and outlier (> 2 SD from the mean) taxa, which were deleted or merged with a larger taxonomic group (e.g. genera pooled within a family). I plotted the first two Principal Components for visual assessment. Biplots of taxa ($r^2 > 0.5$) and environmental variables ($r^2 > 0.3$) were also plotted.

To assess how well patterns of similarity among lakes based on the abundance of rotifer genera corresponded to the presence of trout and/or native fish, cluster analyses were performed. Analyses were done separately for each month using Sorensen (Bray-Curtis) distance measure and group average as the linkage method.

Multiple Response Permutation Procedures (MRPP; McCune and Grace 2002) were performed on abundance data for genera to test for differences among the three lake types in rotifer community composition. MRPPs were also performed on environmental data to test for differences between the three lake types (see Chapter 2).

Mantel Tests were performed on rotifer genera abundance and fish presence/absence data to compare similarities between the two matrices. Fish taxa included were trout, Fathead Minnow, Brook Stickleback, dace species complex, and a "fishless" category to allow inclusion of the fishless lake type. Mantel Tests were also performed on rotifer and environmental data. All Mantel Tests were done separately for each sampling period. Area and maximum depth were initially included in this analysis but always produced significant results with the exception of May (results not shown). For this reason, area and maximum depth were recognized as important contributors to similarities between rotifer and environmental matrices and were removed from the analysis to determine if the remaining environmental variables could produce significant results.

A two-way Variance Partitioning Analysis (VPA; Borcard *et al.* 1992; Hall *et al.* 1999) was used to assess the proportion of variance in the rotifer community composition that could be explained by the environmental variables and the fish assemblage type (stocked, unstocked, and fishless). Analyses were conducted using CANOCO, version 4.5 (ter Braak and Smilauer 2006). A preliminary DCA of the species matrix indicated that a linear model (using redundancy analysis – RDA) was appropriate for VPA (ter Braak and Smilauer 2006). Environmental variables included in the VPA were assessed with forward stepwise selection ($p<0.09$; ter Braak and Smilauer 2006). VPA was conducted for June, July, and August.

Results

Across the 14 study lakes and four sampling periods 42 taxonomic groups of rotifers were identified (Table 3-1). In total, 322,592 rotifers were counted, while 14,390 rotifers were measured from the 130 samples collected.

Rotifer Abundance and Length

Rotifer abundance (Order Ploima) did not differ among lake types (p= 0.744) and months (p= 0.135, Linear Mixed Model, Table 3-2). Brachionidae abundance differed among months (p= 0.018) but not lake types (p= 0.801). Brachionids were more abundant in June compared to July (p= 0.003) and August (p=0.020, Table 3-2).

For the genus *Kellicottia* (Brachionidae), abundance differed marginally among lake types (p= 0.094) and months (p= 0.099). Fishless lakes had a lower abundance than stocked lakes (p= 0.036); other pairwise comparisons did not differ (p> 0.10). *Kellicottia* abundance decreased from May through July, with a slight increase in August (Table 3-3). *K. longispina*, abundance differed among months (p< 0.001) and marginally among lake types (p= 0.061), with a significant interaction (p= 0.002). *K. longispina* was more abundant in stocked lakes than unstocked (p= 0.050) and fishless (p= 0.042) lakes, primarily during May and June (Table 3-4).

Keratella (Brachionidae) abundance differed among months (p= 0.024), peaking in June, but not lake types (p= 0.771; Table 3-3). Within the genus, however, there was some variation. *K. cochlearis* had a lower abundance in fishless lakes than stocked (p= 0.031) and unstocked (p= 0.007) lakes, which did not differ (p= 0.289, Table 3-4). *K. earlinae* was less abundant in fishless lakes compared to stocked (p= 0.029) or unstocked lakes (p= 0.034), which did not differ from each other (p=0.997, Table 3-4). Similar to the genus as a whole, *K. crassa* differed in abundance among months (p= 0.004) but not lake types (p= 0.153), but the interaction was significant (p= 0.036). In stocked and unstocked lakes, *K. crassa* abundance was relatively stable throughout the summer, whereas in fishless lakes, abundance was lowest in May, spiked in June, and then decreased in July and August (Table 3-4).

Gastropidae was less abundant in fishless lakes compared to stocked (p= 0.001) and unstocked (p= 0.003) lakes, which did not differ from each other (p= 0.709, Table 3-2). Overall, abundance increased from May through August (Table 3-2). Within Gastropidae, *Ascomorpha* displayed similar patterns among lake types and months (Table 3-3).

Lecanidae abundance did not differ among lake types (p= 0.744) or months (p= 0.694, Table 3-2). Synchaetidae abundance differed marginally among months (p= 0.090) but not lake types (p= 0.219), with a significant interaction (p= 0.041). In stocked and unstocked lakes, Synchaetidae abundance was high in May, and low in June through August, whereas in fishless lakes abundance remained relatively low throughout the four months (Table 3-2). Within Synchaetidae, *Polyarthra* abundance did not differ among lake types or months (Table 3-3).

Mean individual length of Rotifera (Order Ploima) was not analyzed due to an inability to normalize the data or residuals (Table 3-5). Mean taxon length of rotifers differed marginally among lake types (p= 0.060) and significantly among months (p< 0.001). Mean taxon length was smallest in fishless lakes compared to stocked (p= 0.030) and unstocked (p= 0.032) lakes, which did not differ from each other (p= 0.966). Overall, mean taxon length increased from June to August (Table 3-6).

Brachionidae individual length differed marginally among lake types (p= 0.066) and significantly among months (p= 0.003, Table 3-5). The only significant pairwise comparison revealed that Brachionidae had a larger mean individual length in stocked lakes compared to unstocked lakes (p=0.024). Mean individual length was greatest in May for all three lake types (Table 3-5). Brachionidae taxon length differed among months (p< 0.001) but not lake types (p= 0.872). Overall, mean taxon length was highest in July (Table 3-6).

Gastropidae and Lecanidae individual lengths and taxon lengths could not be analyzed due to inadequate sample sizes. Synchaetidae individual length differed among months ($p< 0.001$, largest in May) but not lake types ($p= 0.112$, Table 3-5). Synchaetidae taxon length differed among months ($p< 0.001$) but not lake types ($p= 0.904$), with a significant interaction ($p= 0.044$). In stocked, but not unstocked or fishless lakes, mean taxon length was high in May and moderate in June-August (Table 3-6).

Rotifer Size Structure

To examine evidence for size-selective predation, I analyzed quantile-quantile (QQ; *sensu* Post and Evans 1989) plots of the mean length distributions for stocked, unstocked, and fishless lakes during the four sampling periods. In the comparison of stocked and unstocked lakes (Appendix C), the average slopes for rotifers as a whole (Order Ploima) (t-test, $t_3= 7.322$, $p= 0.005$) and Synchaetidae (t-test, $t_3= 7.450$, $p= 0.005$) were >1, indicating size selective mortality of small Ploima and Synchaetidae in stocked compared to unstocked lakes. In contrast, the average slope for Brachionidae was <1 (t-test, $t_3= 16.349$, $p< 0.001$), indicating size selectivity for large Brachionidae prey in stocked lakes. In the comparison of stocked versus fishless lakes (Appendix C) the average slope for Ploima was >1 (t-test, $t_3= 7.687$, $p= 0.005$), whereas slopes for Brachionidae (t-test, $t_3= 10.642$, $p= 0.002$) and Synchaetidae (t-test, $t_3= 6.911$, $p= 0.006$) were <1, suggesting selective predation on small Ploima but on large Brachionidae and Synchaetidae in stocked compared to fishless lakes. In the comparison of unstocked and fishless lakes (Appendix C), the average slope for Ploima was >1 (t-test, $t_3= 4.342$, $p= 0.023$), whereas the average slopes for Brachionidae (t-test, $t_3= 7.316$, $p= 0.005$) and Synchaetidae (t-test, $t_3= 5.830$, $p= 0.010$) were <1, again indicating size selective predation on small Ploima but on large Brachionidae and Synchaetidae in unstocked compared to fishless lakes.

Rotifer Community Composition

Rotifer species richness differed significantly among months ($p< 0.001$) but not lake types ($p= 0.625$, Linear Mixed Model). Overall, richness increased from May through July, with a drop in August (Table 3-7). In contrast, rotifer species diversity differed significantly among lake types ($p= 0.045$) but not months ($p= 0.212$), although there was a significant interaction ($p= 0.026$). Stocked lakes supported a greater diversity of rotifers than fishless lakes ($p= 0.015$). Diversity remained relatively constant from May through August in stocked and unstocked lakes, but was high in May and low in June through August in the fishless lake type (Table 3-7). Neither lake area nor depth was correlated with diversity in May ($p> 0.1$) but both were correlated with diversity in June and August (linear regression, Table 3-8).

Rotifera evenness differed significantly among lake types ($p= 0.031$) and months ($p= 0.040$), but the interaction between these factors was also significant ($p= 0.039$, Table 3-7). Evenness was generally higher in stocked lakes vs. fishless lakes; it remained relatively constant from May through August in stocked and unstocked lakes, but was high in May and then low in June through August in fishless lakes (Table 3-7).

No useful ordination of rotifer communities could be constructed for May. In addition, the three major groups that emerged from the cluster analysis for this month did not reflect fish community types, suggesting little effect of fish in structuring rotifer communities during the spring (Figure 3-5). Based on MRPP, however, rotifer community composition differed among lake types in May (p=0.039). Pairwise comparisons revealed a difference between stocked and unstocked lakes (p= 0.013). Similar to ordination and cluster results, rotifer and fish community matrices were not significantly related in May (Mantel Test; p= 0.110) nor were rotifer and environmental matrices (area and maximum depth removed, p= 0.428).

The ordination for June (Figure 3-1) captured 45% of variance in the data set (14 taxa, axis 1: p= 0.05, axis 2: p= 0.70). Rotifer taxa that were strongly correlated with the axes (r^2>0.5) include *Ascomorpha, Gastropus, Kellicottia,* and *Polyarthra*. The environmental variables that were strongly correlated with the axes (r^2>0.3) were TP, TDP, PH, maximum depth, area, and Secchi depth. The ordination separated lake types with fishless lakes on the left, unstocked lakes in the center, and stocked lakes on the right. The ordination indicated that the abundance of all correlated taxa was greater in stocked then fishless lakes (unstocked intermediate) as was maximum depth, area, and Secchi depth, whereas fishless lakes had a higher TP, TDP, and pH. One unstocked lake (Teal) was somewhat of an outlier on the right side of the graph due to high abundances of the correlated taxa. The three major groupings that emerged from cluster analysis strongly reflected the fish community types (Figure 3-5). All three fishless lakes clustered in the first group along with two unstocked lakes. The second group was composed of stocked and unstocked lakes and the third consisted of one stocked lake. Based on MRPP, rotifer community composition differed among lake types (p=0.012). Pairwise comparisons revealed that stocked and fishless lakes differed (p=0.005), as did unstocked and fishless lakes (p= 0.041). The rotifer and fish community matrices were not significantly related in June (Mantel Test; p= 0.100) but a significant relationship was found between the rotifer and environmental matrices (p= 0.046).

The ordination for July (Figure 3-2) captured 48% of variance in the data set (20 taxa, axis 1: p= 0.01, axis 2: p< 0.01). Rotifer taxa that were strongly correlated with the axes (r^2>0.5) included *Notholca, Mytilina, Gastropus, Epiphanes, Monostyla, Trichotria, Asplanchna,* and *Kellicottia.* None of the environmental variables were strongly correlated with the axes (r^2>0.3). The ordination separated lake types with fishless lakes on the left, unstocked lakes in the center, and stocked lakes on the right. The ordination indicated that the abundance of all correlated taxa was greater in stocked then fishless lakes (unstocked intermediate). Two unstocked lakes (Gas Plant and Picard) were outliers on the right side of the graph due to high abundances of taxa correlated with Axis 1. The three major groupings that emerged from cluster analysis strongly reflected lake types (Figure 3-5). Two fishless and two unstocked lakes formed the first group, a fishless lake formed the second group, and the remaining stocked and unstocked lakes formed the third group. Based on MRPP, rotifer community composition did not differed among lake types in July ($p > 0.1$). The rotifer and fish community matrices were significantly related in July (Mantel Test; $p = 0.040$), as were the rotifer and environmental matrices ($p = 0.008$).

The ordination for August (Figure 3-3) represented 54% of variance in the data set (14 taxa, axis 1: $p < 0.01$, axis 2: $p = 0.68$). Rotifer taxa that were strongly correlated with the axes ($r^2 > 0.5$) included *Trichocerca*, *Kellicottia*, *Lecane*, *Gastropus, Monostyla, Asplanchna,* and *Euclanis*. The environmental variables that were strongly correlated with the axes ($r^2 > 0.3$) included area and maximum depth. The ordination separated lake types with fishless lakes on the left, unstocked lakes in the center, and stocked lakes on the right. The ordination indicated that the abundance of all correlated taxa was greater in stocked than fishless lakes (unstocked intermediate) as was maximum depth and area. One unstocked lake (Gas Plant) was somewhat of an outlier on the right side of the graph due to high abundances of the correlated taxa. For August, three major groups emerged from the cluster analysis but did not reflect lake types, suggesting little effect of fish in structuring rotifer communities during the late summer (Figure 3-5). Based on MRPP, rotifer community composition differed among lake types in August ($p=0.010$). Pairwise comparisons revealed that in August, stocked and fishless ($p=0.003$) lakes differed, as did unstocked and fishless lakes ($p= 0.079$). The rotifer and fish community matrices were significantly related in August (Mantel Test; $p= 0.003$), as were the rotifer and environmental matrices ($p= 0.002$).

The ordination of lake-month succession through time (Figure 3-4) captured 28% of the variance in the data set (20 taxa, axis 1: $p < 0.01$, axis 2: $p = 0.01$). Rotifer taxa that were strongly correlated with the axes ($r^2 > 0.5$) included *Trichocerca*, *Asplanchna*, and *Gastropus*. None of the environmental variables were strongly correlated with the axes ($r^2 > 0.3$). The ordination somewhat separated lake types with fishless lakes on the left, and most fish-bearing lakes in the center or on the right. The ordination indicated that the abundance of all correlated taxa was greater in stocked and unstocked lakes during the summer compared to fishless lakes in the spring/summer and fish-bearing lakes in the spring.

The environmental variables that were chosen for VPA through forward stepwise selection were area, TDP, and Secchi depth in June; depth, TDN, TDP, and Chl-a in July; and depth, area, and TP in August. These environmental variables explained between 33.2- 46.8% of variation in the rotifer communities, whereas the fish assemblage explained 7.2- 17.8% of the variation (Figure 3-6) and the variation explained by the combination of environment and fish assemblage was 5.3- 16.5%. Thus, environment conditions were associated with at least twice as much variation in rotifer communities as was the presence and identity of fish.

Discussion

Rotifer Abundance and Length

Similar to crustaceans, few differences were detected in the abundance, biomass, and size of the major rotifer groups between stocked lakes and unstocked lakes containing only native fish, suggesting little additive effect of trout. Several taxa, however, differed significantly between fish-bearing and fishless systems. For example, the family Gastropidae and the LFTL *Ascomorpha*, *Keratella cochlearis* and *K. earlinae* had greater mean abundances in fish-bearing compared to fishless lakes. Studies of alpine lakes in Europe (Schabetsberger *et al*. 2009), and North America (Knapp *et al.* 2001) reported similar results with increased abundance of Gastropidae and *Keratella* species after fish introduction and in trout-bearing compared to fishless lakes.

Larval native fish in stocked and unstocked lakes could impact rotifer communities directly since these newly hatched young are gape-limited to small prey and feed on rotifers within freshwater ecosystems (Thorp and Covich 1991). In addition, although stocked trout and adult native fish do not selectively feed on rotifers, they can impact their microcrustacean competitors. Rotifers may therefore experience improved feeding condition in fish-bearing lakes due to reduced competition with efficient cladoceran grazers such as *Daphnia* (Burns and Gilbert 1986; Ha and Hanazato 2009). Interference competition can also play a role when rotifers are damaged or killed by the filtration appendages of feeding cladocerans (Gilbert 1988; McIsaac and Gilbert 1991). The intensity of competition and lethal interactions increases with increased cladoceran size and density (Gilbert 1985; Burns and Gilbert 1986; Gilbert and MacIsaac 1989). Cladoceran taxa in fish-bearing lakes in my study displayed a significantly smaller mean taxon size compared to fishless lakes, and often contained competitively inferior grazers such as *Bosmina longirostris* and *Diaphanasoma brachyurum/leuchtenbergianum* (Chapter 2). In contrast, fishless lakes often contained several larger and efficient *Daphnia* grazers including *D. middendorffiana, D. pulex,* and *D. schodleri.* The difference in cladoceran community composition and size structure between fish-bearing and fishless lakes could contribute to the greater abundance of Gastropidae (including the genus *Ascomorpha*), and the two *Keratella* species.

In addition to competition, rotifer communities can be impacted through selective predation by invertebrate predators. Fish can influence invertebrate predator communities through size selective predation on large individuals thus indirectly benefiting smaller predators (Carlisle and Hawkins 1998), such as cyclopoids. Rotifers are the preferred prey of cyclopoids, which are selective based on size and adaptations for predator defense (Brandl 1998). I found higher cyclopoid abundances in fish-bearing compared to fishless lakes (Chapter 2), similar to results reported by Carlisle and Hawkins (1998). The cyclopoid species in my study lakes are known to prey upon at least one-third of the rotifer genera with which they coexist (Brandl 2005), with the potential to alter populations of these prey. *Mesocyclops edax*, a cyclopoid common to all 14 study lakes, can have daily consumption rates of between 13-24% of rotifer individuals present (Brandl and Fernando 1981). These predation rates can be high enough to exert top down control and often achieve or exceed reproductive rates of certain rotifer populations (Brandl 2005).

In general, small, soft-bodied species are more vulnerable to cyclopoid predation, although rotifer behavior (e.g. movement and escape reaction) can also affect susceptibility (Brandl 2005). Cyclopoids avoid *Keratella* and Gastropidae (Stemberger 1985). *K. cochlearis* and *K. earlinae* are loricate species possessing external spines and the ability to increase movement to escape predation (Williamson 1987; Gilbert and Kirk 1988). Indeed, abundance of *Keratella* can be positively correlated to cyclopoid populations in fish-bearing lakes (Stemberger and Evens 1984). Gastropidae have a mucus coating that could also confer predator-resistance (Stemberger 1985), with *Ascomorpha* eggs hatch in the adult mucus cavity, providing protection against predators (Stemberger 1985).

A potential impact of trout was detected for one genus (*Kellicottia*); in particular, *K. longispina* had a greater abundance in stocked lakes compared to unstocked and fishless lakes. I suggest that an indirect interaction involving *Chaoborus* could be behind this result. Macroinvertebrate predators, such as *Chaoborus* have been found to feed upon *Kellicottia* species, with a negative relationship documented between *Chaoborus* and *Kellicottia* abundance (Elser *et al.* 1987). Trout had a more drastic impact on *Chaoborus* populations than did native fish; *Chaoborus* in the current study, were 10 times more abundant in fishless compared to stocked lakes and three times more abundant in unstocked than stocked lakes (Chapter 2).

The abundance of all other taxonomic groups investigated did not differ among lake types including Order Ploima, which encompassed all rotifers investigated. These results indicate either an inability to detect an impact at these particular taxonomic levels (e.g., no impact for the genus *Keratella* but an impact on individual species such as *K. cochlearis*) or simply a lack of impact of trout and/or native fish at these particular levels.

The presence of trout and/or native fish affected the size of rotifers. Ploima, encompassing all rotifers investigated, had a larger mean species length in fish-bearing compared to fishless lakes. QQ plots suggest size selective predation by fish (trout and native fish) on small individuals across this order as a whole, but an opposite pattern for the families Brachionidae and Synchaetidae. Large Ploima (e.g. *Asplanchna*) are difficult for cyclopoids to capture (Gilbert and Williamson 1978; Williamson 1983) and are often avoided by these small invertebrate predators (Stemberger 1985). Cyclopoids have been found to prefer smaller, soft-bodied Synchaetidae and even loricate Brachionidae to large-bodied Ploima (Stemberger 1985; Devetter and Seda 2006). Although Brachionidae possess loricate species with external spines or structures (Stemberger 1985), *Brachionus* and *Notholca*, relatively large-bodied genera within this family, posses smaller spines then *Keratella* and *Kellicottia*. Large spines are difficult for cyclopoids to manipulate and increase the rate of rejection once prey is captured (Stemberger and Gilbert 1984). Within the family Synchaetidae, Plassmann *et al.* (1997) recorded cyclopoid preference for the larger, and slower *Synchaeta* species over the smaller *Polyarthra* species, while Stemberger (1985) found selection for the larger and slower of two *Polyarthra* species.

Q-Q plots also suggested a difference in size-selective predation between stocked and unstocked lakes, with greater predation on small Ploima and

Brachionidae, but on large Synchaetidae in stocked compared to unstocked lakes. *Cyclops biscuspidatus thomasi* was present twice as often in stocked compared to unstocked lakes. This species has a relatively high predation rate and a slightly different diet in terms of zooplankton taxa consumed compared to other cyclopoids (Brandl 2005), which could explain the difference in size selectivity between stocked and unstocked lakes.

Rotifer Community Diversity and Composition

Stocked lakes displayed greater species diversity and evenness compared to fishless lakes. As with microcrustaceans, contributing to this diversity pattern could be the somewhat greater size and depth of stocked lakes, which can offer a range of distinct environments for additional species (Tessier and Welser 1991). Linear regression analysis of diversity versus lake area and depth, however, revealed significant relationships in only two of four months.

Predator mediated coexistence of species has also been suggested as a possible cause of greater diversity in systems containing additional predator taxa (Hairston *et al.* 1960). As noted, one of the two cyclopoid taxa present, *Cyclops biscuspidatus thomasi*, was found twice as often in stocked compared to unstocked and fishless lakes. In addition, cyclopoid abundance was greater in stocked compared to fishless lakes (Chapter 2). Cyclopoid predators can facilitate the coexistence of rotifer taxa due to heightened vulnerabilities of competitively superior species (Lapesa *et al.* 2002). Greater cyclopoid richness and higher cyclopoid abundances in stocked compared to fishless lakes supports predator mediated coexistence as a contributing cause for differences in diversity and evenness among lake types.

MRPP analyses and Mantel Tests suggested a moderate fish effect on rotifer communities but only a mild separate effect of trout. *Gastropus, Asplanchna, Kellicottia*, and *Monostyla* displayed a strong affinity to fish-bearing lakes in at least two of the three monthly ordinations with an additional nine genera showing strong affinities in one month. Thus, a strong association with fish-bearing lakes was observed for over half of the rotifer genera, consistent with the findings of Schabetsberger *et al.* (2009) for an alpine rotifer community. Pond mesocosm experiments by Beisner and Peres-Neto (2009) also found favorable responses of many rotifer taxa to the presence of fish. Together with the ordinations, the cluster analyses, which never created groups of fishless and stocked lakes, suggested a gradient effect of stocked trout and native fishes, whereby fishless and stocked lakes harbored distinct rotifer communities, whereas unstocked lakes contained intermediate communities with components of both stocked and fishless lakes.

Seasonal Effects on Rotifers

For a number of my analyses (involving abundance, sizes, and community structure), there were significant month x lake-type interactions that suggested additional impacts of stocked trout or a more general fish effect. In stocked lakes, the abundance of *Kellicottia longispina* was high in May and June but low in July and August, while in unstocked and fishless lakes the abundance remained relatively low throughout the spring/summer period. These results suggest an impact of trout on the seasonal abundance of *K. longispina*. Although differing from Yoshida *et al.* (2001), this pattern could result from seasonal differences in *Chaoborus* populations among lake types, given documented effects of *Chaoborus* on *Kellicottia* abundance (Elser *et al.* 1987).

In stocked and unstocked lakes the abundance of *Keratella crassa* was relatively constant throughout the spring/summer, whereas in fishless lakes abundance spiked in June. Stemberger and Gilbert (1984) reported that larger rotifers (such as *K. crassa*) have higher threshold food levels and are less adapted to food-poor environments. Higher Chl-a levels in fishless lakes may have allowed the spike in *K. crassa* abundance during June, while greater competition with growing cladoceran populations may have limited *K. crassa* abundance later in the summer.

In stocked and unstocked lakes, the abundance of the soft-bodied Synchaetidae family was high in the spring (May) then dropped throughout the summer (June-August), while in fishless lakes the abundance of this family was constant throughout the study period. The abundance results further suggested that the Synchaetidae pattern was driven by changes in *Synchaeta* and not *Polyarthra* abundance. Previous studies (Stemberger and Evans 1984; Plassmann *et al.* 1997; Brandl and Prazakova 2002) have attributed decreased abundances of soft-bodied, fast-reproducing *Synchaeta* species as the summer progressed to selective predation by cyclopoids. Limited mobility and lack of predatory defenses make *Synchaeta* particularly susceptible to cyclopoid predators (Plassmann *et al.* 1997). The proportion of cyclopoid adults increased from spring (May) through summer (June- August) in fish-bearing lakes, which would have increased predation pressure from spring to summer. Low cyclopoid abundance throughout May-August in fishless lakes, however, could be responsible for stable abundance of Synchaetidae throughout this time.

In stocked lakes, Synchaetidae taxon length was high in May and low throughout June-August, while in unstocked and fishless lakes taxon length was low only in June. Decreased Synchaetidae taxon length from May to June in all three lake types likely reflects the removal of individuals of the large genus *Synchaeta* by predatory adult cyclopoids (Plassmann *et al.* 1997) as cyclopoids have matured by June and completed the primarily herbivorous pre-adult stages (Hansen and Santer 1995). Greater taxon length in mid to late summer (July and August) in unstocked and fishless lakes compared to stocked lakes likely reflects the appearance of members of the large-bodied but rare genus *Ploesoma* in several unstocked and fishless lakes.

Rotifer diversity and evenness in fishless lakes were high only in May, in contrast to stocked and unstocked lakes, where values were relatively high or moderate throughout May-August. Fishless lakes experience a relatively low abundance of all taxa present in May, while during the summer the abundance of only two or three taxa drastically increased (e.g. *Keratella*, *Synchaeta,* and *Polyarthra*), whereas the other taxa maintained low abundances near spring levels. In stocked and unstocked lakes, however, the abundance of many taxa increased during the summer (e.g. *Keratella*, *Synchaeta*, *Polyarthra*, *Ascomorpha,* *Gastropus*, and *Kellicottia*) and often many additional taxa that were not present in the spring appeared. Selective predation by invertebrate predators that cannot coexist with fish (e.g., *Chaoborus americana*) and/or greater competition with large cladoceran grazers may have prevented the appearance or increased abundance of susceptible rotifer taxa in fishless lakes. Cyclopoid predator-mediated coexistence of species in fish-bearing lakes (due to greater adult cyclopoid abundance and richness during the summer) could also be a contributing factor to the higher diversity and evenness in fish-bearing lakes during June-August.

The inability to detect differences in rotifer community composition among lake types in May could reflect minimal differences in predation pressure among lake types during spring. Predatory cyclopoid adults were uncommon in May in all three treatments: pre-adult diets consist mostly of algae (Hansen and Santer 1995). The strong increase in adult cyclopoid abundance throughout the summer in fish-bearing lakes undoubtedly increased predation pressure on rotifers in these systems. Greater cyclopoid predation in fish-bearing lakes, combined with selective predation in fishless lakes from *Chaoborus americana* should increase differences in Rotifera communities as the summer progresses. In addition, comparatively low cladoceran abundances in May could create similar competitive regimes across lake types during this time. With the advance of summer, cladoceran communities diverged (small cladocerans dominating fish-bearing lakes, large cladocerans dominating fishless lakes), altering competition within fish-bearing versus fishless lakes.

Previous studies have concluded that selective feeding by cycpopoid predators and food resource levels are the most important determinants of rotifer species succession (Stemberger and Evans 1984, Plassmann *et al.* 1997). Subsequent experiments supported this view and documented a sequence of prey selection by cyclopoids over the course of the summer as preferred species became rare or disappeared. Competition from cladoceran grazers can play an important role later in the summer (Devetter and Seda 2006, 2008).

Fish Community versus Environmental Differences

Environmental variables (maximum depth and area excluded) differed among lake types during two of four sampling periods, whereas rotifer communities differed in three of four months. Environment and rotifer community matrices were correlated in three of four months whereas fish and rotifer community matrices were only correlated during two months. Fish together with environmental variables explained ~60% of the variance in the data set, with environmental variables contributing about three times the explained variation compared to fish. These results imply that, although fish do play a role in structuring rotifer communities, environmental variables are more important. Young-of year native fish may directly impact rotifer communities through predation. In addition, trout and adult native fish that do not select rotifers as prey (Beauchamp 1990; Naud and Magnan 1988) appear to impact rotifer communities indirectly through induced changes in the aquatic community, as described above.

Conclusions

The impact of trout and native fish on their invertebrate prey appears to be the driving force that shapes rotifer communities in my study lakes, resulting in an indirect effect of fish. The presence of at least partially plantivorous fish can reduce the abundance of predatory *Chaoborus* and large, competitively superior cladoceran and calanoid zooplankton, while increasing the abundance of small cladocerans and predatory cyclopoids (e.g. Donald *et al.* 2001). I also found this pattern in my study, with limited differences between stocked and unstocked lakes but significant differences between fish-bearing and fishless lakes (Chapter 2). When large crustaceans dominate aquatic systems, rotifer communities appear to suffer from high competition with cladoceran grazers. When small cladoceran/calanoid grazers and predatory cyclopoids dominate, rotifers appear to benefit from reduced competition, but display a distinct species succession from taxa susceptible to cyclopoid predation (e.g. *Synchaeta*) in the spring to less susceptible taxa (e.g. *Keratella* species and Gastropidae) in the summer, after abundant populations of predatory adult cyclopoids are established.

Limited additional impact of trout was detected in the presence of native fish in the current study systems despite the obvious general impact of fish. The main detectable trout impact was a greater abundance of one taxon (*Kellicottia longispina*) in the presence of trout, which appeared to be driven by the greater impact of trout versus native fish on the invertebrate predator *Chaoborus*. In addition, despite a trend of greater diversity and richness in stocked lakes, both fish-bearing lake types (stocked and unstocked) experienced a high or moderate diversity and richness of rotifer species throughout the spring and summer whereas fishless lakes experienced a drastic drop in these metrics throughout June-August. Again, these changes to the rotifer community appear to result from the impact of trout and native fish on rotifer competitors and predators. These differences, however, could be regarded as positive or neutral in terms of impact on the health of the aquatic community. Based on my results, where stocking trout is deemed an appropriate management strategy, lakes with native small-bodied fish appear to be good candidates for stocking.

Table 3-1 Taxa of pelagic rotifers identified in the 14 boreal foothills study lakes in 2009. All families are within the order Ploima. Species listed together could not always be differentiated.

Family	**Genus**	**Species**
Asplanchnidae	*Asplanchna*	unknown
Brachionidae	*Brachionus*	*angularis*
	Kellicottia	*bostoniensis*
		longispina
	Keratella	*cochlearis*
		crassa
		earlinae
		quadrata
		serrulata
		testudo/hiemalis
	Notholca	*acuminata*
		labis
		michiganensis
	Plationus	*patulus*
Epiphanidae	*Epiphanes*	unknown
Euchlanidae	*Beauchampiella*	*eudactylotum*
	Euchlanis	*dilatata*
Gastropidae	*Ascomorpha*	unknown
	Gastropus	*stylifer*
Lecanidae	*Lecane*	*luna*
		mira
		ohioensis
		stokesi
		tudicola
	Monostyla	*bulla*
		closterocera
		lunaris
		quadridentata
		stenroosi
Lepadellidae	*Colurella*	unknown
	Lepadella	*ehrenbergi*
		ovalis
Lindiidae	*Lindia*	unknown
Mytilinidae	*Mytilina*	*ventralis*
Proalidae	*Proales*	unknown
Synchaetidae	*Ploesoma*	*truncatum*
	Polyarthra	unknown
	Synchaeta	*oblonga/pectinata*
Trichotriidae	*Trichotria*	*tetractis*
Tricocercidae	*Ascomorphella*	*volvocicola*
	Trichocerca	*cylindrica/longiseta*
		multicrinis

Table 3-2 Mean (±SE) abundance (individuals/L) of the major order and families in each of four months in 2009 for each lake type: stocked (n= 6), unstocked (n=5), and fishless (n= 3). Also presented are results from Linear Mixed Models for each taxon with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. S: stocked; U: unstocked; F: fishless; -: taxon not present. *0.1>p>0.05, **p<0.05

Taxa	**Lake Type**	**May**	**June**	**July**	**August**	**Main Effect**	**F-Statistic**
Ploima	S	512.5±166.4	600.2±192.5	304.9±146.8	249.7±95.5	Lake Type	$F_{2, 11}$=0.3
	U	730.1±418.6	580.5±253.9	704.0±473.1	724.4±284.0	Month	$F_{3, 38}$=2.0
	F	263.9±241.6	1194.6±583.9	405.4±282.9	245.5±156.0	Interaction	Removed
Brachionidae	S	282.6±100.9	526.8±172.1	267.6±140.3	173.5±82.5	Lake Type	$F_{2, 11}$=0.2
	U	424.9±270.7	477.4±226.6	529.5±409.8	613.0±266.2	Month	$F_{3, 38}$=3.8**
	F	158.2±139.5	1114.0±544.5	282.3±274.6	169.1±129.6	Interaction	Removed
Gastropidae	S	1.3±0.7	26.8±14.2	25.9±9.9	26.1±8.5	Lake Type	$F_{2, 11}$=9.4**
	U	1.6±0.5	4.7±3.2	44.7±23.7	47.4±25.0	Month	$F_{3, 38}$=14.4**
	F	-	-	3.8±2.7	0.8±0.3	Interaction	Removed
Lecanidae	S	0.8±0.3	0.3±0.1	0.4±0.1	0.7±0.3	Lake Type	$F_{2, 11}$=0.3
	U	0.9±0.5	1.5±0.9	1.0±0.6	0.6±0.4	Month	$F_{3, 38}$=0.5
	F	0.3±0.1	1.0±0.5	0.3±0.3	0.3±0.2	Interaction	Removed
Synchaetidae	S	227.7±79.5	40.3±19.9	4.9±1.5	39.7±18.1	Lake Type	$F_{2, 11}$=1.7
	U	302.1±160.5	91.6±35.0	112.2±51.7	58.3±14.7	Month	$F_{3, 32}$=2.4*
	F	101.4±98.6	79.5±42.8	118.5±60.8	74.4±25.5	Interaction	$F_{6, 32}$=2.5**

Table 3-3 Mean (±SE) abundance (individuals/L) of major genera in each of four months in 2009 for each lake type: stocked (n= 6), unstocked (n=5), and fishless (n= 3). Also presented are results from Linear Mixed Models for each taxon with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. S: stocked; U: unstocked; F: fishless; -: taxon not present. *0.1>p>0.05, **p<0.05

Taxa	**Lake Type**	**May**	**June**	**July**	**August**	**Main Effect**	**F-Statistic**
Ascomorpha	S	0.2±0.2	5.5±2.6	6.6±3.3	18.7±9.5	Lake Type	$F_{2, 11}$=4.2**
	U	0.8±0.4	1.5±0.9	18.0±10.9	12.7±3.0	Month	$F_{3, 38}$=11.1**
	F	-	-	3.7±2.8	0.8±0.3	Interaction	Removed
Kellicottia	S	115.4±61.7	100.7±42.1	7.0±3.1	48.7±27.6	Lake Type	$F_{2, 11}$=2.9*
	U	15.9±14.6	50.5±48.3	48.2±30.0	240.7±217.1	Month	$F_{3, 38}$=2.2*
	F	6.7±3.5	1.7±0.8	0.5±0.3	0.4±0.1	Interaction	Removed
Keratella	S	166.1±90.8	424.9±173.4	260.6±140.8	124.7±77.1	Lake Type	$F_{2, 11}$=0.3
	U	400.2±247.6	401.3±213.5	480.8±385.5	372.1±112.1	Month	$F_{3, 38}$=3.5**
	F	148.0±139.1	1110.9±545.8	281.5±274.1	168.7±129.6	Interaction	Removed
Polyarthra	S	124.0±47.5	39.7±19.7	4.4±1.4	38.3±17.6	Lake Type	$F_{2, 49}$=2.0
	U	178.1±146.2	91.5±35.0	107.4±48.8	51.1±9.5	Month	$F_{3, 49}$=1.5
	F	95.5±93.9	40.3±4.5	79.2±36.9	61.5±15.4	Interaction	Removed

Table 3-4 Mean (±SE) abundance (individuals/L) of major species in each of four months in 2009 for each lake type: stocked (n= 6), unstocked (n=5), and fishless (n= 3). Also presented are results from Linear Mixed Models for each taxon with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. S: stocked; U: unstocked; F: fishless. *0.1>p>0.05, **p<0.05

Taxa	**Lake Type**	**May**	**June**	**July**	**August**	**Main Effect**	**F-Statistic**
Keratella cochlearis	S	29.7±9.1	122.9±44.1	37.6±17.5	37.8±14.4	Lake Type	$F_{2, 11}=5.5$**
	U	123.7±47.0	351.6±219.0	381.6±335.9	157.4±56.6	Month	$F_{3, 38}=1.3$
	F	7.8±7.1	4.5±1.4	3.8±2.0	1.4±0.4	Interaction	Removed
Keratella crassa	S	0.6±0.5	42.4±39.3	107.1±89.6	70.9±66.2	Lake Type	$F_{2, 13}=2.2$
	U	10.5±9.3	24.3±11.0	11.0±6.2	22.6±19.2	Month	$F_{3, 31}=5.6$**
	F	30.8±25.2	1091.3±544.0	276.6±275.8	166.0±128.9	Interaction	$F_{6, 31}=2.6$**
Keratella earlinae	S	6.0±4.3	136.1±67.6	17.4±11.3	7.4±3.8	Lake Type	$F_{2, 11}=3.6$*
	U	2.3±2.3	20.9±18.0	85.4±53.6	190.6±119.3	Month	$F_{3, 38}=3.6$**
	F	0.1±0.1	1.7±0.9	0.7±0.6	0.1±0.0	Interaction	Removed
Kellicottia longispina	S	114.8±61.5	97.9±40.3	5.7±1.9	3.2±0.5	Lake Type	$F_{2, 11}=3.6$*
	U	15.0±14.3	49.4±48.4	20.1±20.0	8.5±8.4	Month	$F_{3, 32}=17.7$**
	F	6.5±3.3	1.6±0.7	0.4±0.4	0.1±0.0	Interaction	$F_{6, 32}=4.6$**

Table 3-5 Mean (±SE) individual length (mm; see text for definition) of the major order and families in each of four months in 2009 for each lake type: stocked (n= 6), unstocked (n=5), and fishless (n= 3). Also presented are results from Linear Mixed Models for each taxon with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis ($p>0.05$), it was removed from the model. n/a: insufficient sample size for analysis or (in the case of Ploima) data and residuals from the model were not normal. S: stocked; U: unstocked; F: fishless. *$0.1>p>0.05$, **$p<0.05$

Taxa	Lake Type	May	June	July	August	Main Effect	F-Statistic
Ploima	S	0.135±0.008	0.119±0.007	0.140±0.021	0.128±0.008	Lake Type	n/a
	U	0.116±0.004	0.098±0.004	0.108±0.001	0.106±0.003	Month	n/a
	F	0.121±0.004	0.100±0.004	0.113±0.005	0.116±0.005	Interaction	n/a
Brachionidae	S	0.121±0.004	0.114±0.004	0.110±0.004	0.110±0.002	Lake Type	$F_{2, 11}=3.5$*
	U	0.109±0.006	0.098±0.005	0.103±0.003	0.102±0.004	Month	$F_{3, 38}=5.7$**
	F	0.118±0.005	0.100±0.004	0.101±0.004	0.111±0.006	Interaction	Removed
Gastropidae	S	n/a	n/a	n/a	n/a	Lake Type	n/a
	U	n/a	n/a	n/a	n/a	Month	n/a
	F	n/a	n/a	n/a	n/a	Interaction	n/a
Lecanidae	S	n/a	n/a	n/a	n/a	Lake Type	n/a
	U	n/a	n/a	n/a	n/a	Month	n/a
	F	n/a	n/a	n/a	n/a	Interaction	n/a
Synchaetidae	S	0.148±0.013	0.107±0.003	0.104±0.003	0.116±0.004	Lake Type	$F_{2, 49}=2.3$
	U	0.125±0.001	0.094±0.001	0.110±0.001	0.111±0.004	Month	$F_{3, 49}=17.7$**
	F	0.133±0.011	0.096±0.008	0.111±0.006	0.116±0.005	Interaction	Removed

Table 3-6 Mean (±SE) taxon length (mm; see text for definition) of the major order and families in each of four months in 2009 for each lake type: stocked (n= 6), unstocked (n=5), and fishless (n= 3). Also presented are results from Linear Mixed Models for each taxon with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis (p>0.05), it was removed from the model. n/a: insufficient sample size for analysis. S: stocked; U: unstocked; F: fishless. *0.1>p>0.05, **p<0.05

Taxa	Lake Type	May	June	July	August	Main Effect	F-Statistic
Ploima	S	0.125±0.005	0.137±0.009	0.147±0.005	0.154±0.002	Lake Type	$F_{2,11}$=3.7*
	U	0.128±0.002	0.136±0.006	0.147±0.005	0.149±0.004	Month	$F_{3,38}$=12.7**
	F	0.130±0.005	0.113±0.007	0.132±0.011	0.137±0.016	Interaction	Removed
Brachionidae	S	0.116±0.002	0.117±0.004	0.122±0.003	0.115±0.002	Lake Type	$F_{2,11}$=0.1
	U	0.122±0.003	0.115±0.003	0.120±0.004	0.113±0.002	Month	$F_{3,38}$=8.0**
	F	0.119±0.004	0.105±0.006	0.130±0.002	0.113±0.002	Interaction	Removed
Gastropidae	S	n/a	n/a	n/a	n/a	Lake Type	n/a
	U	n/a	n/a	n/a	n/a	Month	n/a
	F	n/a	n/a	n/a	n/a	Interaction	n/a
Lecanidae	S	n/a	n/a	n/a	n/a	Lake Type	n/a
	U	n/a	n/a	n/a	n/a	Month	n/a
	F	n/a	n/a	n/a	n/a	Interaction	n/a
Synchaetidae	S	0.153±0.012	0.123±0.006	0.117±0.005	0.124±0.006	Lake Type	$F_{2,11}$=0.1
	U	0.136±0.012	0.097±0.004	0.136±0.016	0.130±0.007	Month	$F_{3,32}$=10.1**
	F	0.143±0.003	0.103±0.014	0.124±0.005	0.129±0.001	Interaction	$F_{6,32}$=2.5**

Table 3-7 Mean (±SE) lowest feasible taxonomic level (often species but sometimes genus) richness, Shannon-Weiner diversity, and evenness (%) for each of four months in 2009 and each lake type: stocked (n=6), unstocked (n=5), and fishless (n=3). Also presented are results from Linear Mixed Models with lake type, month, and their interaction as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis ($p>0.05$), it was removed from the model. *$0.1>p>0.05$, **$p<0.05$

Metric & Lake Type	**May**	**June**	**July**	**August**	**Main Effect**	**F-Statistic**	**Comparisons of Lake Types**
Richness							
Stocked	12.5±1.5	15.7±1.1	22.7±1.3	15.3±0.6	Lake Type	$F_{2,11}$= 0.5	Stocked vs. Unstocked
Unstocked	15.2±1.8	18.0±0.6	19.2±2.8	16.6±1.2	Month	$F_{3,38}$= 10.4**	Stocked vs. Fishless
Fishless	14.5±0.5	12.7±1.5	19.3±3.9	15.3±3.3	Interaction	Removed	Unstocked vs. Fishless
Diversity							
Stocked	1.46±0.07	1.66±0.13	1.47±0.13	1.68±0.10	Lake Type	$F_{2,10}$= 4.3**	Stocked vs. Unstocked
Unstocked	1.26±0.10	1.26±0.30	1.41±0.22	1.38±0.14	Month	$F_{3,32}$= 1.6	Stocked vs. Fishless**
Fishless	1.65±0.29	0.67±0.15	0.95±0.36	0.73±0.29	Interaction	$F_{6,31}$= 2.8**	Unstocked vs. Fishless
Evenness							
Stocked	59.7±5.5	61.2±5.5	47.2±4.6	61.7±4.1	Lake Type	$F_{2,11}$= 4.4**	Stocked vs. Unstocked
Unstocked	47.6±5.5	44.2±11.0	48.0±7.1	49.2±4.6	Month	$F_{3,32}$= 3.3**	Stocked vs. Fishless**
Fishless	62.0±10.0	26.7±5.9	31.3±9.9	26.0±9.8	Interaction	$F_{6,32}$= 2.6**	Unstocked vs. Fishless

Table 3-8 Results from linear regression analysis of lowest feasible taxonomic level (often species but sometimes genus) diversity for May-August 2009 versus lake area and maximum depth. Degrees of freedom were 1 and 12 for all months except May (1 and 11).
*0.1>p>0.05, **p<0.05

Analysis & Results	**May**	**June**	**July**	**August**
Diversity vs. Area				
r^2 -value	0.179	0.415	0.015	0.354
F -value	2.403	8.517**	0.179	6.576**
Diversity vs. Depth				
r^2 -value	0.077	0.256	0.544	0.434
F -value	0.921	4.124*	14.324**	9.208**

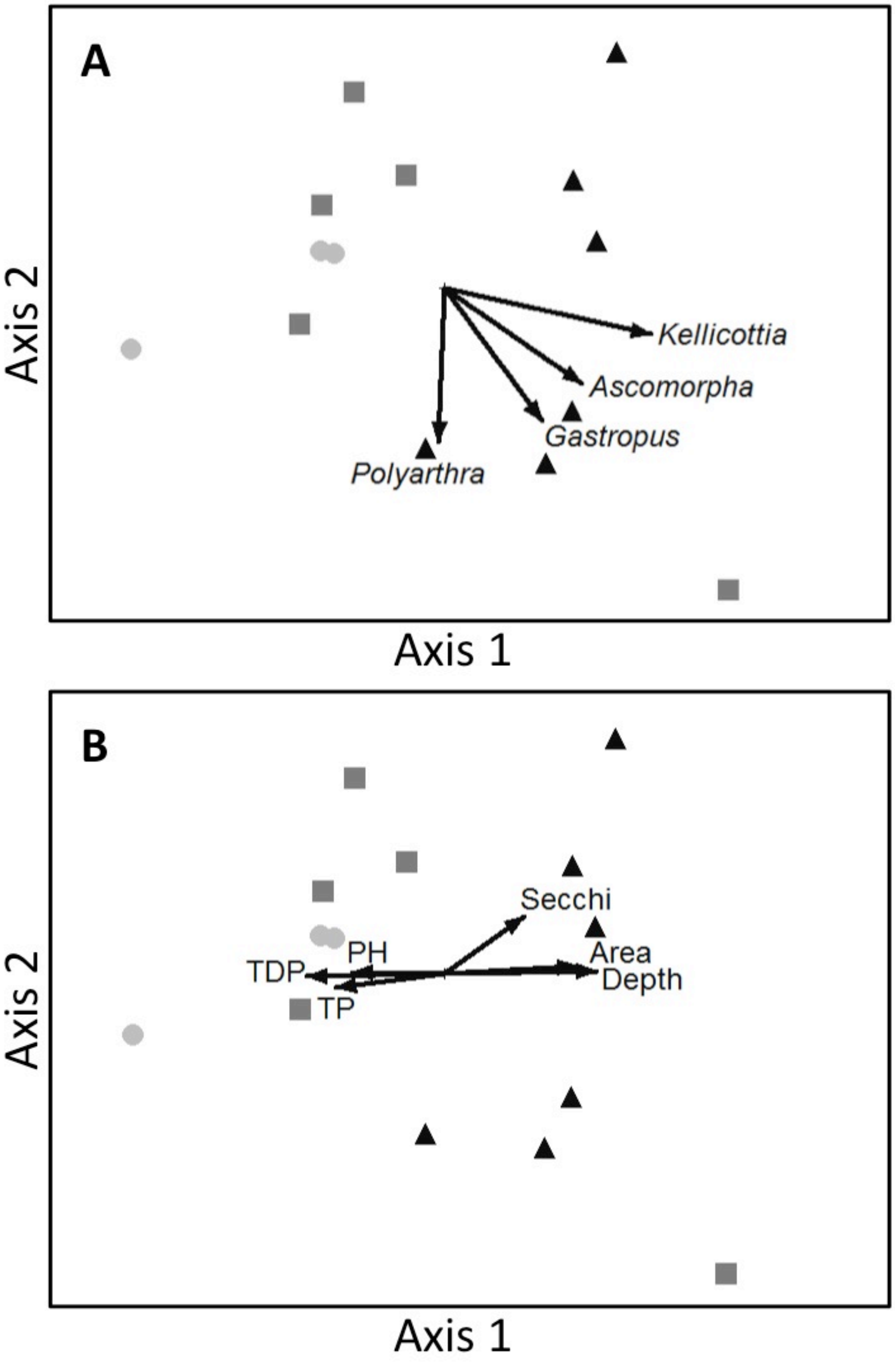


Figure 3-1 Principal component analysis (PCA) joint plots of pelagic rotifer communities in study lakes in June 2009. Vectors point in the direction of increased (A) abundance ($r^2>0.5$) and (B) levels of environmental variables ($r^2>0.3$), and the length of the vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

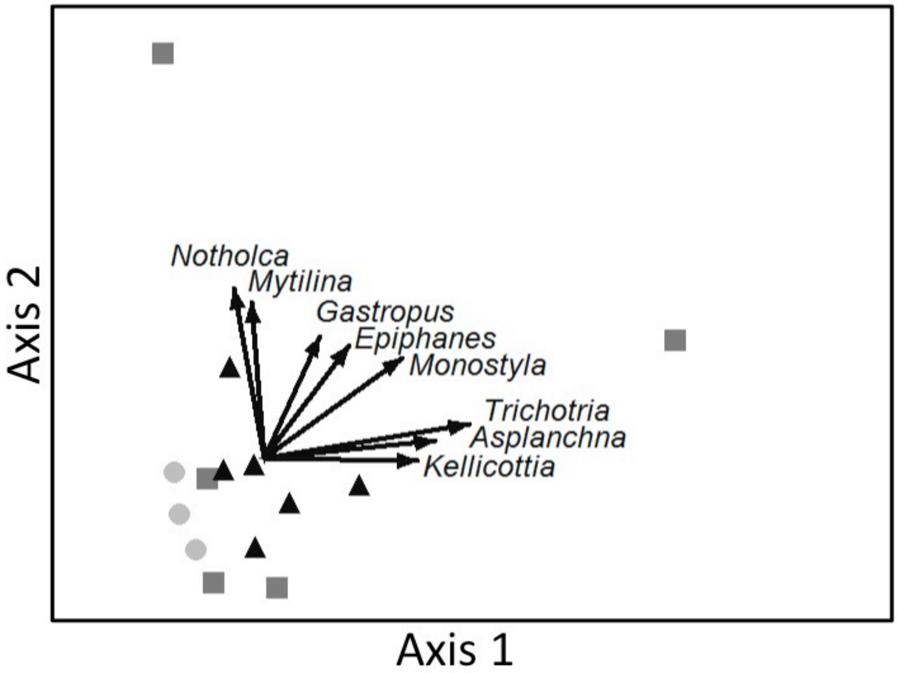


Figure 3-2 Principal component analysis (PCA) joint plots of pelagic rotifer communities in study lakes in July 2009. Vectors point in the direction of increased abundance (r^2>0.5) and the length of the vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3). None of the environmental variables were strongly correlated with the axes (r^2>0.3).

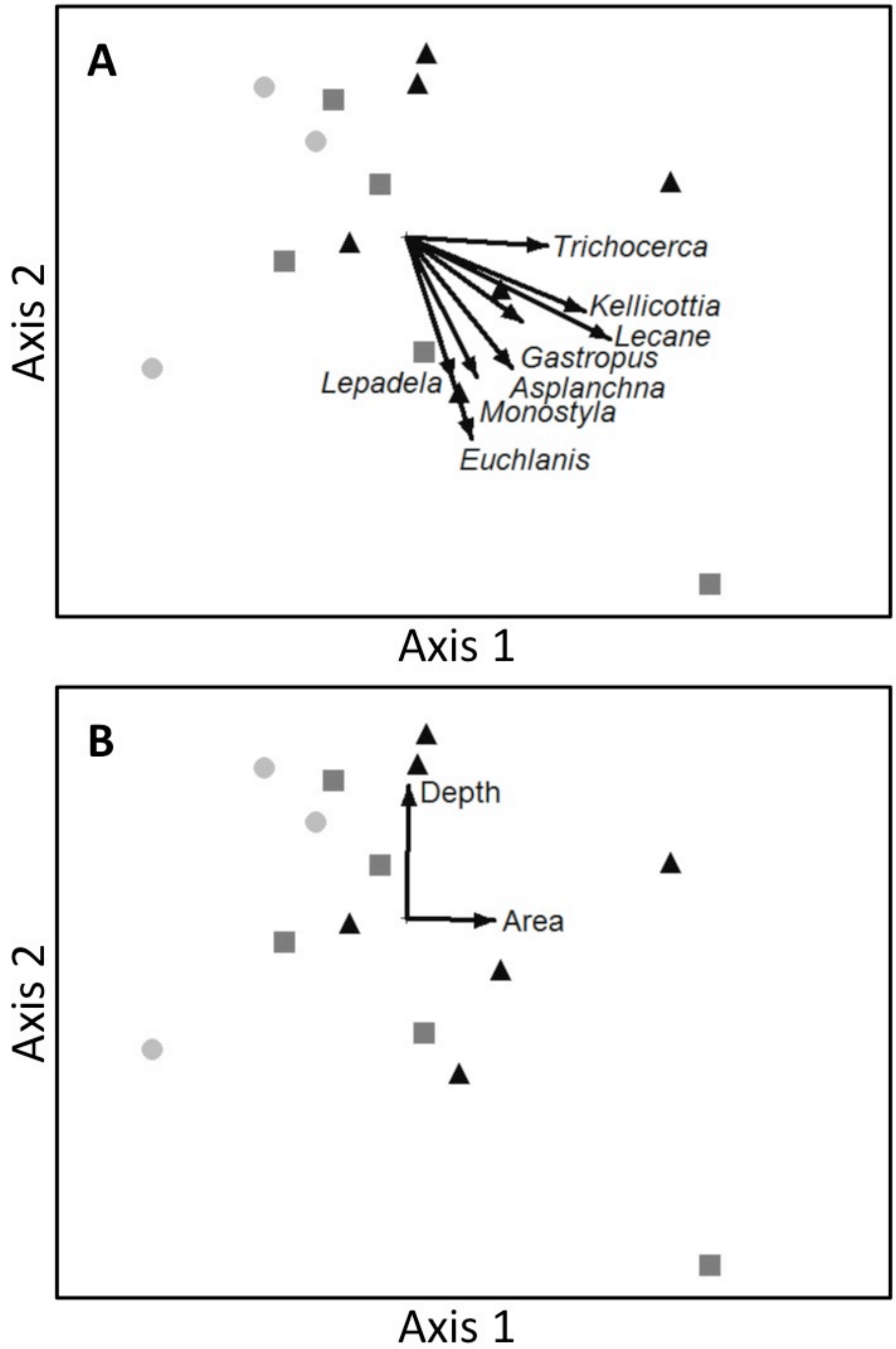


Figure 3-3 Principal component analysis (PCA) joint plots of pelagic rotifer communities in study lakes in August 2009. Vectors point in the direction of increased (A) abundance (r^2>0.5) and (B) levels of environmental variables (r^2>0.3), and the length of the vectors indicate the strength of the relationship. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

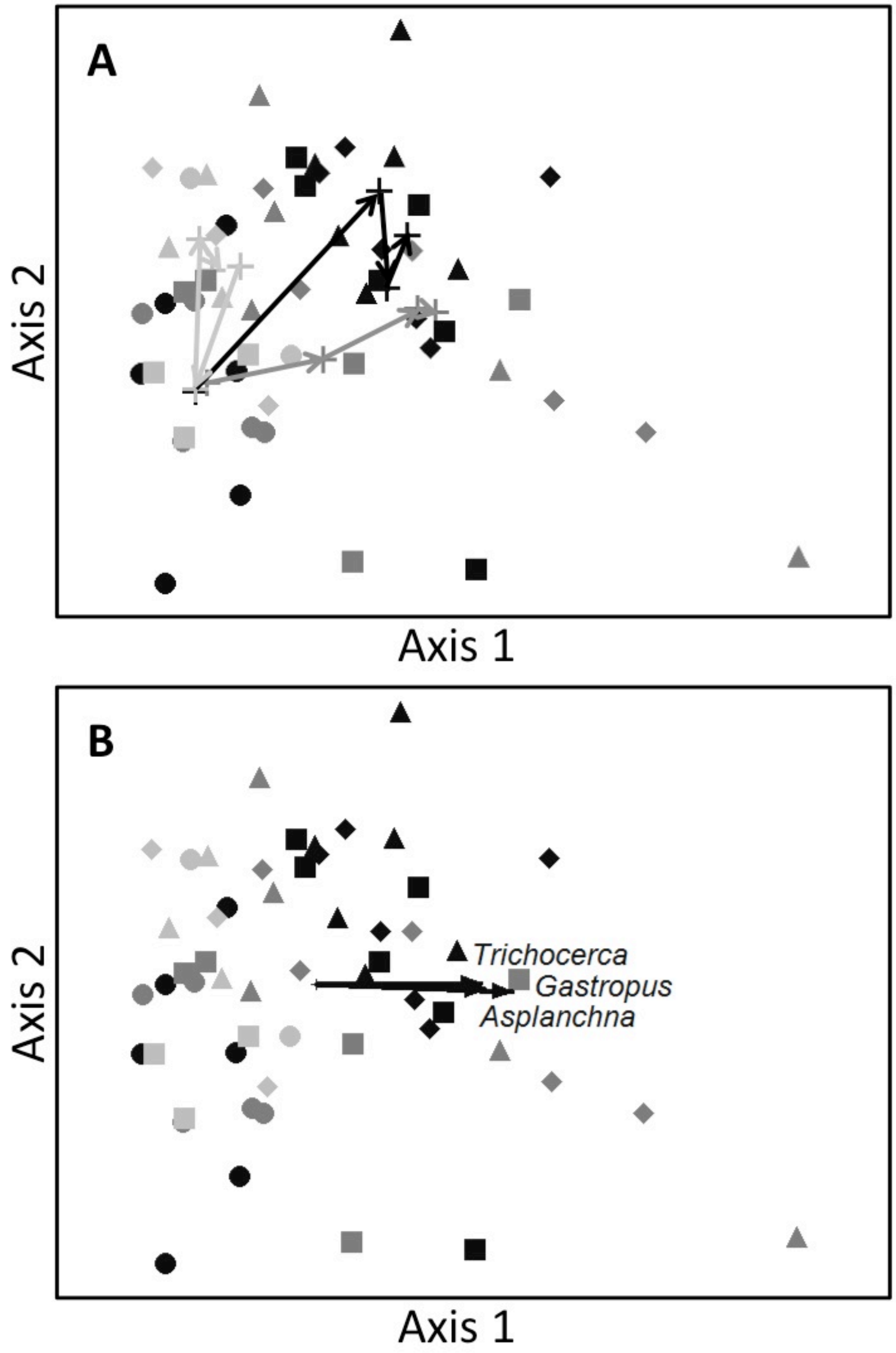
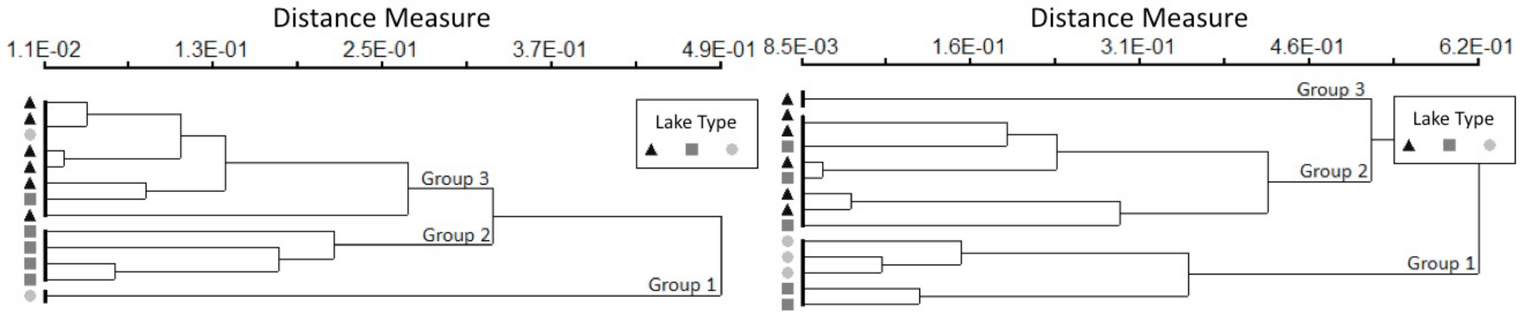
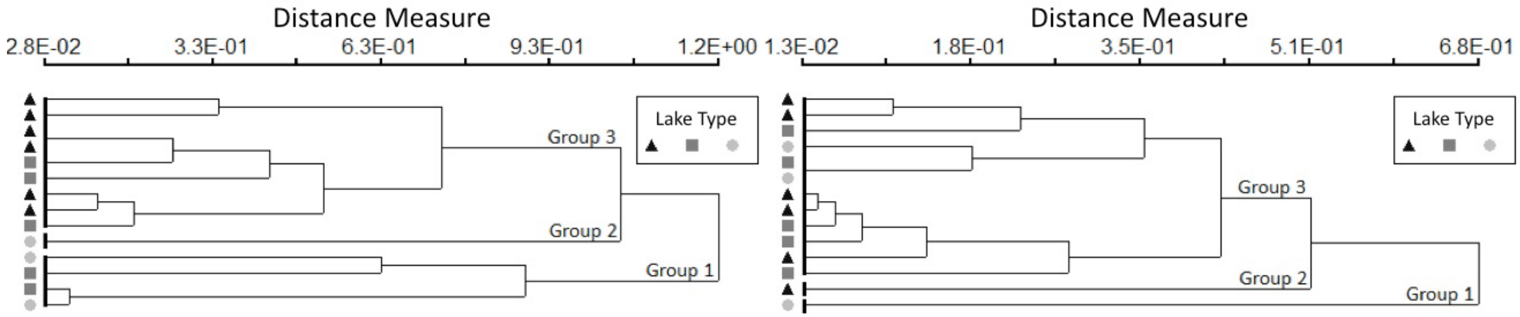


Figure 3-4 Principal component analysis (PCA) of pelagic rotifer communities in study lakes during the four sampling periods in 2009. (A) successional vectors follow lake type-month centroids through time and (B) joint plot vectors point in the direction of increased abundance (r^2>0.5) and the length of joint plot vectors indicate the strength of the relationship. Black symbols: stocked lake-months (n=18), dark grey symbols: unstocked lake-months (n=15), light grey symbols: fishless lake-months (n=8), circles: May, squares: June, triangles: July, diamonds: August. None of the environmental variables were strongly correlated with the axes (r^2>0.3).



May June



July August

Figure 3-5 Dendrograms of rotifer communities for each of the four sampling periods (May-August 2009). Lakes were grouped by their similarity in rotifer composition based on abundance data using group average linkage. Clusters have been divided into the three major groups formed. Black triangles: stocked lakes (n=6), dark grey squares: unstocked lakes (n=5), light grey circles: fishless lakes (n=3).

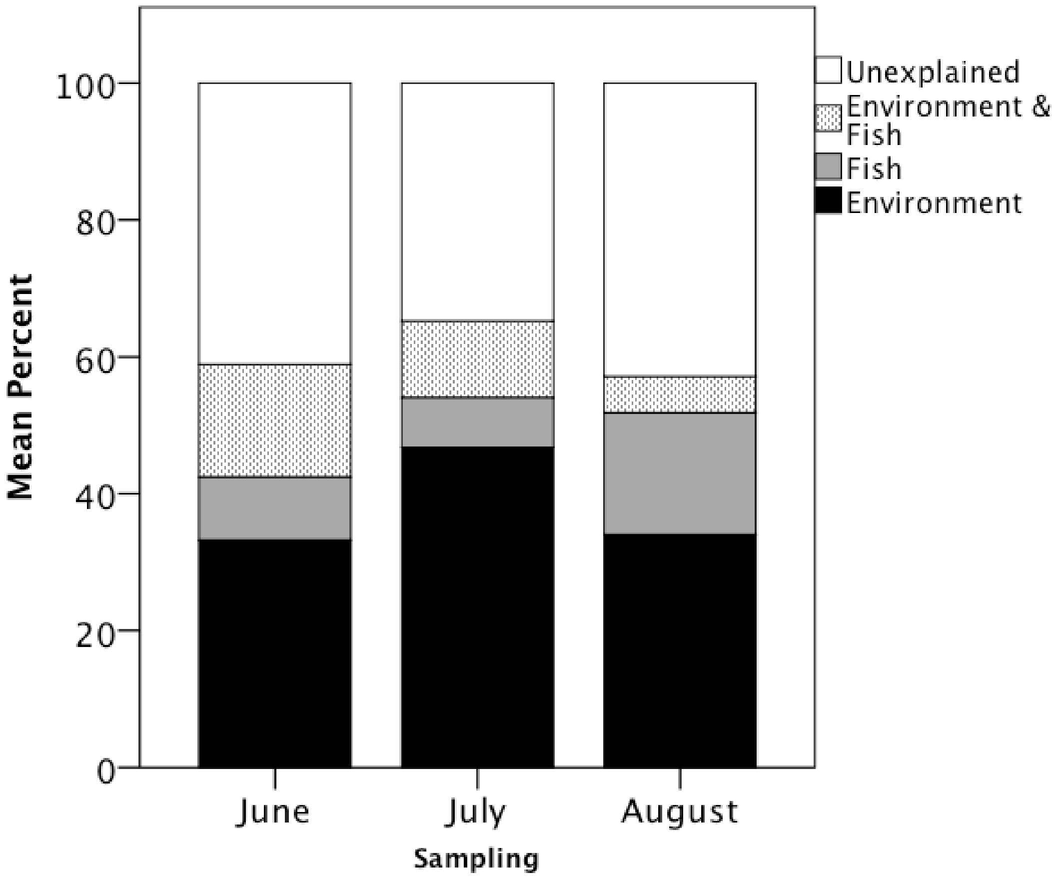


Figure 3-6 Results from a two-way variance partitioning analyses for three sampling periods in 2009. Values represent the percentage of variance in the composition of rotifer communities explained independently by environmental variables and fish taxa, the percentage shared by environment and fish, and the variation left unexplained.

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Chapter 4. Effects of stocked trout and native small-bodied fish on the vertical distribution of pelagic zooplankton in small boreal foothills lakes

Introduction

Zooplankton exhibit distinct vertical distributions within freshwater lakes such as higher daytime densities in upper layers or greater daytime densities in the deeper meta- or hypolimnion of lakes. Different patterns in vertical distribution are thought to result from optimal habitat selection, which depends on trade offs between predation risk, food availability, exposure to damaging ultraviolet radiation, and favourable temperatures that facilitate development and growth (Haney 1988; Lampert 2005). Pelagic zooplankton can also undergo diel vertical migration in the presence of zooplanktivorous fish, migrating to deeper and darker waters during the day to avoid these visual predators (Dodson 1988; Loose 1993; Semyalo and Nattabi 2009). During the night, pelagic zooplankton will migrate back towards the surface exploiting abundant phytoplankton resources and warmer water. Often diel vertical migration is more pronounced in relatively large taxa, such as many groups of microcrustaceans but is absent in the smallest taxa, including most rotifer species (Semyalo and Nattabi 2009). These size-dependent differences likely result from fish predation as fish show a strong preference for large zooplankton prey (e.g. Naud and Magnan 1988; Laurich *et al.* 2003; Budy *et al.* 2005).

Stocked trout have been found to influence the distribution of zooplankton in a similar manner to other vertebrate planktivores (Hembre and Megard 2003). Trout, however, feed on a variety of prey in addition to zooplankton including macoinvertebrates and small-bodied fish (Beauchamp 1990; Nelson and Paetz 1992; Lynott *et al.* 1995). For this reason trout could impact the vertical distribution of zooplankton both directly through predation and indirectly as the result of a trophic cascade. Trout predation has been found to alter macroinvertebrate assemblages in mountain streams and lakes (Bradford *et al.* 1998; Herbst *et al.* 2009; Martinez-Sanz *et al.* 2010) often through the absence or reduced abundance of invertebrate predators such as *Chaoborus* (Carlisle and Hawkins 1998). Trout predation can also decrease the abundance (Townsend 1996) and recruitment of native planktivorous fish (Jellyman and McIntosh 2010). In addition to direct impacts on these prey taxa, trout can also modify the behaviour of native fish (Naud and Magnan 1988) and invertebrate predators like *Chaoborus* (Luecke 1986), through altered habitat selection including greater time spent in littoral versus pelagic habitats or hypo- versus epi-limnetic zones.

In the absence of fish, lakes typically contain a greater diversity and abundance of large, free-swimming predatory macroinvertebrates, including *Chaoborus* (Carlisle and Hawkins 1998; Schiling *et al.* 2009). *Chaoborus* often dominates the pelagic region of fishless lakes (Schiling *et al.* 2009) feeding on smaller zooplankton than typically eaten by fish (Campbell 1991). Despite this difference in size selectivity, dense *Chaoborus* populations can still exert strong selective pressures on larger taxa, such as *Daphnia*, due to predation on small juveniles (Liljendahl-Nurminen *et al.* 2003). *Chaoborus* do not depend on vision for prey detection and can undergo vertical migration (Teraguchi and Northcote 1966; Borkent 1981). In the presence of migratory *Chaoborus* populations, zooplankton are typically non-migratory, with vertical distributions influenced more by temperature and food availability, often resulting in higher zooplankton densities closer to the surface.

As rotifers are not favoured prey of stocked trout and adult native fish, a direct impact of these vertebrate predators on rotifers is not typically seen (Semyalo and Nattabi 2009). Certain rotifer taxa, such as Synchaetidae, however, could experience strong indirect effects on habitat selection due to fish induced changes in the distribution of predatory cyclopoid copepods. Unlike many rotifers, Synchaetidae are soft-bodied and without protective spines, which makes them susceptible prey of cyclopoids (Stemberger 1985). In contrast, swimming appendages possessed by the genus *Polyarthra* allows diel vertical migration away from high densities of invertebrate predators (Gilbert and Hampton 2001).

The present study systems are located in Alberta's boreal plain where native small-bodied fish coexist with stocked trout and where naturally fishless lakes are not uncommon. Minimal impacts of introduced trout have been observed for prey taxa in these lakes; this pattern has largely been attributed to the high productivity of these systems and the dense populations of native fish they support. (e.g. *Chrosomus* spp). In the study lakes, trout stocking did not impact the density and recruitment of native small-bodied fish (Nasmith *et al.* 2010), community composition and size structure of macroinvertebrates (Nasmith *et al.* 2012), amphibian abundance (Schank *et al.* 2011), and zooplankton abundance, biomass, and size (Chapter 2 and 3). Trout stocking, however, did alter native fish behaviour as cyprinids allocated greater amounts of time to littoral versus pelagic habitats where dense macrophyte beds appear to provide native fish with refuge from picivorous trout (Nasmith *et al.* 2010; Hanisch *et al*. 2012).

To examine the separate effects of introduced trout and native fish on the daytime vertical distribution of zooplankton, I collected samples at discrete depths of stocked, unstocked (but fish-bearing) and fishless lakes. The vertical distribution of all major microcrustacean and rotifer taxa in the upper layers of 12 lakes was contrasted among lake types to determine any differences caused by the presence of fish. For larger, more conspicuous prey (microcrustaceans), I also compared the mean individual and taxon lengths between depths.

Native fish and trout are visual predators that show similar patterns of size-selectivity for zooplankton prey (Hambright and Hall 1992; Laurich *et al.* 2003; Budy *et al.* 2005), which should translate into similar predation pressure. As trout in the current study have not significantly affected the abundance of native fish (Nasmith *et al.* 2010), trout introduction might simply increase overall planktivore density and therefore predation pressure on zooplankton prey. Native small-bodied fish in the study system, however, respond to stocked trout predation by greater use of littoral habitat (Hanisch *et al.* 2012). This could result in the alternative expectation that pelagic zones could have similar or lower planktivore densities after trout stocking as trout are stocked at densities at least 5 times below that of existing minnow populations. For this reason, I expected the distributions of zooplankton in stocked lakes to show the same or reduced effects of fish relative to unstocked lakes.

I did expect fish-bearing (stocked and unstocked) and fishless lakes to differ in the distribution of microcrustaceans prey, as microcrustaceans are relatively large-bodied compared to rotifers and the preferred prey of native and stocked planktivorous fish. I expected a greater abundance and biomass of microcrustaceans at a deeper vs. shallower depth in fish-bearing lakes due to darker waters that could provide refuge from visual predation by fish but a greater abundance and biomass at the shallower depth of fishless lakes due to more favourable abiotic conditions for growth and reproduction (e.g warmer temperatures, greater abundance of phytoplankton food). Due to greater size variability and slow mobility in cladocerans relative to copepods, I also expected larger cladoceran individuals and/or taxa at a deeper vs. shallower depth in fish-bearing lakes as larger cladocerans would be conspicuous prey with greater ease of capture. I did not expect a difference in the distribution of most rotifer taxa between fish-bearing and fishless lakes, as rotifers have limited mobility and are relatively small and not favoured food of fish. I did, however, expect *Polyarthra* to exhibit the opposite pattern in vertical distribution compared to its cyclopoid predators as this rotifer genus is the preferred prey of these invertebrate predators and posses swimming appendages for greater mobility, allowing migration.

Methods

Study Area

Pelagic zooplankton were sampled from 12 lakes in Canada's boreal foothills near the towns of Rocky Mountain House (52°22'39''N and 144°54'37''W) and Caroline (52° 5'36''N and 114°45'28''W) Alberta (Table 4-1). Lakes were relatively small and shallow, and primarily surrounded by boreal forest. Typically shorelines supported thick patches of *Typha latifolia*. The dense littoral macrophyte beds were dominated by *Potamogeton* spp., *Sparganium angustifolium*, and *Nuphar variegatum* (Nasmith *et al.* 2010).

Samples were collected at the end of July 2009 from lakes representing three distinct lake types. Lakes were either stocked with non-native trout (n=6), unstocked (n=4), or fishless (n=2). Rainbow Trout (*Oncorhynchus mykiss*) was stocked in five of the study lakes, one of which also contained Brown Trout, *Salmo trutta*. The sixth stocked lake contained only Brook Trout (*Salvelinus fontinalis*). Lakes had been stocked for two to >50 years; stocking densities in 2009 ranged from 80 to 790 fish/ha, with higher densities of small fish for family-oriented put-and-take fisheries in some lakes and lower densities of larger trout providing a catch-and-release "trophy" fishery in other lakes (S. Herman and R. Konynenbelt, ASRD, pers. comm.). In addition, four of six stocked lakes were also aerated using one to three floating aerators with ½ to 1 hp motors. One lake was aerated throughout the year, while the other three lakes received only winter aeration, from mid-October to early April.

Stocked and unstocked lakes supported population of native fish that included Fathead Minnow (*Pimephales promelas*), Brook Stickleback (*Culaea* *inconstans*), Pearl Dace (*Margariscus margarita*), and a dace species complex consisting of Northern Redbelly Dace (*Chrosomus eos*), Finescale Dace (*Chrosomus neogaeus*) and their hybrids (Appendix A). Between 2005 and 2009, native fish densities varied among years and lakes but typically averaged 4,000-6,000 fish/ha for both stocked and unstocked lakes (Nasmith *et al.* 2010; Hanisch *et al.* 2012).

The dominant pelagic invertebrate predator in all three lake types was the larva of the dipteran *Chaoborus*. Stocked lakes contained two of four species present in the study lakes (*C. flavican* and *C. punctipennis*) with July abundances between 0-8.7 individuals/L. Unstocked lakes supported three of four species (*C. flavican*, *C. punctipennis*, and *C. trivitatus*) and had July abundance between 0-22.6 individuals/L. Fishless lakes also supported three of four species (C. *flavican*, C. *trivitatus*, and C. *americana*) but were the only lakes that contained *C. americana*, a large *Chaoborus* species incapable of diel vertical migration to avoid predatory fish. The fishless lakes also had the highest July abundance values of *Chaoborus* that ranged between 15.6-31.1 individuals/L.

Zooplankton Collection and Laboratory Processing

Discrete zooplankton samples were collected over the deepest location of lakes using a 30-L Schindler-Patalas Trap, fitted with a 63-µm net, at depths of 1 and 2 m in each lake. We contrasted distributions at depths of 1 m vs. 2 m for several reasons. Study lakes were characterized by a variety of depths, water clarities, and extent of temperature-based stratification, which precluded other contrasts, e.g., epi- versus hypo-limnion, photic versus aphotic zone, shallow versus deep, that could be applied across all lakes. For lakes that did stratify, the metalimnion was located below 2 m, thus sample collection was standardized to the epilimnion of lakes.

I believe that comparisons between depths of 1 and 2 m is justifiable in my study systems for a number of reasons. Most studies of zooplankton vertical distribution focus on a single lake or large stratified oligortophic lakes with high water clarity and maximum depths greatly exceeding 20 m (e.g. Hembre and Megard 2003; Kessler *et al.* 2008; Kahilainen *et al.* 2009). The present study, however, compares the vertical distribution of zooplankton among a dozen lakes that are meso- to meso-eutrophic with low water clarity and maximum depths of only 4 m to 13 m. An average secchi depth of 3.5±0.5 m in the current study systems suggests a drastic decrease in the ability of visual fish predators to detect their zooplankton prey between 1 m and 2 m depths. For this reason comparing 1 m and 2 m depths should be a viable means of detecting changes in habitat selection by zooplankton that may be induced by planktivorous fish. In addition, zooplankton concentrations can vary by as much as 4 times over vertical distances less then 1 m (Hembre and Megard 2003) with zooplankton demonstrating fish induced daytime distributions in lakes as shallow as 1.6 m (Castro *et al.* 2007). Finally, although depths of 1 m and 2 m were used for statistical comparisons, the distribution of zooplankton throughout the entire vertical water column was examined for each lake with a clear pattern from shallow to deep depths that was consistently reflected in the first 2 meters (e.g. microcrustacean distributions from each lake type in Figure 4-1). The only exception was near lake bottom waters, where zooplankton abundance was always low, likely due to dissolved oxygen concentrations lower than levels favourable for zooplankton (<3 mg/L).

All lakes were sampled within a 5-day period with samples collected during daylight hours. July was chosen over other ice-free months as vertical migration is most pronounced during the summer (July and August) in temperate lakes (Stich and Lampert 1981) and due to the fact that temperature stratification, to which zooplankton can respond (Pinel-Alloul *et al.* 2004), was greatest during this month. The mean temperature difference between the 2 meters sampled in July was 1.7±0.4 °C. In addition to stronger temperature gradients, young-of-year small-bodied fish have hatched by the end of June and began foraging on zooplankton, while spring and early summer trout stocking programs have been completed. These factors should create significant predation pressure from fish during July, which can then directly or indirectly shape the vertical distributions of their zooplankton prey. Samples were processed using the same methods described in Chapter 2, except that discrete samples from each depth were not combined into composite samples.

Statistical Analysis

Abundance and biomass were determined at depths of 1 and 2 m in each lake for all major zooplankton groups (i.e., those with an average abundance across all lakes that was greater then 25 individuals/L). Major taxa included the microcrustacean orders Cladocera, Calanoida, and Cyclopoida, the rotifer families Brachionidae, Synchaetidae, and Gastropidae, the rotifer genus *Polyarthra* (from the family Synchaetidae) and the rotifer species *Keratella cochlearis* and *Keratella crassa* (from the family Brachionidae); other rotifer groups were mostly benthic (e.g. Bdelloidea) and littoral (e.g. Flosculariacea). Mean individual and taxon lengths were also determined at 1 and 2 m in each lake for the microcrustacean orders only, as microcrustaceans are larger than rotifers (and thus more vulnerable to size-selective predation from fish), show more variability in size, and therefore are more likely to show size-based differences in vertical distribution. Juvenile *Daphnia* and copepod copepodites were included in all analysis as adults were rare in several lakes.

For the taxonomic groups mentioned above, I determined the relative mean (±SE) abundance (% of individuals), relative mean (±SE) biomass (% biomass) and mean (±SE) individual and taxon lengths at 1 and 2 m for each lake type (stocked, unstocked, and fishless). Relative data were used to standardize the proportion of individuals at each depth, as lakes could vary in the overall density of different zooplankton taxa. Relative abundance and biomass data were arcsine square root transformed, while length data were normally distributed and did not require transformations. Univariate analyses were conducted using SPSS Statistics 19.0 (SPSS for Mac OS X, Rel. 19.0.0 2010). Analyses of dependent variables (mean relative abundance, mean relative biomass, mean individual length, and mean taxon length) at depths of 1 and 2 m within the water column among lake types consisted of Linear Mixed Models, with treatment, depth, and the treatment*depth interaction as explanatory variables, and lake as a random variable. A significant interaction in this analysis would indicate a potential impact of trout and/or native fish on zooplankton vertical distribution. A value of $p < 0.05$ was considered significant while $0.05 < p < 0.1$ was considered marginally significant.

Results

The mean abundances (±SE) of Cladocera, Calanoida, and Cyclopoida were 44±8, 21±3, and 12±3 individuals/L, respectively, within the top 2 m of lakes in this study. The most abundant rotifer families were Brachionidae, Sychaetidae, and Gastropidae (299±102, 41±13, and 31±12 individuals/L respectively), which made up 64, 10, and 6 percent of all rotifers present (relatively rare rotifer taxa made up the remaining 20 percent). The two most abundant taxa within Brachionidae were *Keratella cochlearis* and *Keratella crassa* (169±92 and 80±45 individuals/L), which made up 56 and 38 percent of brachionids, respectively. The most abundant taxon within Sychaetidae was *Polyarthra* (26±7 individuals/L), which made up 63 percent of all synchaetids.

Vertical Distribution of Microcrustaceans

A significant treatment*depth interaction was detected for mean relative abundance and mean relative biomass in all three microcrustacean orders (Cladocera, Calanoida, and Cycopoida; Figure 4-2). In lakes with fish (stocked and unstocked), these taxa had either a similar or lower mean relative abundance and biomass at 1 m compared to 2 m, whereas abundances and biomasses of these taxa in fishless lakes were higher at 1 m. Significant treatment*depth interactions were not detected for mean individual length and mean taxon length in all three microcrustacean orders (Cladocera, Calanoida, and Cyclopoida; Figure 4-3), although cladoceran individuals did show a non-significant pattern of smaller individuals at 1 m vs. 2 m in both fish-bearing lake types, whereas in fishless lakes cladoceran individuals were similar in size at both depths.

Vertical Distribution of Rotifers

Non-significant treatment*depth interactions were detected for mean relative abundance and mean relative biomass in the family Brachionidae and also for the two most abundant taxa within this family, *Keratella cochlearis* and *Keratella crassa* (Figure 4-4 and 4-5). The family Synchaetidae also displayed non-significant treatment*depth interactions for mean relative abundance and mean relative biomass. For Synchaetidae, however, a non-significant pattern of greater abundance and biomass at 1 m vs. 2 m was present in both fish-bearing lake types, whereas fishless lakes had similar abundances and biomasses between depths. Significant treatment*depth interactions were detected for mean relative abundance and mean relative biomass in *Polyarthra*, the most abundant taxon in Synchaetidae. (Figure 4-4 and 4-5). In contrast to microcrustaceans, fish-bearing lakes (stocked and unstocked) had relatively greater abundance and biomass of *Polyarthra* at 1 m compared to 2 m, whereas fishless lakes showed the reverse pattern. Significant treatment*depth interactions were also detected for mean relative abundance and biomass in the family Gastropidae (Figure 4-4 and 4-5). Unlike pattern for *Polyarthra* mean relative abundance and biomass were similar or lower at 1 m vs. 2 m in stocked and unstocked lakes, but were higher at 1 m vs. 2 m in fishless lakes as was also seen for microcrustaceans.

Discussion

Vertical distribution patterns of zooplankton in stocked and unstocked lakes showed strong similarities, but distributions in fishless lakes differed in many respects (Table 4-2), even with my limited contrast between 1 and 2 m strata. The taxa responsible for these patterns included the three microcrustacean orders Cladocera, Calanoida, and Cyclopoida, along with the rotifer family Gastropidae and genus *Polyarthra*. With the exception of *Polyarthra* (which showed the opposite pattern), mean relative abundance and biomass of these taxa were much greater at 1 m vs. 2 m in fishless lakes, but were lower (or similar) at 1 m vs. 2 m in both types of fish-bearing lakes, regardless of the presence of stocked trout. Vertical distributions of the rotifer families Synchaetidae and Brachionidae, and of *K. cochlearis* and *K. crassa,* did not differ among lake types for either abundance or biomass. Size-related vertical distribution patterns of Cladocera, Calanoida and Cyclopoida did not differ between lake types, although cladoceran individuals did show a non-significant pattern of smaller individuals at 1 m compared to 2 m in both fish-bearing lake types, whereas fishless lakes had similar-sized cladoceran individuals at both depths.

Similar patterns in stocked and unstocked lakes suggest that trout stocking does not affect the vertical distribution of zooplankton in lakes containing native small-bodied fish. Contrasting patterns between fish-bearing (stocked and unstocked) and fishless lakes, however, indicate that planktivorous fish do affect the vertical distribution of zooplankton but effects are independent of the fish species present. Previous studies have proposed that effects of fish on zooplankton distribution are mediated by detection by zooplankton of predator-derived chemical cues (Dodson 1988; Neill 1990). Although slight variations exist in the chemical composition of these cues among fishes, overall similarities in chemical characteristics of kairomones exist across species (Elert and Loose 1996). Similar chemical characteristics suggest similar influences of chemical cues on zooplankton behaviour, which could explain why trout stocking did not result in zooplankton distributions different from that observed in lakes possessing populations of native zooplanktivorous fish.

Although trout stocking did not alter the vertical distribution of zooplankton in lakes with native fish, the presence of fish (trout and/or native) significantly affected the distribution of common zooplankton groups. The vertical distribution of all major microcrustacean groups was strongly influenced by the presence of planktivorous fish, whereas rotifers experienced more taxa-specific impacts. Similarly, the effects of fish on the vertical distribution of zooplankton in a lake in Uganda was more pronounced for large compared to small taxa and was absent in many rotifer species (Semyalo and Nattabi 2009). Zooplanktivorous fish are generally size-selective predators, with a strong preference for larger-bodied prey. This selectivity likely results in variable predation pressure across different zooplankton taxa, which could contribute, directly and/or indirectly, to the different impacts of fish that I observed for microcrustacean versus rotifer taxa.

Vertical Distribution of Microcrustaceans

Fishless lakes had a greater mean relative abundance and biomass of Cladocera, Calanoida, and Cyclopoida at 1m versus 2 m, while fish-bearing lakes had similar or lower levels at 1 m versus 2 m. This pattern suggests that cladocerans (Dini and Carpenter 1991) and copepods (Gliwicz and Pijanowska 1988; Doulka and Kehayias 2011) moved to deeper waters during the day, in response to predation by fish, but remained near surface waters in the absence of fish (Lampert *et al.* 2003). Studies, such as those cited, often show changes in day/night vertical distributions over many meters. Drastic densities changes in zooplankton, however, have also been found to occur over a single meter in more productive lakes, similar to those in my study (Hembre and Megard 2003; Castro *et al.* 2007). Although not statistically significant, the mean length of individual cladocerans at 1 m was also smaller in fish-bearing lakes, whereas lengths in fishless lakes were similar between depths. In laboratory experiments, Dodson (1988) found similar results as smaller cladocerans were less inclined to migrate vertically in the presence of fish predators. Semyalo and Nattabi (2009) also observed smaller zooplankton occupying shallower depths during the day compared to larger individuals in a large eutrophic lake with planktivorous fish.

These patterns in vertical distribution are based on trade-offs between predation risk and growth (Lampert 1989). During the day, shallow waters of meso- to eutrophic lakes often harbor optimal conditions for rapid zooplankton growth and high reproductive potential, including warmer temperatures and abundant phytoplankton food (Johnsen and Jakobsen 1987; Leibold 1990; Dini and Carpenter 1992), with little impact of damaging ultraviolet radiation due to low water clarity (Ringelberg *et al.* 1984). Occupying shallow water, however, can also increase susceptibility of zooplankton to visual predation by fish. Trout (Budy *et al.* 2005) and native fish (Naud and Magnan 1988; Laurich *et al.* 2003) rely heavily on microcrustaceans as food for at least a portion of their lives (Beauchamp 1990; Lynott *et al.* 1995) and feed selectively on large individuals. Cladocerans are known to be particularly susceptible to fish predation relative to copepod crustaceans due to their slower mobility (Thorp and Covich 1991). This difference could contribute to the additional effect of planktivorous fish on the mean size of individual cladocerans between depths, as large cladocerans would be relatively slow and conspicuous prey. In fish-bearing lakes, higher midday light levels (Semyalo and Nattabi 2009) and fish densities (Dorazio *et al.* 1987) can greatly influence the amplitude of vertical migration in zooplankton prey, supporting the idea that visual predation is the leading factor influencing vertical distributions in productive fish-bearing lakes.

With the presence of planktivorous fish, some studies have attributed greater daytime densities of microcrustaceans in deep waters and diel vertical migration to avoidance of damaging ultraviolet radiation and not the direct and indirect impacts of fish predation (Kessler *et al.* 2008; Leech *et al.* 2009). Indeed, damage by solar radiation can be an important selective force in nature (Ringelberg *et al.* 1984). The lakes with high ultraviolet penetration, however, are deep oligotrophic systems with high water clarity, unlike my study systems, which are shallow and meso- to meso-eutrophic with relatively high concentrations of Chl-a and low water clarity. The infiltration depth of damaging ultraviolet radiation can change by almost 4 m with a 3 µg/L change in Chl-a (Ringelberg *et al.* 1984), with many studies suggesting a strong influence of ultraviolet radiation on zooplankton vertical distribution in lakes with high ultraviolet penetration, but a greater influence of other factors, such as predation, in lakes with low penetration (e.g. Leech *et al.* 2005).

In the absence of fish, zooplankton should occupy optimal habitat based on the Ideal Free Distribution (Tyler and Gilliam 1995). The Ideal Free Distribution for zooplankton has been observed in fishless systems, where microcrustaceans were distributed based on temperature (Gliwicz and Pijanowska 1988) and availability of phytoplankton resources (Johnsen and Jakobsen 1987; Leibold 1990; Dini and Carpenter 1992). In productive lakes, phytoplankton are often abundant in warm shallow waters (Dawidowicz and Loose 1992), aggregating in response to available light (Wang *et al.* 2011). Assuming that phytoplankton are more abundant at 1 m than 2 m in our fishless lakes, this could attract greater densities of microcrustaceans at 1 m, as the absence of visually feeding fish predators would negate the refuge provided by deeper, darker waters. In addition, zooplankton growth and development benefit from higher temperatures up to a maximum of 25°C (Orcutt and Porter 1983). With a mean temperature of 22.4±0.4 °C at 1 m and 20.7±0.5 °C at 2 m in the present study systems, zooplankton should benefit from the almost 2°C increase between depths.

The presence of *Chaoborus* as the dominant predator in the pelagic zone of fishless lakes (T. Holmes, unpublished data) could also contribute to the observed patterns, as this invertebrate predator is often the major source of mortality for zooplankton such as *Daphnia* in fishless lakes and ponds (Lynch 1979; Spitze 1991). *Chaoborus* does not depend on vision for prey detection, and numerous species have a tendency to migrate vertically to deeper waters during the day and then ascend at night in both fish-bearing (Stahl 1966; Halat and Lehman 1996) and fishless lakes (Xie *et al.* 1998). In fishless lakes with migratory *Chaoborus* populations, deeper waters would not protect zooplankton from the top predator; as a result, warmer temperatures, higher food availability, and lower predator densities should make shallow waters optimal habitat during the day. Indeed, similar to my study, field experiments in fishless systems have found that microcrustaceans migrate towards the waters surface in the presence of *Chaoborus* (Dodson 1988; Gonzalez 1998).

Daytime migration to deeper strata has also been observed in fishless lakes and ponds (Gilbert and Hampton 2001; Karabin and Ejsmont-Karabin 2005) unlike my study systems. Karabin and Ejsmont-Karabin (2005) attributed this behaviour to strong competition for scarce resources that were depleted from surface layers after a night of intense grazing in an oligotrophic lake. Deep, cool waters can result in energy-saving metabolic shifts (McLaren 1963), especially during periods of food limitation (Geller 1986). In contrast to the system just discussed, my study lakes were both highly productive and relatively shallow, making significant depletion of phytoplankton unlikely in the surface waters, limiting the thermal advantage of migration in fishless lakes. Indeed daytime Chl-a samples from just below the surface in my study indicate abundant phytoplankton food in upper layers. Gilbert and Hampton (2001), in turn, attributed diel vertical migration of zooplankton in their fishless study pond to predation by notonectids. Notonectides prefer foraging in shallow littoral waters (Gilbert *et al.* 1999), and thus should have less impact on pelagic zooplankton in lakes compared to ponds. Conversely, the dominant invertebrate predator in my fishless lakes, *Chaoborus*, are not only pelagic, but often migrate vertically to deeper waters during the day.

Vertical Distribution of Rotifers

In contrast to microcrustaceans, vertical distributions of many rotifer taxa were not impacted by the presence of trout or native fish. Distributions of Synchaetidae, Brachyonidae, *K. cochlearis*, and *K. crassa* were similar among lake types, however, patterns for *Polyarthra*, and Gastropidae differed in fish-bearing versus fishless lakes. As size-selective predators, fish should prefer microcrustaceans over rotifers, since rotifers are generally smaller then microcrustaceans, alleviating much of the predation pressure from fish on rotifer taxa. Indeed, microcrustaceans are common components of both trout and adult native fish diets, whereas rotifers are rarely ingested (Naud and Magnan 1988; Beauchamp 1990). Predatory cyclopoids, however, are size-selective for small individuals and show a strong preference for small, soft-bodied rotifer prey (Stemberger 1985; Brandl 2005). Because planktivorous fish altered the vertical distribution of cyclopoids in the current study and all cyclopoids species present are highly predacious as adults (Brandl 2005), one might expect a cascading effect on the vertical distribution of their preferred or susceptible prey.

The rotifer family Synchaetidae contains soft-bodied taxa that are known to be preferred and often susceptible prey of cyclopoids over such alternate taxa such as Brachionidae and Gastropidae (Stemberger 1985), which posses external structures for predator defense. As noted, however, the vertical distribution of Synchaetidae as a whole was not significantly affected by the presence of planktivorous fish. A non-significant trend, however, did exist where Synchaetidae had a higher mean relative abundance and biomass at a depth of 1 m versus 2 m in the two fish bearing lake types but had similar abundances at 1 m and 2 m in fishless lakes. This suggests aggregations, of at least some Synchaetidae individuals, away from optimal conditions for growth and reproduction to avoid predatory cyclopoids.

The genus *Polyarthra* was the most abundance taxa of Synchaetidae (63 percent of individuals), and did show the predicted pattern in vertical distribution opposite to that of its cyclopoid predators. Gilbert and Hampton (2001) also observed an opposite pattern in vertical migration between cyclopoid predators and *Polyarthra,* supporting predator avoidance as the mechanism driving the distribution of *Polyarthra*. Unlike the other Synchaetidae and taxa from Brachionidae and Gastropidae, *Polyarthra* posses swimming appendages that greatly enhance mobility. These swimming appendages could facilitate vertical migration as a predator-avoidance behaviour in *Polyarthra*, whereas the absence of these structures could make daily migrations unfeasible for other taxa (Zhou *et al.* 2007). Predation pressure from abundant cyclopoids at specific depths combined with enhanced mobility could explain the pattern observed in *Polyarthra* that was not seen for less mobile taxa or those with structures for predator defense.

Vertical distributions of Brachionidae, including those of the dominant species *K. cochlearis* and *K. crassa*, were similar across all treatments, with a generally higher abundance and biomass at 1 m. This suggests that these taxa occupy optimal conditions for growth regardless of predator distributions. *K. cochlearis* and *K. crassa* are loricate species possessing spines for protection from cyclopoid predation. These defensive structures could eliminate the need for Brachionidae to alter distributions relative to cyclopoid predators.

Interestingly, the rotifer family Gastropidae was the only rotifer taxon that was distributed in the same pattern as the microcrustaceans. The most abundant genus in this family (*Gastropus*) has been described as the most colourful rotifer in North America, consisting of a violet epidermis and a blue stomach embedded with bright orange fat globules (Edmondson 1966). This conspicuous appearance could increase susceptible to visual predation by fish compared to other rotifers, as seen with pigmented versus non-pigmented copepods (Hairston 1979; Luecke and O'Brien 1981) resulting in the same distribution pattern as that observed for microcrustaceans (highest densities at 1 m only in fishless lakes). In particular, young-of-year native fish, may contribute to the Gastropidae pattern, as these small fishes are gape-limited to small-bodied invertebrate prey and are known to feed on rotifers in freshwater systems. In addition, Gastropidae have a mucus coating that could confer resistance to cyclopoid predators (Stemberger 1985), allowing this rotifer to occupy depths with high cyclopoid densities. To my knowledge, this is the first documentation of non-uniform Gastropidae distributions within the vertical water column of freshwater lakes.

Conclusions

Vertical distribution patterns of zooplankton can be quite variable and are thought to result from differences in predation pressure, food availability, exposure to damaging ultraviolet radiation, and water temperatures (Haney 1988). Nevertheless, the most generally observed pattern involves diel vertical migration (of most microcrustaceans and some rotifers) to deeper waters during the day. In my small boreal foothill lakes, planktivorous fish, including stocked trout and native small-bodied species, appear to exert strong direct effects on the daytime vertical distribution of Cladocera, Calanoida, Cyclopoida, and Gastropidae, even between the first and second meter of the water column. In addition, fish presence may have indirectly resulted in the reverse distribution of *Polyarthra* through changes in depth selection by predatory cyclopoids. Stocked trout did not have an additive effect on any vertical distribution patterns, suggesting that fish identity does not change prey behaviour.

In the absence of fish, temperature, food concentration, and predation by *Chaoborus* may create optimal habitat in surface waters for all taxa, with the exception of *Polyarthra*, which can migrate to deeper strata with lower densities of their cyclopoid predators. Overall microcrustacean vertical distribution was strongly and uniformly affected by fish presence, not trout presence *per se,* but fish impacted only two out of the six major rotifer taxa. Microcrustaceans and Gastropidae avoided surface waters, where they are easily detected, in lakes with visual predators (trout and/or native fish), but in lakes with a non-visual predators (*Chaoborus*), these taxa prefer surface waters, with warmer temperatures and likely more abundant phytoplankton food.

Table 4-1 Physical, chemical, and biological properties of study lakes, in July 2009 and means (±SE) of lake types. TN: total nitrogen; TDN: total dissolved nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; Chl-a: specrophometric chlorophyll-a; DO: dissolved oxygen.

Lake Type/ Lake	**TN µg/L**	**TDN µg/L**	**TP µg/L**	**TDP µg/L**	**Chl-a µg/L**	**Secchi Depth m**	**Min. DO mg/L**	**Surface Temp. °C**	**PH**	**Conduct-ivity µS/cm**
Stocked										
Beaver	613	578	17	10	1.09	4.8	1.3	21.3	7.7	153.6
Birch	698	620	12	7	1.21	4.1	1.5	22.3	8.1	83.2
Fiesta	770	710	17	9	1.39	3.4	1.3	23.0	7.6	178.8
Ironside	602	544	9	5	0.91	4.6	1.1	24.1	7.7	252.0
Mitchell	884	765	12	5	0.90	3.8	3.2	22.9	7.3	47.9
Strubel	475	454	7	4	0.01	6.9	6.7	22.5	8.3	188.8
Unstocked										
Dog Leg	964	886	31	14	5.03	2.0	1.0	25.3	7.6	115.9
Gas Plant	903	760	35	13	7.02	1.3	1.5	25.6	6.7	104.8
Gun Range	1,190	866	15	8	2.77	2.0	1.1	24.2	8.2	226.0
Picard	1,090	997	21	10	2.70	2.5	1.0	23.8	7.5	70.1
Fishless										
Conundrum	769	722	15	9	0.34	4.6	7.4	22.7	8.9	272.0
Dog Paw	1,270	1,130	44	30	7.36	2.2	0.9	26.5	7.5	35.9
Mean±SE										
Stocked	674 ±58	612±46	12±2	7±1	0.9±0.2	4.6±0.5	2.5±0.9	22.7±0.4	7.8±0.1	151±30
Unstocked	1037±64	877±49	26±5	11±1	4.4±1.0	2.0±0.2	1.2±0.1	24.7±0.4	7.5±0.3	129±34
Fishless	1020±251	926±204	30±15	20±11	3.9±3.5	3.4±1.2	4.1±3.2	24.6±1.9	8.2±0.7	154±118

Table 4-2 Summaries of vertical distribution patterns (1 m vs. 2 m) of major zooplankton taxa in stocked (n=6), unstocked (n=4; except Gastropidae n=3), and fishless (n=2) lakes. A. Vertical distributions based on mean relative abundance. B. Vertical distributions based on mean individual lengths (microcrustaceans only). Downward arrows indicate a smaller mean relative value at 1 m versus 2 m; upward arrows indicate a larger mean relative value at 1 m versus 2 m; sideways arrows indicate no difference between depths. Also shown are the statistical significance of treatment*depth interactions based on Linear Mixed Models with treatment and depth as the main effects and lake as a random variable. The pattern in mean biomass was comparable to mean relative abundance for all taxa and the pattern in mean taxon length was comparable to individual length.

A. Mean relative abundance

Taxa	Significant Interaction	Stocked	Unstocked	Fishless
Cladocera	**	↓	↓	↑
Calanoida	**	↔	↔	↑
Cyclopoida	**	↔	↔	↑
Brachionidae	None	↑	↑	↑
K. cochlearis	None	↑	↑	↑
K. crassa	None	↑	↑	↑
Synchaetidae	None	↑	↑	↔
Polyarthra	**	↑	↑	↓
Gastropidae	**	↔	↔	↑

B. Mean relative individual length

Taxa	Significant Interaction	Stocked	Unstocked	Fishless
Cladocera	*	↓	↓	↔
Calanoida	None	↓	↓	↓
Cyclopoida	None	↓	↓	↓

*0.10>p>0.05, ** p <0.05

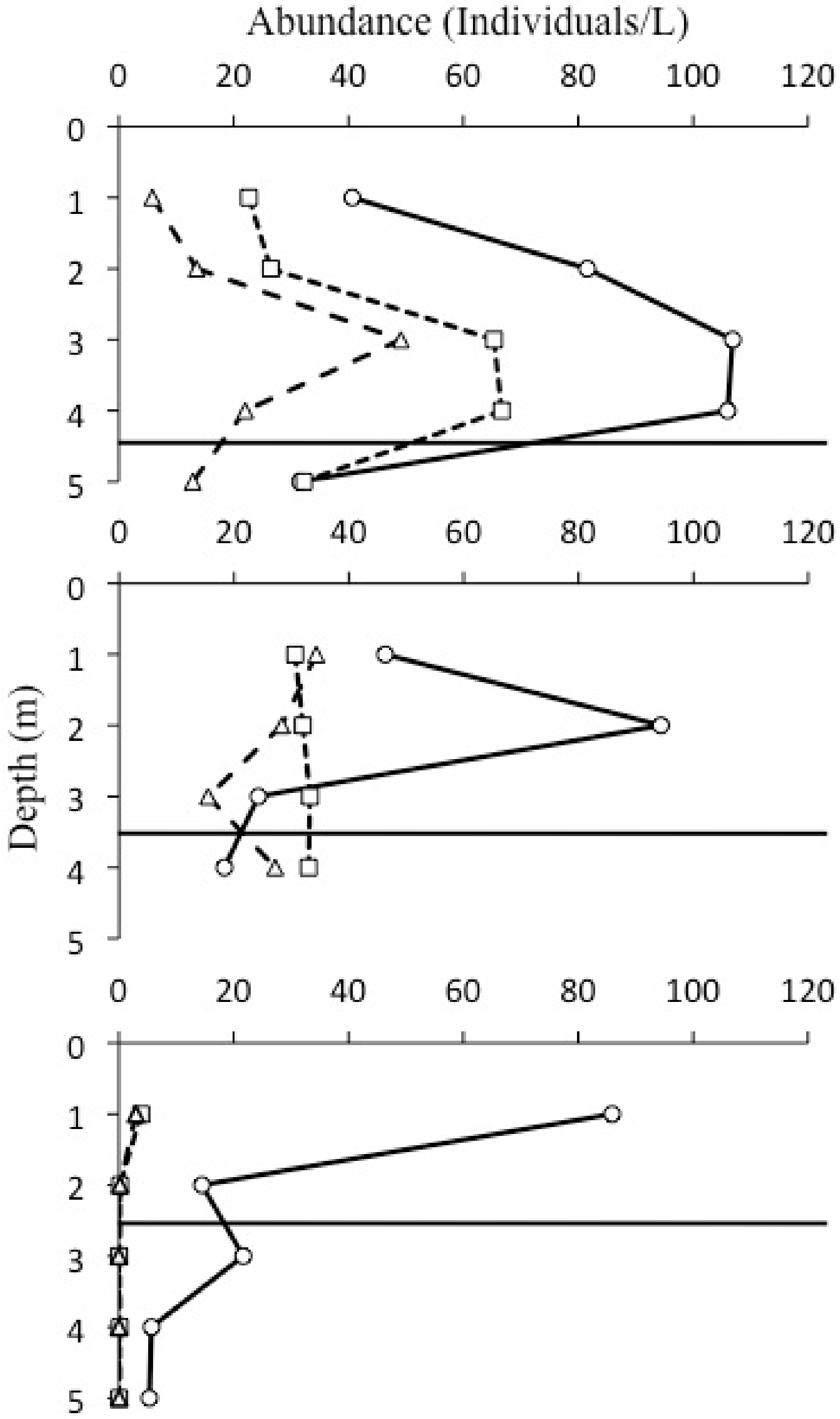

Figure 4-1 Vertical distributions of 3 microcrustacean orders at 1 meter intervals in a stocked lake (top), unstocked lake (middle), and fishless lake (bottom) in July 2009. Horizontal lines represent oxygen levels unfavourable to zooplankton (<3 mg/L). Cladocera: circles with solid line; Calanoida: squares with short dashed lines; Cyclopoida: triangles with long dashed lines.

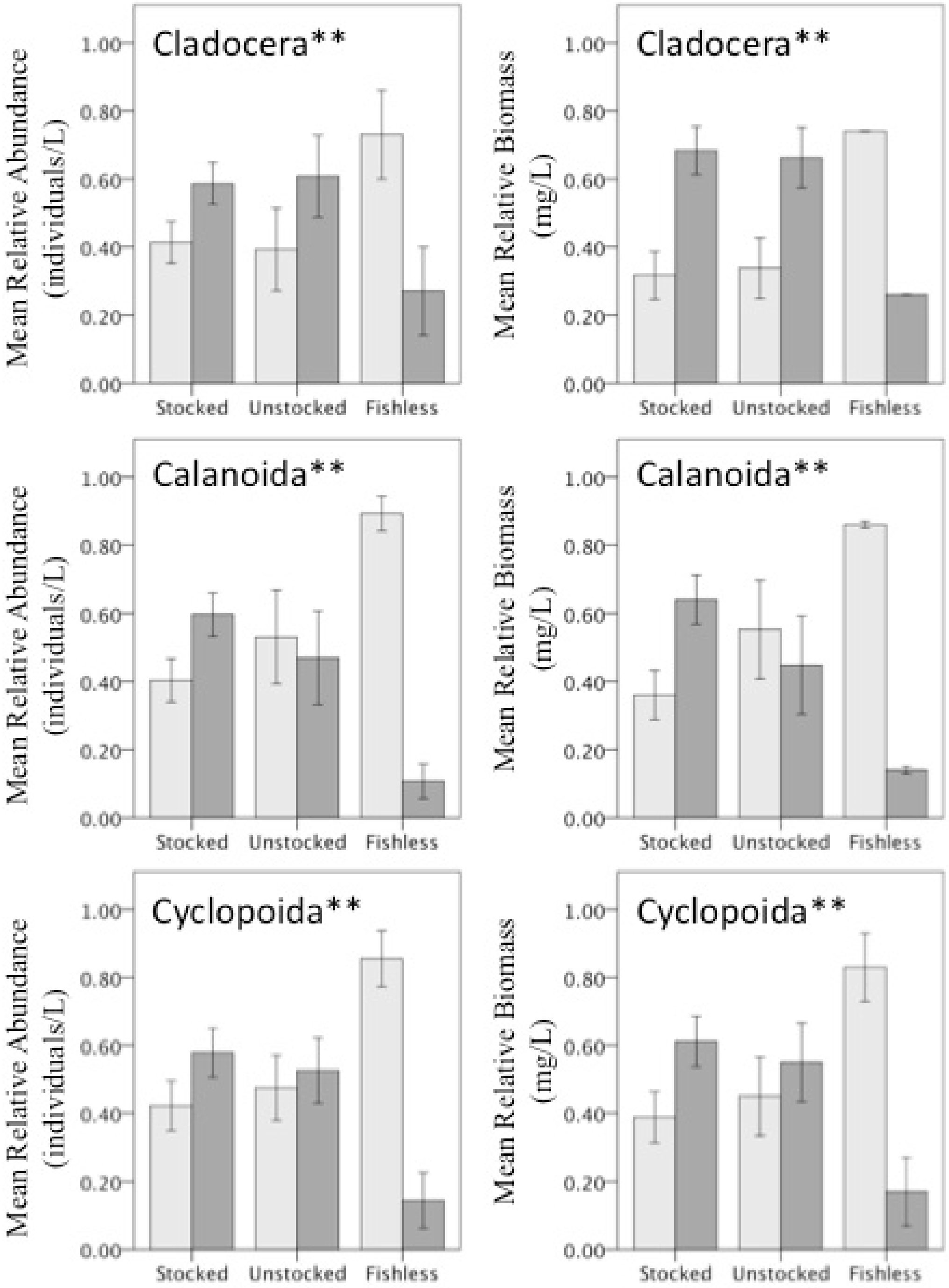

Figure 4-2 Mean (±SE) relative abundance (left) and biomass (right) of Cladocera ($F_{2, 18}$= 5.15; $F_{2, 18}$= 10.07), Calanoida ($F_{2, 18}$= 10.27; $F_{2, 18}$= 8.67), and Cyclopoida ($F_{2, 18}$= 10.32; $F_{2, 18}$= 7.81) at 1 m (light grey) and 2 m (dark grey) depths within stocked (n=6), unstocked (n=4), and fishless (n=2) lakes. F-values and degrees of freedom are for treatment*depth interactions from Linear Mixed Models with treatment and depth, as main effects and lake as a random variable. For significant interactions *0.10>p>0.05 and **p <0.05.

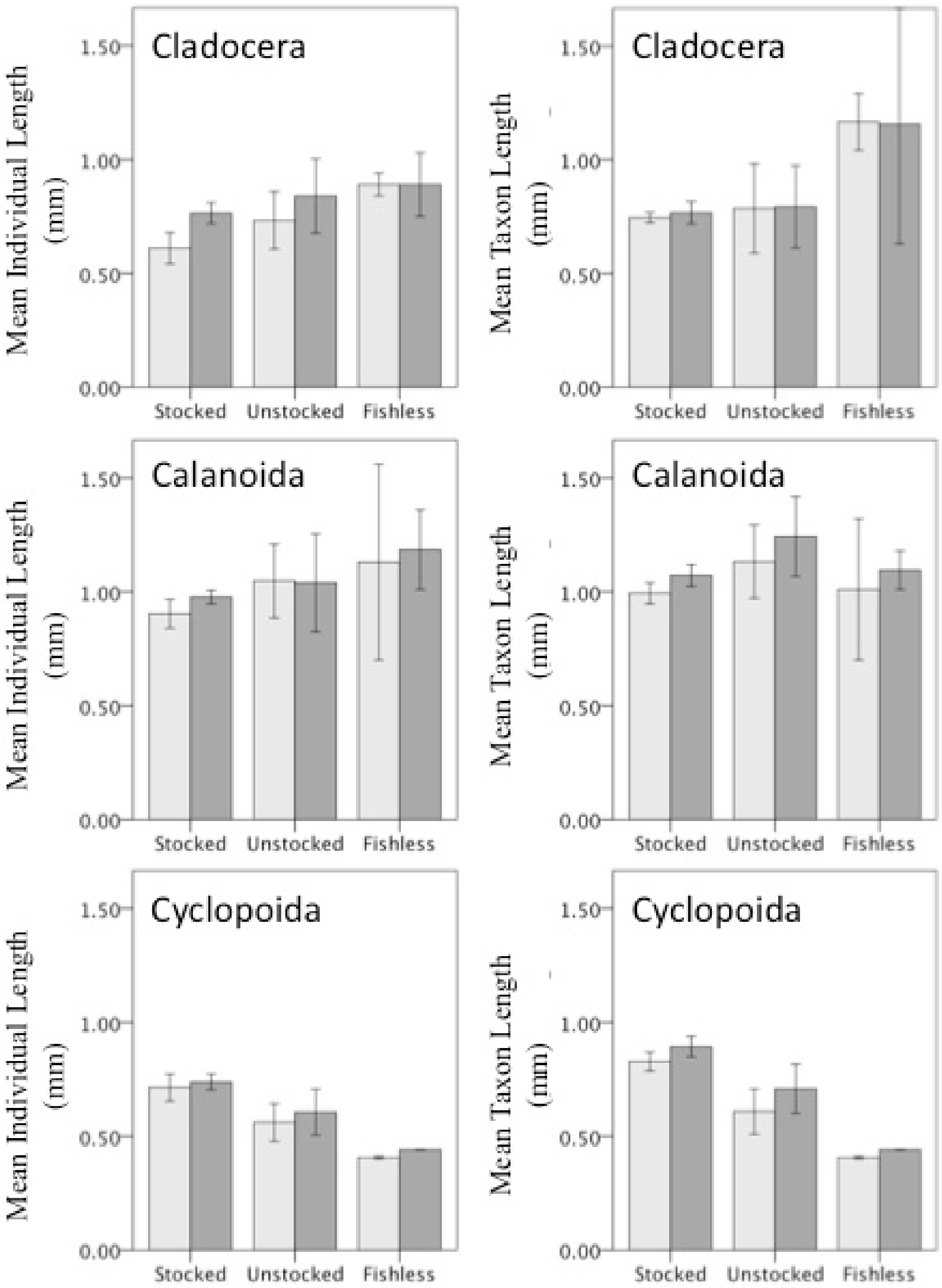

Figure 4-3 Mean (±SE) individual length (left) and taxon length (right) of Cladocera ($F_{2, 18}$= 3.30; $F_{2, 18}$= 0.34), Calanoida ($F_{2, 18}$= 1.41; $F_{2, 18}$= 0.15), and Cyclopoida ($F_{2, 18}$= 0.04; $F_{2, 18}$= 0.34) at 1 m (light grey) and 2 m (dark grey) depths within stocked (n=6), unstocked (n=4), and fishless (n=2) lakes. F-values and degrees of freedom are for treatment*depth interactions from Linear Mixed Models with treatment and depth as main effects and lake as a random variable. For significant interactions *0.10>p>0.05 and **p <0.05.

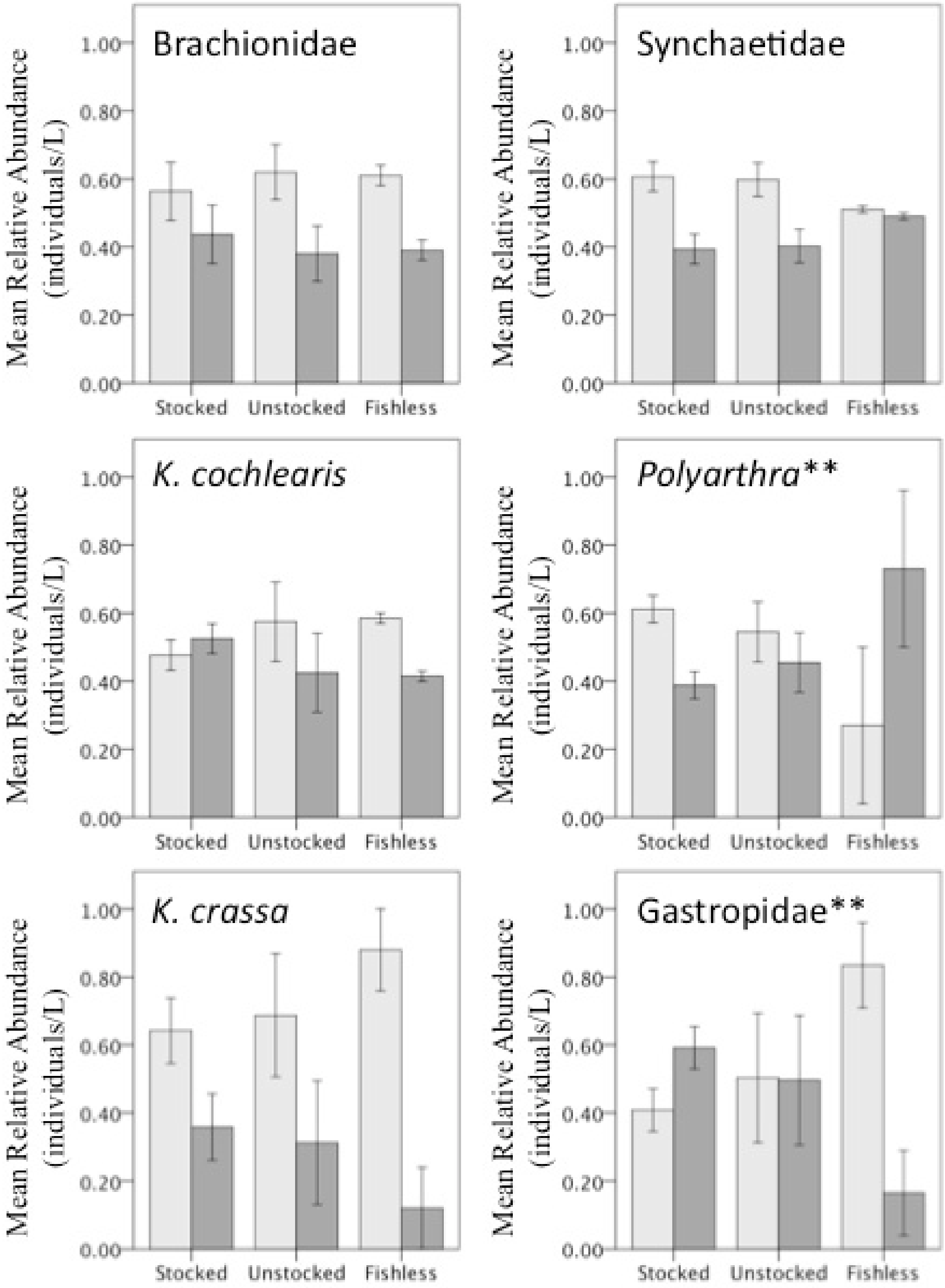

Figure 4-4 Mean (±SE) relative abundance of Brachionidae ($F_{2,\,18}$= 0.07), *K. cochlearis* ($F_{2,\,18}$= 1.28), *K. crassa* ($F_{2,\,18}$= 1.22), Synchaetidae ($F_{2,\,18}$= 1.47), *Polyarthra* ($F_{2,\,18}$= 7.00), and Gastropidae ($F_{2,\,18}$= 6.40) at 1 m (light grey) and 2 m (dark grey) depths within stocked (n=6), unstocked (n=4, except Gastropidae n=3), and fishless (n=2) lakes. F-values and degrees of freedom are for treatment*depth interactions from Linear Mixed Models with treatment and depth as the main effects and lake as a random variable. For significant interactions *0.10>p>0.05 and **p <0.05.

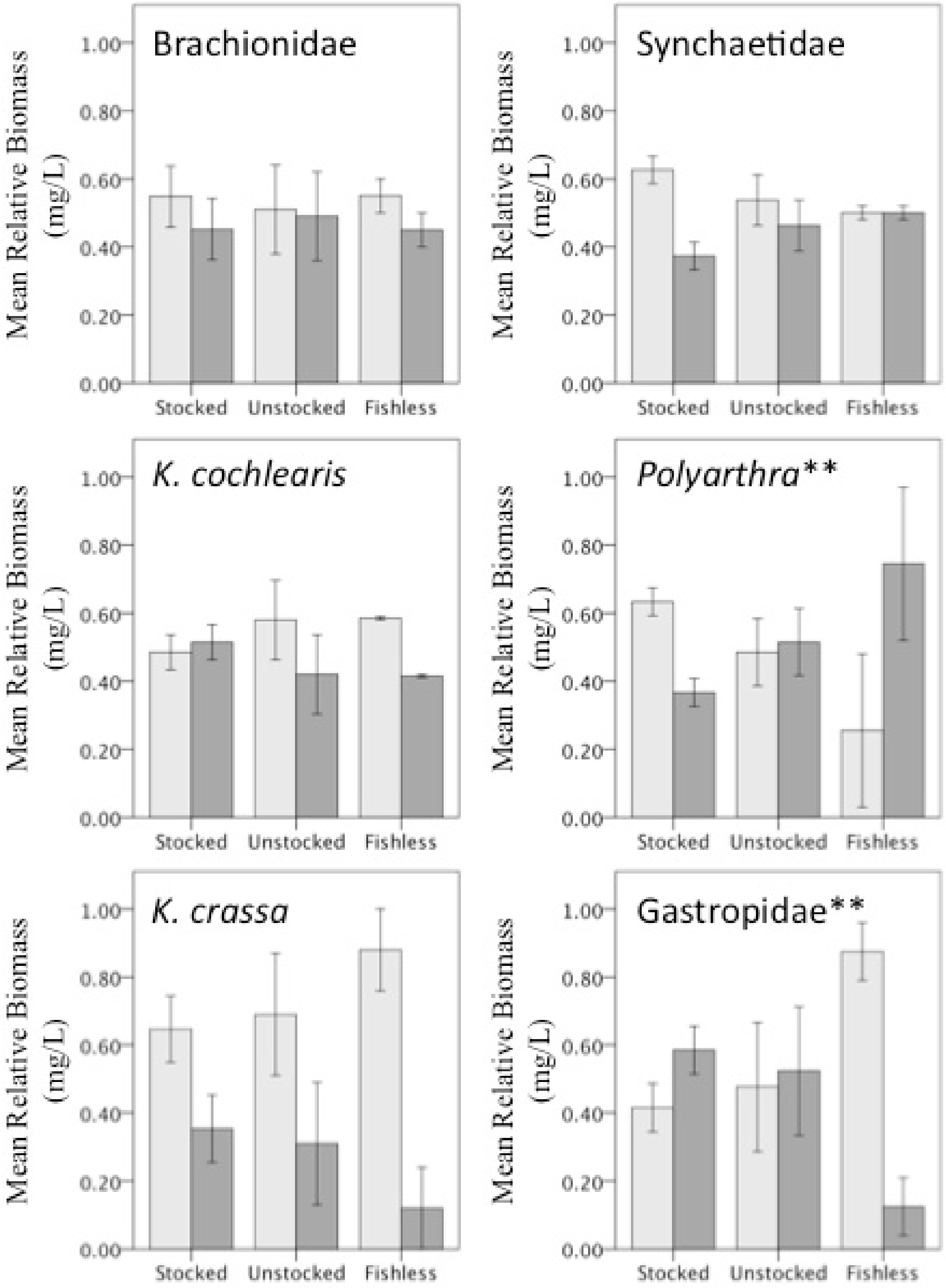

Figure 4-5 Mean (±SE) relative biomass of Brachionidae ($F_{2,\,18}$= 0.14), *K. cochlearis* ($F_{2,\,18}$= 1.07), *K. crassa* ($F_{2,\,18}$= 1.18), Synchaetidae ($F_{2,\,18}$= 2.51), *Polyarthra* ($F_{2,\,18}$= 7.85), and Gastropidae ($F_{2,\,18}$= 7.41) at 1 m (light grey) and 2 m (dark grey) depths in stocked (n=6), unstocked (n=4, except Gastropidae n=3), and fishless (n=2) lakes. F-values and degrees of freedom are for treatment*depth interactions from Linear Mixed Models with treatment and depth as the main effects and lake as a random variable. For significant interactions *0.10>p>0.05 and **p <0.05.

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Chapter 5. Effects of winter surface aeration on pelagic zooplankton communities in a small boreal foothills lake

Introduction

Extensive ice-cover on boreal lakes can have adverse effects on lake water quality and biota due to the development of hypoxia that can cause mortality of fish and other organisms, termed winterkill. Winterkill can range from an annual to an occasional phenomenon, and can have severe to mild consequences (Greenbank 1945; Scidmore 1957; Barica 1977; Danylchuk and Tonn 2003). Winter oxygen depletion results from the respiration of the biotic community and the decomposition of previous organic production during a period when oxygen is not replaced by wind mixing or primary production. Shallow, productive lakes run a particularly high risk of frequent or severe winterkill because of significant decomposition and limited oxygen stores (Barica and Mathias 1979).

Given the occurrence of hypoxia and winterkill in ice-covered lakes, lake aeration is often implemented to support valued recreational fisheries. Winter aeration is often used in conjunction with trout stocking, in part because of the limited tolerance of trout to hypoxia (Dean and Richardson 1999), but can also be used to support other gamefish year-round, improve water quality, or treat the symptoms of eutrophication (reviewed by Nordin and McKean 1982). There are two basic types of aeration: surface aeration and subsurface aeration. Subsurface techniques are used more in lake management to improve water quality, reduce eutrophication, and increase production of cool- and cold-water biota (Prepas *et al.* 1997), rather than in fisheries management to prevent winterkill.

Surface aeration consists of a fountain or spray-like device that allows and/or increases oxygen-exchange at the lake surface and slowly mixes the water column. Surface aerators are often implemented to prevent winterkill due to high oxygen input rates, low power consumption, and minimum maintenance requirements. These systems maintain an opening in the ice that results in a net gain of dissolved oxygen (DO) and a net loss of heat. A lower rate of deep-water mixing and reduced sediment disturbance makes surface aeration the ideal system for winterkill prevention (McCord *et al.* 2000). Effects of subsurface aeration on the limnological properties of freshwater systems have received considerable attention. Little to no information, however, is available on the effects of surface aeration on native taxa within lakes.

In freshwater systems, variations in thermal stratification and/or the concentration of DO can impact the distribution and physiology of zooplankton (Pennak 1944; Fast 1971). Subsurface aeration that increases hypolimnetic DO and/or temperatures can affect zooplankton communities though overall decreased abundance (Cowell *et al.* 1987; Taggart 1984), shifts in community size structure (Strus 1976) and migration of plankton to deeper depths (Fast 1971; Ellis and Tait 1981) after implementation of aeration systems. These effects could be the direct result of changes in DO and/or temperature but could also be the consequence of altered interactions between zooplankton and their phytoplankton food or altered predator-prey interactions between fish and their zooplankton prey.

Winter surface aeration could impact zooplankton communities in boreal foothills lakes for a number of reasons. These systems often contain dense populations of native, small-bodied fish that are size selective predators on large zooplankton taxa (Naud and Magnan 1988; Laurich *et al.* 2003), similar to non-native trout (Lynott *et al.* 1995) that are the management targets of aeration. Aeration could increase the overwinter survival of both non-native trout and native fish (Nasmith *et al.* 2010), which could increase predation on large-bodied zooplankton (Sosnovsky and Quiros 2009). Native fish in boreal foothills lakes, however, favor littoral habitat in the presence of trout (Hanisch *et al.* 2012), potentially offsetting the impact of increased native fish abundance on zooplankton within the pelagic region of lakes. Over the long term, increased survival of non-native trout through the winter could lead to a size shift to larger-bodied trout that do not rely heavily on zooplankton for prey, reducing predation pressure on zooplankton communities.

Winter aeration could also impact zooplankton communities by decreasing algal growth in spring through reduced nutrient availability. Under anaerobic conditions at the sediment-water interface, phosphorus is mobilized from lake sediments into the water column and becomes available for biological uptake by algae (reviewed by Nordin and McKean 1982). When aeration systems alleviate those anoxic conditions, the phosphorus remains bound to iron, aluminum, or manganese in the sediments and is not available to phytoplankton in lakes (reviewed by Nordin and McKean 1982). Decreased algal growth in the spring could limit zooplankton abundance or exclude small, competitively inferior taxa (Brooks and Dodson 1965; Gliwicz *et al.* 2010). Lakes within Alberta's boreal foothills, however, are meso- to meso-eutrophic. Although internal cycling can represent a substantial amount of nutrient input to water bodies (Jacoby *et al.* 1983; Lazoff 1983), in the absence of nutrient release from lake sediments, the surrounding watershed of boreal plain lakes (including boreal foothills lakes) could supply ample nutrients to maintain algal growth at levels that prevent declines in zooplankton densities (Prepas *et al.* 1997).

Alberta Conservation Association, along with Alberta Sustainable Resource Development, manages a trout stocking program in a number of small boreal and prairie lakes to enhance angling opportunities. In many of the stocked lakes, winter surface aeration accompanies stocking. I conducted a Before-After-Control-Impact (BACI) study (Stewart-Oaten *et al.* 1986) on the effects of winter surface aeration on spring and summer zooplankton populations. Birch Lake, in Alberta's boreal foothills, contained both stocked trout and native small-bodied fish when it was aerated for the first time in winter 2009-2010. I used two types of nearby control lakes (both containing stocked trout and native fish): one that had never been aerated (Strubel) and one that had been aerated for six years (Mitchell). In BACI designs, changes that occur in the focal lake (Birch) post-impact are compared against changes over the same time period in similar, but non-impacted, control sites (Strubel and Mitchell lakes). The BACI design has the ability to remove potentially confounding effects of natural variation, allowing the isolation of the "true" effects of the impact under investigation. This study design is considered among the most powerful for detecting ecological impacts (Downes *et al.* 2002). The strength of a BACI design resides in the number of lakes within each lake type and the sampling occasions before and after stocking, that is, it is the structure of the BACI design that ultimately determines its utility. For this reason, our ability to detect an effect may have been limited by sampling only one lake in each category and only one year before and after the initiation of aeration.

Specifically, I investigated zooplankton abundance, biomass, size, and community composition in the spring and summer 1 year before and 1 year after the start of aeration in Birch Lake, comparing values for these metrics in Birch Lake with values in control lakes. Given the paucity of studies on impacts of overwinter surface aeration and the conflicting nature of some potential impacts, a priori predictions were difficult. Increased survival of native fish through the winter could be offset by avoidance of pelagic habitat by zooplankton in the presence of trout. Increased trout survival could also be offset by a lower spring stocking density producing an ageing trout populations made of larger individuals that rely less on zooplankton as food. Finally, the potential for decreased nutrient release from sediments could be offset by the meso- to meso-eutrophic status of the lake and inputs from the nutrient rich catchment that could support algal growth at high enough levels to maintain zooplankton populations (Prepas *et al.* 1997).

Methods

Study Area

Birch, Strubel, and Mitchell lakes are located in the boreal foothills near the towns of Rocky Mountain House (52°22’39’’N and 144°54’37’’W) and Caroline (52° 5’36’’N and 114°45’28’’W), Alberta. Birch Lake received winter aeration for the first time in 2009/2010 to prevent winterkill of stocked trout, while Mitchell had received winter aeration for 6 years. Birch and Mitchell lakes each had two 1-hp floating aerators and received winter aeration from mid-October to early April. Alberta Conservation Association is responsible for lake aeration in the area and often monitors the dissolved oxygen and temperature profiles of aerated lakes during winter application. This data was obtained for Birch, and Mitchell lakes the winter before and the first winter of Birch Lake aeration but could not be obtained for Strubel Lake, since Strubel Lake does not receive winter aeration. In addition to winter aeration in Birch and Mitchell lakes, a third lake in the area (Fiesta Lake) is also aerated during winter to support stocked trout, thus winter data for Fiesta Lake was obtained during the same time periods for comparisons with Birch Lake.

Birch, Strubel, and Mitchell lakes all supported stocked trout populations for 15+ years. Birch is stocked with Brook Trout (*Salvelinus fontinalis*), whereas Strubel and Mitchell are stocked with Rainbow Trout (*Oncorhynchus mykiss*) and/or Brown Trout (*Salmo trutta*, Table 5-1). Depending on lake size (maximum depth and area) and the management strategy, between 5,000-24,000 trout were stocked in spring 2009 and again in spring 2010. Similar numbers of trout were stocked into the two control lakes in both years, whereas the number of fish stocked in Birch Lake in 2010 was only one third of that stocked in 2009 due to overwinter trout survival. All three lakes also supported native fish populations, including Fathead Minnow (*Pimephales promelas*), Brook Stickleback (*Culaea inconstans*), Pearl Dace (*Margariscus margarita*), and a dace species complex consisting of Northern Redbelly Dace (*Chrosomus eos*), Finescale Dace (*Chrosomus neogaeus*) and their hybrids (Appendix A). Native small-bodied fish densities, monitored in 2005 and 2006, ranged from 1,100 to 3,500 fish/ha (Nasmith *et al.* 2010).

Water Chemistry

Study lakes were monitored monthly (May- August 2009 and 2010) for chemical, physical and biological factors. Epilimnetic pH and Secchi transparency were measured at the deepest location within lakes, while water samples were collected just below the surface at the same locations. Water samples (200 mL) were filtered through GFF filters in the field and then frozen for chlorophyll-a (Chl-a) analysis. Other water samples (500 mL) were refrigerated until analysed for total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorous (TP), and total dissolved phosphorous (TDP). Samples were processed within seven days of collection by the Biogeochemical Analytical Laboratory at the University of Alberta, Edmonton, Alberta. Procedures followed the guidelines of the Canadian Association for Environmental Analytical Laboratories (M. Ma, Biogeochemical Analytical Laboratory, personal communication).

Temperature and DO profiles were taken at the end of May, June, and July using an OxyGuard International Handy Mark II meter, with readings taken at every meter, from just below the surface to about 1 meter above the lake bottom. Readings were recorded for both up- and down-casts, with the average of the two used for vertical profiles. Residual effects of winter aeration on the above characteristics of lakes could potentially appear in May measurements as aeration continues until early April.

Winter temperature and dissolved oxygen profiles were also acquired on a monthly basis (January- April 2009 and January- March 2010) for Birch, Mitchell, and Fiesta lakes based on sampling by Alberta Conservation Association. This resulted in winter data for Birch Lake before and during the first winter of aeration and parallel data for two additional lakes in the area (Mitchell and Fiesta) that have received winter aeration for 3+ years.

Zooplankton Collection and Laboratory Processing

Before-aeration samples of zooplankton were collected during daylight hours on a monthly basis (May- August) from Birch, Strubel, and Mitchell lakes in 2009. After-aeration samples were collected on the same schedule in 2010. Pelagic zooplankton was collected as discrete samples at 1-m intervals at the deepest location in each lake using a 30-L Schindler-Patalas Trap fitted with a 63 μm mesh dolphin-cup. Samples were preserved in 80% ethanol until laboratory processing. For May, June, and August, samples from each meter were combined to produce a single composite sample for each lake. In contrast, discrete samples from each depth were processed separately for July to examine depth distribution as discussed in Chapter 4. Procedures for sample processing are presented in Chapter 2.

Statistical Analysis

I conducted BACI analyses to assess the impact of winter surface aeration on mean density, biomass, and length of different zooplankton taxa for 2009 and 2010. I analysed taxa that occurred in all three lakes during each of the eight sampling periods (four months from 2009 and four months from 2010). To achieve these criteria, lower-level taxa were combined into the orders Cladocera, Calanoida, Cyclopoida, and Ploima, along with the families Brachionidae, Gastropidae, and Synchaetidae. Individual and taxa lengths were analysed only for taxonomic groups with sufficient sample sizes (>15 lengths/lake/sample period), thus, Gastropidae was not included. Year (Before, After) and Lake (Control, Impact) were analyzed as main effects in Linear Mixed Models with month as a repeated variable using SPSS Statistics 19.0 (SPSS for Mac OS X, Rel. 19.0.0 2010). Data were $\log_{10}(x+1)$ transformed. A non-parametric K-S tests assessed normality and Levene's test of Equality of Variances assessed the homogeneity of variance. Linear Mixed Models were also performed on water chemistry variables, including TN, TDN, TP, TDP, Chl-a, maximum DO, minimum DO, pH, surface temperature, and Secchi transparency.

To assess the impact of aeration on microcrustacean and rotifer community composition, I conducted PerMANOVA analyses on the Sorensen (Bray-Curtis) distance measure, calculated from density data at the species level for microcrustacean and the genus level for rotifer, in a two-factorial design that included Lake and Year as independent factors. I also conducted a Principal Component Analysis (PCA) on density data for zooplankton, plotting lake-year centroids and successional vectors to indicate qualitatively changes in communities between years. PCA was chosen based on the results from a preliminary detrended correspondence analysis (DCA) of the species matrix that calculated the length of the dominant axis. DCA determined that a linear model (using PCA) was appropriate. PerMANOVA and PCA analyses were performed using PC-ORD (Version 6, McCune and Mefford 2011). Densities and environmental data were $\log_{10}(x+1)$ transformed and rare taxa (occurring in < 2 samples or with a density < 1 individuals/L) were removed from the data set before analysis along with copepod copepodites, *Daphnia* juveniles, and nauplii that could not be identified down to species. Biplots of taxa and environmental variables ($r^2 > 0.5$ and $r^2 > 0.3$, respectively) were produced to aid interpretation of ordination results.

Results

Water Chemistry

All three lakes stratified by the end of July in 2009 and 2010, when epilimnetic temperatures approached or exceeded 20 ^{o}C, well above the thermal optimum for Brook Trout growth (10-12 ^{o}C; Xu *et al.* 2010); stratification appeared to be stronger in 2009 compared to 2010 (Figure 5-1). Thermal stratification often resulted in depleted oxygen concentrations (near or below 5 mg/L) in the lower depths of all lakes, although a metalimnetic DO peak was detected in at least one month (May, June, and/or July) for all three lakes (Figure 5-2). Otherwise, the top half of the water columns remained well mixed.

Chl-a, TP, and Secchi transparency values indicated that all three lakes were mesotrophic in both years (Carlson 1977), however, the three lakes varied in their year-to-year changes in water quality, particularly in spring (May), which could reflect residual effects of aeration on the abiotic feature of the lakes. Birch and Mitchell lakes both displayed decreases in TP and TDP and increases in Secchi transparency in May 2010 compared to 2009, whereas Strubel showed the opposite patterns (Table 5-3). For TN and TDN, Mitchell differed from the pattern shared by Birch and Strubel lakes. For Chl-a, Birch Lake differed from both control lakes, with concentrations increasing in Mitchell and Strubel between May 2009 and May 2010, but decreasing in Birch Lake. Finally, all three lakes displayed lower minimum DO concentrations and surface temperatures in May 2010 compared to May 2009.

Results from Linear Mixed Models of spring/summer (May-August) water chemistry variables detected marginally significant Lake*Year interactions only for TP and TDP. For TP, separate Linear Mixed Models of each lake pair (results not shown) indicated that the significant interaction was due to an increased TP in Strubel Lake but a decrease in Mitchell in spring/summer 2009 versus 2010. For TDP, separate Linear Mixed Models of each lake pair (results not shown) indicated that the significant interaction was the result of increased TDP in Strubel Lake but a decrease in Birch (Table 5-4).

In Birch Lake during winter 2009 (no aeration) DO at 1 m ranged from 8.6- 2.4 mg/L, while the temperature ranged from 2.0- 2.3 °C. At depths of 2 m to 7 m DO ranged from 2.9- 0.1 mg/L, while temperature ranged from 3.8- 3.4 °C. A steady decrease in DO and temperature was observed from January through April with DO and temperature profiles indicating little mixing between 1 m and lower depths. In Birch Lake during winter 2010 (first year of winter aeration) the top 3 m of the water column appeared well mixed with DO ranging from 8.0- 5.4 mg/L, while DO from 4 m to 5 m ranged from 4.4- 1.0 mg/L, though DO was recorded as low as 0.1 mg/L at shallower sample stations farther from surface aerators. In 2010, the temperature profile formed a gradient from 1.5- 4.2 °C from 1 m to 5 m depths. Again, DO and temperature readings decreased as winter progressed. By the end of March 2010, meters 1- 5 appeared well mixed with DO ranging from 9.6- 7.8 mg/L and temperature varying by only 0.3 °C over 5 meters. It should be noted that the maximum depth of Birch Lake is 9.0 m thus profiles to 7 m in 2009 and 5 m in 2010 were not taken at the deepest locations.

In Mitchell and Fiesta lakes, the two lakes that have received winter aeration for 3+ years, the entire water columns appeared well mixed throughout the 2009 and 2010 winters. DO in Mitchell Lake ranged from 9.2- 7.9 mg/L from 1 m to 6 m, while in Fiesta Lake DO ranged from 6.7- 5.0 mg/L from 1 m to 5 m, though readings as low as 0.4 mg/L (Mitchell) and 3.5 mg/L (Fiesta) were detected at shallower sample stations farther from surface aerators. Temperature profiles from the surface to the bottom in both lakes rarely varied by more then

0.3 °C. Again, DO and temperature reading decreased throughout the 2009 and 2010 winters, but by the end of March 2010, DO readings in the vertical column of both lakes increased to a range between 11.0- 9.7 mg/L. Although DO and temperature readings did not reach the sediment water interface in these two lakes (where anoxia can lead to nutrient release), they were within 1.5 m to 0.5 m of maximum lake depths (Mitchell and Fiesta lakes are 6.8 m and 6.6 m deep, respectively).

Zooplankton Communities

Results from Linear Mixed Models of May-August zooplankton abundance, biomass, individual length and taxon length did not detect significant Lake*Year interactions for any of the taxa investigated (Table 5-4), although lake was occasionally, and year was often, significant or marginally significant.

The lake*year interactions were also not significant for the PerMANOVAs of microcrustacean (F= 1.20, d.f.= 2, p= 0.31) and rotifer (F= 0.90, d.f.= 2, p=0.51) community data. Lake and year were, respectively, significant and marginally significant on their own for microcrustacean community data (F= 3.87, d.f.= 2, p< 0.01 and F= 2.27, d.f.= 1, p= 0.07, respectively) but were not significant for rotifers (F= 1.37, d.f.= 2, p=0.21 and F= 0.49, d.f.= 1, p= 0.79, respectively).

The first two principal components of the crustacean density ordination represented 48% of the variance in the dataset (12 taxa; Figure 5-3A). Randomization tests showed the first two axes to be significant (axis 1: p= 0.04, axis 2: p=0.02). Crustacean taxa that were correlated with the two axes include *Diaphanosoma, Skistodiaptomus oregonensis,* and *Mesocyclops edax* (Axis 1), and *Cyclops biscuspidatus thomasi* and *Daphnia catawba* (Axis 2; Figure 5-3B). Environmental variables that correlated with the two axes were surface temperature and maximum DO (Axis 1), and secchi transparency and Chl-a (Axis 2; Figure 5-3C). The area enclosed by each plotted lake-month was consistently larger in 2009 (before) versus 2010 (after) for all three lakes, ca. 3 times bigger for Birch, 5 times bigger for Mitchell, and 6 times bigger for Strubel. All three lakes moved toward the right on Axis 1 between 2009 and 2010, suggesting cooler temperatures and higher oxygen concentrations and corresponding decreases in *Diaphanosoma, Skistodiaptomus oregonensis,* and *Mesocyclops edax.* On Axis 2, the centroids of both Birch and Strubel lakes moved in an upward direction through time, suggesting higher Chl-a and lower Secchi depths, and corresponding decreases in *Daphnia catawba* and *Cyclops biscuspidatus thomasi*. In contrast, Mitchell Lake's centroids showed a slightly downward trajectory. Only one axis was recommended for rotifer community data using PCA analysis, thus multivariate results are not presented.

Discussion

There was no effect of winter surface aeration on mean May-August zooplankton abundance, biomass, size, and community composition in Birch Lake, based on the results of several BACI analyses. The zooplankton community in the aerated control lake (Mitchell Lake) displayed a slightly different trajectory through time compared to Birch Lake and the non-aerated control (Strubel Lake), although this could not be statistically linked to changes in specific taxa or environmental factors over the two years of the study.

Aeration appeared to impact the May concentration of Chl-a in Birch Lake based on qualitative analysis of data. Chl-a concentration decreased in Birch Lake but displayed greater spring concentrations in the control lakes in the after aeration time period (May 2010). Aeration in Birch Lake, however, did not impact the mean values for May through August for most environmental variables.

During winter, surface aeration increased the depth of well mixed water in Birch Lake from 1 m in 2009 to a depth of 3 m in 2010 and the minimum DO content of this well mixed area from levels as low as 2.4 mg/L in 2009 to 5.4 mg/L in 2010. Trout have a minimum requirement of 5mg/L DO (Wang *et al.* 1996), thus aeration increased the DO concentration in Birch Lake from unsuitable to suitable for stocked trout. Despite aeration, DO levels below 3 m were often far below 5 mg/L and dropped as low as 1.0 mg/L at a depth of 5 m (still 4 m above lake bottom). Though measurements were not taken at the sediment-water interface, it is likely that aeration did not prevent hypoxic conditions at this depth. The open water around the aerator, however, would have reduced the albedo effect, melting the ice-cover at a more rapid rate, and potentially shortening the anoxic period. DO profiles from two other lakes in the area that received winter aeration indicate that mixing of the entire water column with well oxygenated water (9.2- 5.0 mg/L) throughout the winter is possible. These lakes, however, were at least 2 m shallower and 1/4 to 3/4 the area of Birch Lake (maximum depths of Birch, Mitchell, and Fiesta lakes are 9.0 m, 6.8 m, and 6.6 m, respectively; maximum areas are 20.0 ha, 15.0 ha, and 7.1 ha, respectively). These responses indicate the potential importance of lake size and depth in determining the ability of surface aerators to mix entire water columns before deep water oxygen becomes depleted.

Aeration, Fish, and Zooplankton in Birch Lake

Surface aeration could impact zooplankton communities in freshwater systems through several different mechanisms, including direct effects of altered oxygen concentrations and water temperatures as well as indirect effects resulting from prevention of fish winterkill and changes in phytoplankton communities. Limited effects on water column mixing due to differences in lake size and the seasonality of application could affect the overall outcome. Nevertheless, greater fish survival could increase predation pressure on zooplankton, resulting in changes to zooplankton abundance, biomass, size, and/or community composition. Results from the BACI analysis of Birch Lake, however, showed that no initial effects of winter surface aeration on zooplankton were detectable.

Despite indications of greater survival of both native small-bodied fish and non-native trout due to aeration in the current study area (Nasmith *et al.* 2010), effect of greater native fish abundance on pelagic zooplankton in Birch Lake could be offset by increased use of littoral habitat by these fishes in the presence of trout (Hanisch *et al.* 2012). In the long run, increased overwinter survival of non-native trout in Birch Lake could result in lower spring stocking rates (as seen the first spring after winter aeration). In turn, lower spring stocking rates could decrease predation on zooplankton as trout are stocked at small sizes (usually < 15 cm in my study area) that heavily use zooplankton for food. Thus, a trout population dominated by older, larger fish would be expected due to increased survival and decreased stocking in conjunction with aeration. This should decrease predation on zooplankton since Brook Trout switch to piscivory at a fork length > 25cm (Browne and Rasmussen 2009).

Aeration, Phytoplankton, and Zooplankton in Birch Lake

Winter surface aeration could also impact zooplankton communities through changes in nutrient availability and composition of phytoplankton communities. Subsurface aeration can reduce nutrient availability for phytoplankton populations by eliminating or shortening the anoxic period at the sediment-water interface (Grochowska and Gawronska 2004). Although decreased algal growth in the spring could limit zooplankton abundance due to limiting resources, many studies to date have not detected a lasting impact of aeration on Chl-a concentrations and algal abundance (e.g. McQueen and Story 1986; Grochowska and Gawronska 2004). Although surface aerators are capable of mixing the entire water column of shallow lakes (Miller *et al.* 2001), this takes days, and during this time oxygen may become depleted from deep waters.

Qualitative BACI analysis of spring water chemistry variables did reveal a lower May Chl-a concentration after aeration in Birch Lake; both control lakes showed the opposite pattern. Results from quantitative BACI analysis of May-August water chemistry variables demonstrated decreased TDP in Birch Lake between years relative to the non-aerated control. TP did not illustrate the same pattern as TDP, which should not be a surprise as phosphorus released from anoxic sediments is dissolved not particulate phosphorus (Lazoff 1983). In addition, dissolved phosphorus is more available for biological uptake by phytoplankton, and thus is more strongly correlated with Chl-a concentrations. No overall effect of aeration on May-August Chl-a concentration in Birch Lake was detected, however, suggesting that any changes to phytoplankton populations as a result of winter aeration are short lived and do not persist throughout the summer.

Alberta’s boreal foothill lakes are mesoeutrophic, collecting runoff from relatively nutrient rich soils. As a result, the surrounding catchment could supply enough nutrients to support algal growth at levels that avoid adverse effects to zooplankton, even in the absence of nutrient release from lake sediments. The lack of effect of winter aeration on overall spring/summer Chl-a concentration could thus contribute to the lack of effects on the spring/summer zooplankton community.

Conclusions

This study was the first to investigate the potential impacts of winter surface aeration on zooplankton communities despite the numerous lakes currently managed under this strategy. BACI and other analyses indicated that winter surface aeration of Birch Lake did not affect its May-August pelagic zooplankton community the first summer after the initiation of aeration, including no effects on abundance, biomass, size, and community composition. In addition, reduced spring Chl-a concentrations did not translate into lower mean summer Chl-a and there were no detectable effects on the zooplankton community during this time. Over many years, winter aeration could potentially alter zooplankton communities due to increased winter survival of non-native trout and reduced spring stocking creating a population of older and larger trout that rely less on zooplankton and more on native fish for food. Additional research into the effects of winter surface aeration on zooplankton should prove valuable in increasing our understanding of this management technique.

Table 5-1 Stocking data for Birch, Strubel, and Mitchell lakes. Numbers, months, and stocking sizes are data from 2009 and 2010 (Alberta Sustainable Resource Development). Adult sizes are from trout caught by angling in Strubel and Mitchell (2009; J. Hanisch unpublished data) and by a combination of ice-fishing and multi-mesh gill-netting (2009; R. Konynenbelt, ASRD, unpublished data). All three lakes are open all year for angling with a daily trout limit of 5.

Lake	Year Initially Stocked	Trout Species	Area (ha)	Max. Depth (m)	Months & Numbers Stocked 2009	Stocking Size (cm) 2009	Months & Numbers Stocked 2010	Stocking Size (cm) 2010	Resident Size Mean ±SE (n) (cm)
Birch	1983	Brook	20.0	9.0	May 15,800	9	May 5,000	8	316±10 (60)
Strubel	1950	Rainbow	25.9	12.5	May 20,300	12	April 24,000	13	248±6 (79)
Mitchell	1950	Rainbow	15.0	6.8	May 4,000	17	May 4,000	18	269±5 (85)
	2003	Brown			June 500	25	June 500	15	327±20 (15)

Table 5-2 Limnological properties of Birch, Strubel, and Mitchell lakes; data were collected during May-August of 2009 and 2010. TN: total nitrogen; TDN: total dissolved nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; Chl-a: spectrophometric chlorophyll-a; DO: dissolved oxygen; Temp: temperature.

Lake Year	**Month**	**TN µg/L**	**TDN µg/L**	**TP µg/L**	**TDP µg/L**	**Chl-a µg/L**	**Max. DO mg/L**	**Min. DO mg/L**	**pH**	**Surface Temp °C**	**Secchi Depth m**
Birch 2009	May	675	553	14	6	5.1	11.80	3.10	7.7	12.0	3.0
	June	706	594	14	5	1.6	9.40	0.30	8.2	16.4	4.0
	July	698	620	12	7	1.2	8.80	1.50	8.1	22.2	4.1
	August	651	589	13	6	1.7	7.60	2.30	7.6	17.6	3.8
Birch 2010	May	619	568	10	5	2.2	8.30	2.60	-	8.5	3.9
	June	636	591	15	6	-	8.90	0.60	8.5	19.3	3.5
	July	686	639	14	3	2.4	8.70	0.20	8.6	20.7	2.6
	August	675	614	17	6	1.6	9.20	0.20	7.2	17.9	2.9
Strubel 2009	May	518	454	10	3	0.5	11.20	9.20	7.8	11.6	4.5
	June	503	423	8	2	0.1	15.40	9.30	7.2	16.9	6.1
	July	475	454	7	4	0.01	13.30	6.70	8.3	22.5	6.9
	August	484	424	10	5	0.03	7.90	2.40	8.2	18.1	6.1
Strubel 2010	May	500	467	14	5	0.7	13.00	5.60	-	10.0	4.0
	June	470	466	8	3	-	13.20	3.40	8.8	17.6	5.3
	July	841	829	12	8	0.01	11.20	0.20	8.6	19.1	6.0
	August	474	478	12	7	0.6	9.70	0.20	8.4	17.3	5.8
Mitchell 2009	May	856	774	17	7	1.6	13.70	10.80	8.1	13.3	3.7
	June	844	755	14	5	0.8	11.00	7.50	6.9	18.2	4.8
	July	884	765	12	5	0.9	9.10	3.20	7.3	22.9	3.8
	August	815	714	11	6	1.3	7.40	2.90	7.6	20.2	4.4
Mitchell 2010	May	869	773	9	7	2.3	10.80	9.70	-	10.8	3.9
	June	818	826	15	6	-	9.60	6.10	7.7	18.1	5.5
	July	468	475	8	5	1.3	8.80	1.50	6.6	20.6	4.8
	August	823	781	11	7	1.5	8.60	7.10	7.4	18.0	4.1

Table 5-3 Limnological properties of Birch, Strubel, and Mitchell lakes in 2009 and 2010. All values are the mean (±SE) of May-August measurements, with the exception of Chl-a, which is May, July, and August, and pH, which is June, July, and August. TN: total nitrogen; TDN: total dissolved nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; Chl-a: spectrophometric chlorophyll-a; DO: dissolved oxygen; Temp: temperature. Also presented are F-statistics and p-values from the Lake*Year interaction of Linear Mixed Models with Lake and Year as the independent variables and month as a repeated variable. Analyses have 2, 18 degrees of freedom except Chl-a and pH, which have 2, 12 degrees of freedom.

Lake Year	**TN µg/L**	**TDN µg/L**	**TP µg/L**	**TDP µg/L**	**Chl-a µg/L**	**Max. DO mg/L**	**Min. DO mg/L**	**pH**	**Surface Temp °C**	**Secchi Depth m**
Birch										
2009	683±12	589±14	13±0.5	6±0.4	2.7±1.2	9.40±0.88	1.80±0.60	8.0±0.2	17.1±2.1	3.7±0.3
2010	654±16	603±15	14±1.5	5±0.7	2.0±0.2	8.78±0.19	0.90±0.57	8.1±0.5	16.6±2.8	3.2±0.3
Strubel										
2009	495±10	439±9	9±0.8	4±0.6	0.2±0.2	11.95±1.60	6.90±1.62	7.9±0.4	17.3±2.2	5.9±0.5
2010	571±90	560±90	12±1.3	6±1.1	0.4±0.2	11.78±0.83	2.35±1.32	8.6±0.1	16.0±2.0	5.3±0.4
Mitchell										
2009	850±14	752±13	14±1.3	6±0.5	1.3±0.2	10.30±1.35	6.10±1.89	7.3±0.2	18.7±2.0	4.2±0.3
2010	745±93	714±80	11±1.5	6±0.5	1.7±0.3	9.45±0.50	6.10±1.71	7.2±0.3	16.9±2.1	4.6±0.4
F-statistic	1.32	1.64	2.99	2.83	0.41	0.08	1.43	0.80	0.02	1.20
p-value	0.29	0.22	0.076	0.086	0.67	0.92	0.27	0.47	0.98	0.32

Table 5-4 Results of Linear Mixed Models of abundance, biomass, individual length, and taxon length for major taxonomic groups of zooplankton from Birch, Strubel, and Mitchell lakes during May-August, 2009-2010. Lake and year were the main effects, while month was included as a repreated measure. *0.1>p>0.05, **p<0.05

Taxa	**Dependent Variables**	**Independent Variables** **Lake**	**Year**	**Interaction**
Cladocera	Abundance	$F_{2,18}$= 0.44	$F_{1,18}$= 0.44	$F_{2,18}$= 0.18
	Biomass	$F_{2,18}$= 0.48	$F_{1,18}$= 2.70	$F_{2,18}$= 0.22
	Individual length	$F_{2,18}$= 1.36	$F_{1,18}$= 3.81*	$F_{2,18}$= 0.67
	Taxon length	$F_{2,18}$= 1.58	$F_{1,18}$= 2.22	$F_{2,18}$= 0.03
Calanoida	Abundance	$F_{2,18}$= 0.61	$F_{1,18}$= 0.02	$F_{2,18}$= 0.10
	Biomass	$F_{2,18}$= 0.81	$F_{1,18}$= 15.08**	$F_{2,18}$= 0.02
	Individual length	$F_{2,18}$= 0.29	$F_{1,18}$= 6.46**	$F_{2,18}$= 0.18
	Taxon length	$F_{2,18}$= 2.31	$F_{1,18}$= 4.31*	$F_{2,18}$= 0.63
Cylopoida	Abundance	$F_{2,18}$= 1.03	$F_{1,18}$= 0.01	$F_{2,18}$= 0.74
	Biomass	$F_{2,18}$= 2.24	$F_{1,18}$= 19.21**	$F_{2,18}$= 0.52
	Individual length	$F_{2,18}$= 0.81	$F_{1,18}$= 6.44**	$F_{2,18}$= 1.90
	Taxon length	$F_{2,18}$= 0.83	$F_{1,18}$= 2.85	$F_{2,18}$= 0.15
Ploima	Abundance	$F_{2,18}$= 1.64	$F_{1,18}$= 0.17	$F_{2,18}$= 0.55
	Biomass	$F_{2,18}$= 1.82	$F_{1,18}$= 4.35*	$F_{2,18}$= 2.28
	Individual length	$F_{2,18}$= 0.72	$F_{1,18}$= 11.44**	$F_{2,18}$= 1.66
	Taxon length	$F_{2,18}$= 0.65	$F_{1,18}$= 0.02	$F_{2,18}$= 0.22
Brachionidae	Abundance	$F_{2,18}$= 1.21	$F_{1,18}$= 0.11	$F_{2,18}$= 0.12
	Biomass	$F_{2,18}$= 0.21	$F_{1,18}$= 0.42	$F_{2,18}$= 0.79
	Individual length	$F_{2,18}$= 0.25	$F_{1,18}$= 31.11**	$F_{2,18}$= 0.60
	Taxon length	$F_{2,18}$= 0.467	$F_{1,18}$= 3.29*	$F_{2,18}$= 0.87
Gastropidae	Abundance	$F_{2,18}$= 2.03	$F_{1,18}$= 2.66	$F_{2,18}$= 0.41
	Biomass	$F_{2,18}$= 1.43	$F_{1,18}$= 0.16	$F_{2,18}$= 0.18
	Individual length	NA	NA	NA
	Taxon length	NA	NA	NA
Synchaetidae	Abundance	$F_{2,18}$= 2.93*	$F_{1,18}$= 0.41	$F_{2,18}$= 0.58
	Biomass	$F_{2,18}$= 1.44	$F_{1,18}$= 0.53	$F_{2,18}$= 0.32
	Individual length	$F_{2,18}$= 0.62	$F_{1,18}$= 2.53	$F_{2,18}$= 0.99
	Taxon length	$F_{2,18}$= 3.65**	$F_{1,18}$= 0.16	$F_{2,18}$= 2.16

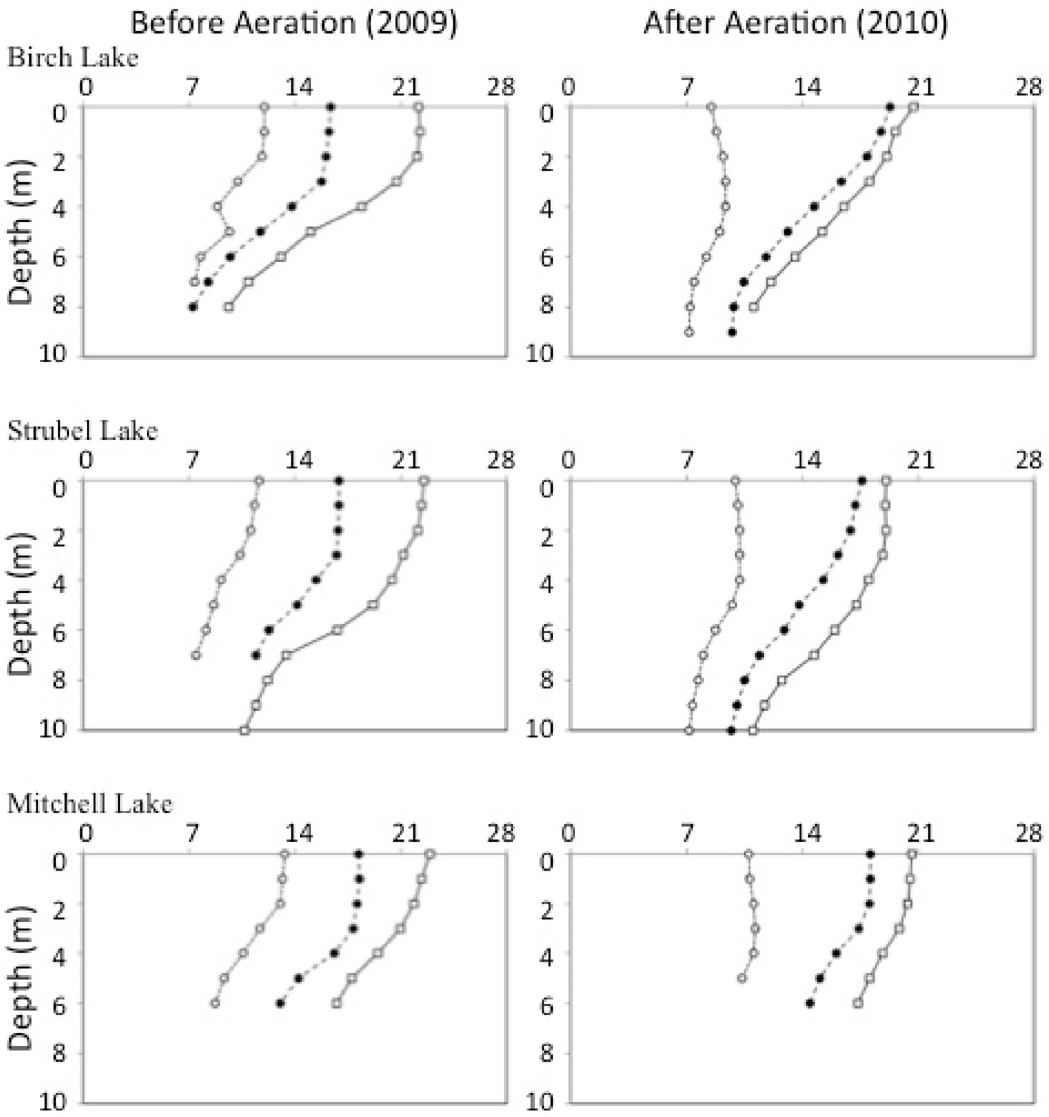

Figure 5-1 Temperature profiles taken in the last week of each month during the spring/summer of 2009 and 2010 for Birch, Strubel, and Mitchell lakes. May: open circles with short dashed lines; June: closed circles with long dashed lines; July: open squares with solid lines.

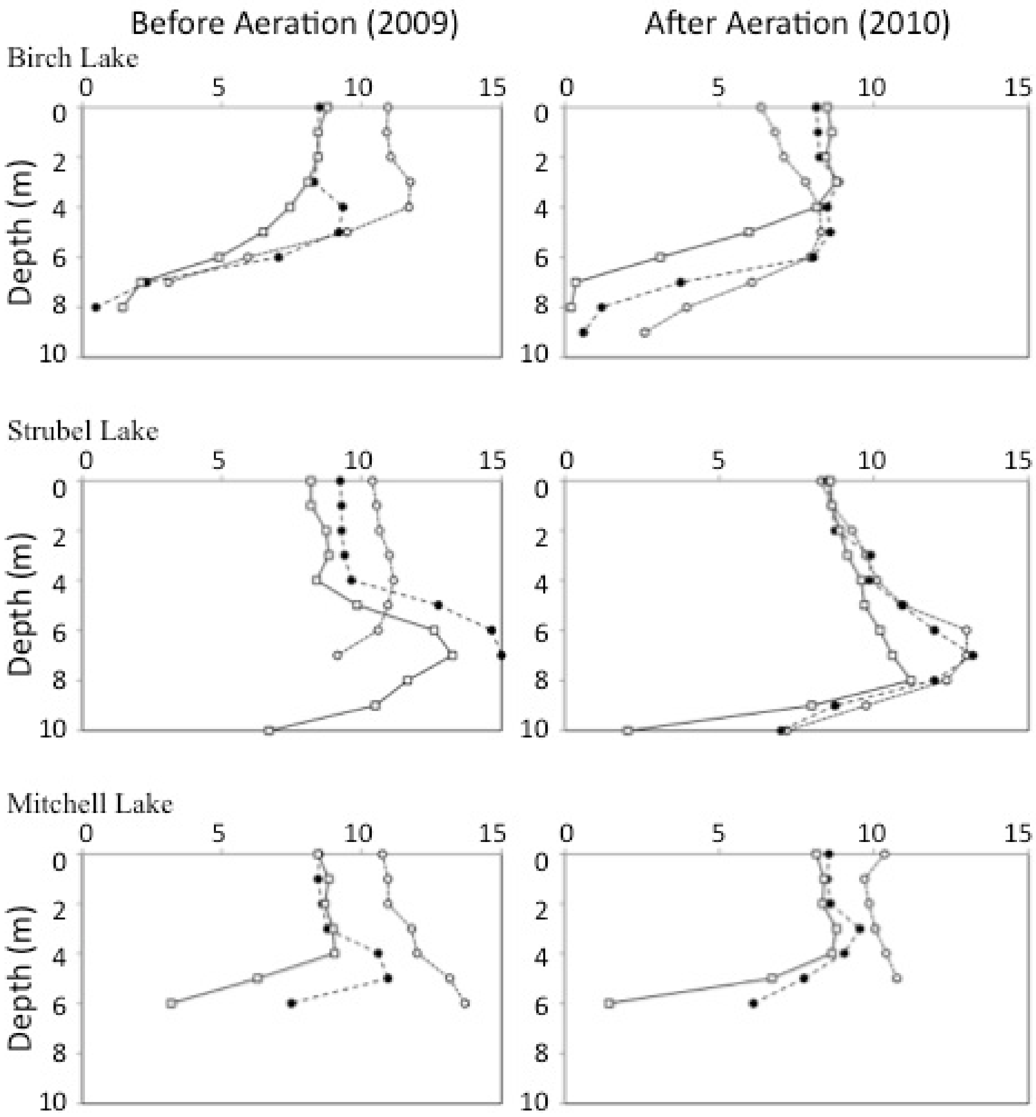

Figure 5-2 Dissolved oxygen profiles taken in the last week of each month during the spring/summer of 2009 and 2010 for Birch, Strubel, and Mitchell lakes. May: open circles with short dashed lines; June: closed circles with long dashed lines; July: open squares with solid lines.

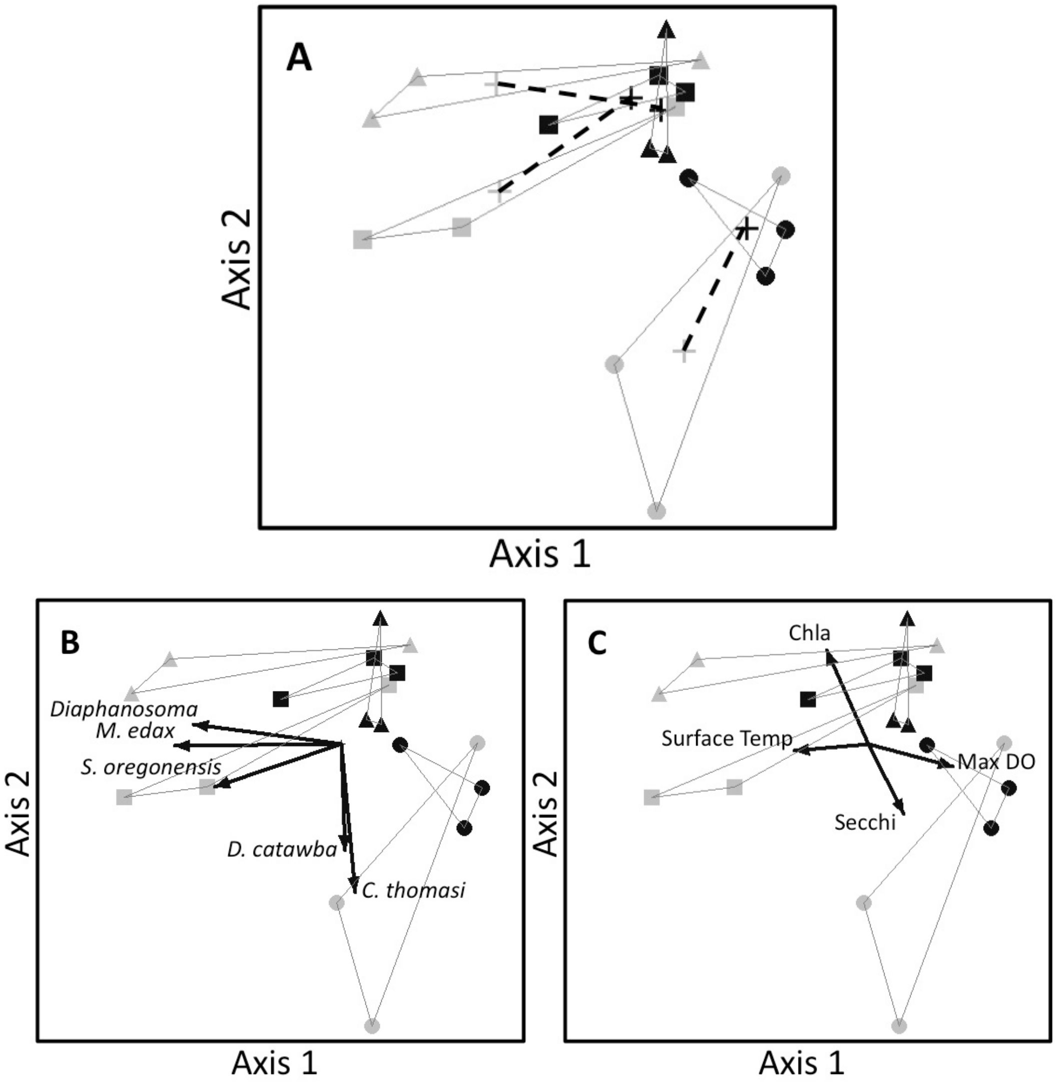

Figure 5-3 Principal Component Analysis (PCA) of microcrustacean density data from June, July and August 2009 (grey) and 2010 (black) in 3 lakes. Circles= Strubel Lake (never aerated), Squares= Birch Lake (initially aerated in winter 2009/2010), Triangles= Mitchell Lake (aerated for 6 years), Crosses= Centroid of each lake-year. Species correlated with the two axes ($r^2 > 0.5$) and environmental variables correlated with the two axes ($r^2 > 0.3$) are presented.

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Chapter 6. General Discussion

The introduction of non-native sport fish to natural aquatic ecosystems is a management practice that continues throughout North America and the world. In some cases, the introduction of these exotic species is viewed as negative due to potential impacts on receiving systems. The creation and maintenance of recreational fisheries, however, are often considered desirable, resulting in conflict between the protection of natural ecosystems and the availability of fishing opportunities for the public. Although negative impacts of gamefish introduction have been extensively recorded and discussed (e.g. Schindler 2000), more recent studies have found that under some circumstances, successful fisheries can be created without significant harm to the environment (e.g. Hickley and Chare 2004).

In particular, various species of trout have been viewed as superior sport fish, compared to native species, resulting in introductions of trout to aquatic ecosystems across the globe. For this reason, many species of trout are non-native in much of their current ranges, which encompass diverse habitat types. Among the negative effects on receiving ecosystems, introduced trout have been found to drastically alter zooplankton communities in high altitude headwater lakes and streams. A decrease in the biomass and size of zooplankton resulting from fish predation on large microcrustaceans (e.g. *Daphnia* and large calanoid copepods) has been documented in mountain lakes in North America (Carlisle and Hawkins 1998), Europe, and New Zealand (reviewed by Jeppesen *et al.* 1997; Jeppesen *et al.* 2000). In fact, the complete extirpation of populations of large microcrustacean species has been commonly recorded (Schindler 2000; Parker *et al.* 2001). Fish predation can, in turn, translate into indirect benefits to rotifer communities.

The introduction of trout into so many ecosystem types, however, makes it difficult to generalize or predict possible effects on the native fauna within systems. In North America, trout stocking of Canadian (Drouin *et al.* 2009) and American Boreal Shield lakes (Hembre and Megard 2005) appeared to positively affect microcrustacean communities, leading to greater abundances of large-bodied *Daphnia*, suggesting little negative impacts of trout predation on zooplankton communities in these systems. Mild effects have also been observed outside North America, such as tropical high Andes lakes in Bolivia, where non-native trout did not have negative impacts on zooplankton, including both microcrustacean and rotifer taxa (Aguilera *et al.* 2006). These findings indicate that a variety of trout effects can develop, likely contingent on the biotic and abiotic characteristics of receiving systems (Dunham *et al.* 2004).

My research offers another example of minimal impacts of stocked trout on zooplankton communities. In Alberta’s boreal foothills lakes with native small-bodied fish, I observed no difference in the abundance, biomass, mean individual length, mean taxon length, size structure, and vertical distribution of the major microcrustacean groups present and all rotifer groups in the presence of trout, when compared to lakes without trout. The single exception was one rotifer species (*Kellicottia longispina*) that was more abundant in stocked lakes. In addition, trout had limited effects on the community composition of microcrustaceans and rotifers, although greater species richness was observed for microcrustaceans in stocked lakes. Similarly, studies on native fish (Nasmith *et al.* 2010), amphibian (Schank *et al.* 2011), and macroinvertebrate (Nasmith *et al.* 2012) populations and communities in these lakes found no strong or consistent effects of trout.

The failure to detect statistically significant differences between stocked and unstocked lake types could be the result of the null hypothesis being (essentially) correct or it could be the result of low statistical power, that is, a relatively low probability that my analysis would reject the null hypothesis when that hypothesis is false (i.e. the probability of committing a Type II error). Statistical power may depend on a number of factors, including the statistical criterion used (i.e. the alpha level used to consider a result significant), sample size, and the magnitude of the effect of interest on the population. One way to increase the power in my analysis would be to adjust the alpha-level used for my significance criterion (such as using 0.10 instead of 0.05), which would increase the chances of rejecting the null hypothesis when the null hypothesis is false; however, that would also increase the risk of committing a Type I error (i.e., incorrectly rejecting a true null hypothesis). A second way to increase the statistical power in my analysis would be increasing the sample size (i.e., number of lakes), which determines the amount of sampling error inherent in the test results. This, however, was not feasible given the number of lakes in the area that could be contrasted based on fish community, while maintaining relatively similar physical and chemical characteristics among lakes. The magnitude of the effect (i.e., predation pressure) on zooplankton populations may have differed among lakes within a lake type due to variation in stocking rates and native fish populations, which could also effect the ability to detect a difference. Given the statistical criterion and sample size that I used, however, it is likely that significant differences were not detected between stocked and unstocked lakes due to small differences in fish predation effects between stocked and unstocked lakes on zooplankton populations, rather than limited power of my statistical tests, suggesting little biological difference to zooplankton communities. This is supported by numerous statistical differences between fish-bearing and fishless lakes in my study (as described below) as well as the previous studies done on other native taxa in the same lakes that also found null hypotheses correct during comparisons of stocked and unstocked lakes (Schank *et al.* 2011; Nasmith *et al.* 2010, 2012).

Despite the lack of significant differences in zooplankton communities between stocked and unstocked lakes, which all contained native small-bodied fishes, I did observe strong differences between fish-bearing lakes (stocked and unstocked) and fishless lakes. The presence of fish, whether non-native trout or native cyprinids and sticklebacks, strongly influenced zooplankton populations. Cladocerans and calanoids in fish-bearing lakes had a greater mean abundance, but smaller mean individual and/or species lengths, compared to fishless lakes, with smaller proportions of large cladoceran and calanoid individuals within populations. Cyclopoids and several groups of rotifers (Gastropidae, *Ascomorpha*, *Keratella cochlearis*, and *Keratella earlinea*) displayed greater abundances and biomasses in fish-bearing compared to fishless lakes. Communities in fish-bearing lakes were dominated by rotifers and small microcrustacean taxa (e.g. *Bosmina* and cyclopoid species), whereas communities in fishless lakes were dominated by large *Daphnia* and calanoid species.

The vertical distribution of all microcrustacean orders and two groups of rotifers (Gastropidae and *Polyarthra*) differed in fish-bearing lakes compared to fishless lakes. Higher abundances of microcrustaceans and Gastropidae were collected in shallow versus deeper water in fishless lakes. In contrast, lower or equal abundances of these taxa were detected in shallow versus deeper water in fish-bearing lakes. This suggests active avoidance by these taxa of areas of the lakes where fish (native or non-native) as visual predators would be more likely to detect planktonic prey because of higher light levels. The rotifer *Polyarthra* displayed the opposite pattern from microcrustaceans, which may be an indirect effect of trout, since members of this genus can migrate away from areas with abundant cyclopoid predators (Gilbert and Hampton 2001).

Due to the relative high productivity and shallow depth of Alberta's boreal foothills lakes, winter surface aeration is often used after trout stocking to prevent oxygen depletion during ice-cover and the subsequent winterkill of introduced gamefish. Winter surface aeration did not appear to impact zooplankton communities within Birch Lake, despite the potential for greater vertebrate planktivore densities after aeration. Greater survival of native small-bodied fish may have been offset by selection for littoral versus pelagic habitat in the presence of trout (Hanisch *et al.* 2012), whereas greater survival of non-native trout may have been offset by the resulting decrease in spring stocking densities and a trout population made up of proportionally larger fish that rely less on zooplankton for food. In addition, decreased anoxia near sediments and the subsequent reduction in nutrient release did not translate into an overall decrease in Chl-a throughout spring/summer (May-August) and thus did not affect zooplankton populations.

Recommendations and Conclusion

It has recently been demonstrated in a number of systems (e.g. Hickley and Chare 2004) that the successful creation of recreational fisheries with non-native sport fish is possible without the "classic" detrimental effects to native fauna observed in high altitude headwater lakes and streams. Identifying characteristics of aquatic ecosystems that make them vulnerable to or protected from stocking effects appears to be the first step in recognizing suitable locations for future stocking. The lakes that I studied within Alberta's boreal foothills seem to posses characteristics that structure zooplankton communities to fish predation and buffer the activities of introduced trout and the presence or absence of these characteristics can be used to assess other lakes to determine if they are candidates for stocking.

Alberta's boreal foothills lakes are inherently different from high-altitude lakes in many regards. Often these lakes contain dense populations of native small-bodied fish that can structure invertebrate prey communities prior to stocking, as seen in both the current study and Nasmith *et al.* (2012). Boreal foothills lakes also have moderate productivity, which could contribute resilience to native populations during the summer, while decreasing water clarity and the ability of fish to detect invertebrate prey (Liljendahl-Nurminen *et al.* 2008). Boreal foothills lakes are often stratified during the summer, with warm epilimnia and hypoxic hypolimnia; both regions could function as refuges from fish for invertebrates such as zooplankton (Hembre and Megard 2005). Boreal foothills lakes are also small and shallow, containing dense macrophyte beds that extend out from littoral habitats (Bayley and Prather 2003), which could provide additional refuge for native fauna, as seen with native fish in my study lakes (Hanisch *et al.* 2012) and invertebrates in other systems (Crowder and Cooper 1982). Finally, unlike headwater lakes, these productive, structurally complex boreal foothill lakes contain complex invertebrate communities shaped by coexistence with fish (Nasmith *et al.* 2012). In contrast, headwater lakes in alpine habitats are often naturally fishless, relatively unproductive, and unstratified with cold water suited to introduced trout. In addition, these headwater lakes frequently possess rocky or scree shorelines with low coverage by macrophytes and simple, depauperate, and naïve invertebrate communities (Schindler 2000; Donald *et al.* 2001).

Due to high angler demand for recreational fisheries and growing human populations, it is likely that new systems will be stocked in the future. Pre-stocking assessments should be done on lakes to determine the suitability of sites for gamefish stocking. The stocked lakes in the current study varied in a number of limnological respects (e.g. size, depth, the degree of thermal stratification, Chl-a concentration, small-bodied fish density and the species of small-bodied fish present), but their native taxa (Nasmith *et al.* 2010, 2012; Schank *et al.* 2011; present study) all showed similar, limited responses to trout. There thus appears to be a range of biotic and abiotic conditions that lend lake ecosystems resilience to the introduction of a new top predator. In particular, moderately high primary productivity appears to be important for providing refugia from trout, while the presence of native fish appears to be important for structuring invertebrate communities to the addition of a visual fish predator. In addition to trout stocking, winter surface aeration did not impact the zooplankton community in Birch Lake, and for this reason should be considered an appropriate management tool to increase the overwinter survival of gamefish in boreal foothills lakes.

Understanding how trout stocking programs influence native fauna is essential for the conservation of ecosystem function. Due to the position of zooplankton as primary consumers within lakes, they have the potential to control algal biomass and species composition. The use of lakes for recreational purposes such as swimming and boating depends on water quality. The presence of algal blooms or toxic species may inhibit the use of lakes for recreation and pose health concerns for humans, pets and livestock, making zooplankton herbivory extremely important due to its direct impact on algal populations. In addition, zooplankton are important food for many vertebrate and invertebrate predators.

My study showed that stocked trout have few effects on zooplankton communities in Alberta's boreal foothills lakes. It also demonstrated strong effects of fish populations, regardless of the identity of the fish species, on zooplankton communities and revealed the biotic distinctness of fishless lakes that should be preserved. Studies such as mine provide insight to resource managers on the potential effects of common practices on natural environments, allowing government agencies to reduce human effects through a greater understanding of the systems they manage.

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Appendix A: Water Chemistry

Table A-1 Physical, chemical, and biological properties of individual study lakes, 2009. With the exception of area, maximum depth and *Chaoborus* abundance, values for each lake are means ± SE of four monthly measurements (May-August), except Conundrum, which is the mean ± SE of two months (July- August). *Chaoborus* abundances (individuals/L) were calculated from July plankton samples. TN: total nitrogen; TDN: total dissolved nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; Chl-a: specrophometric chlorophyll-a; DO: dissolved oxygen.

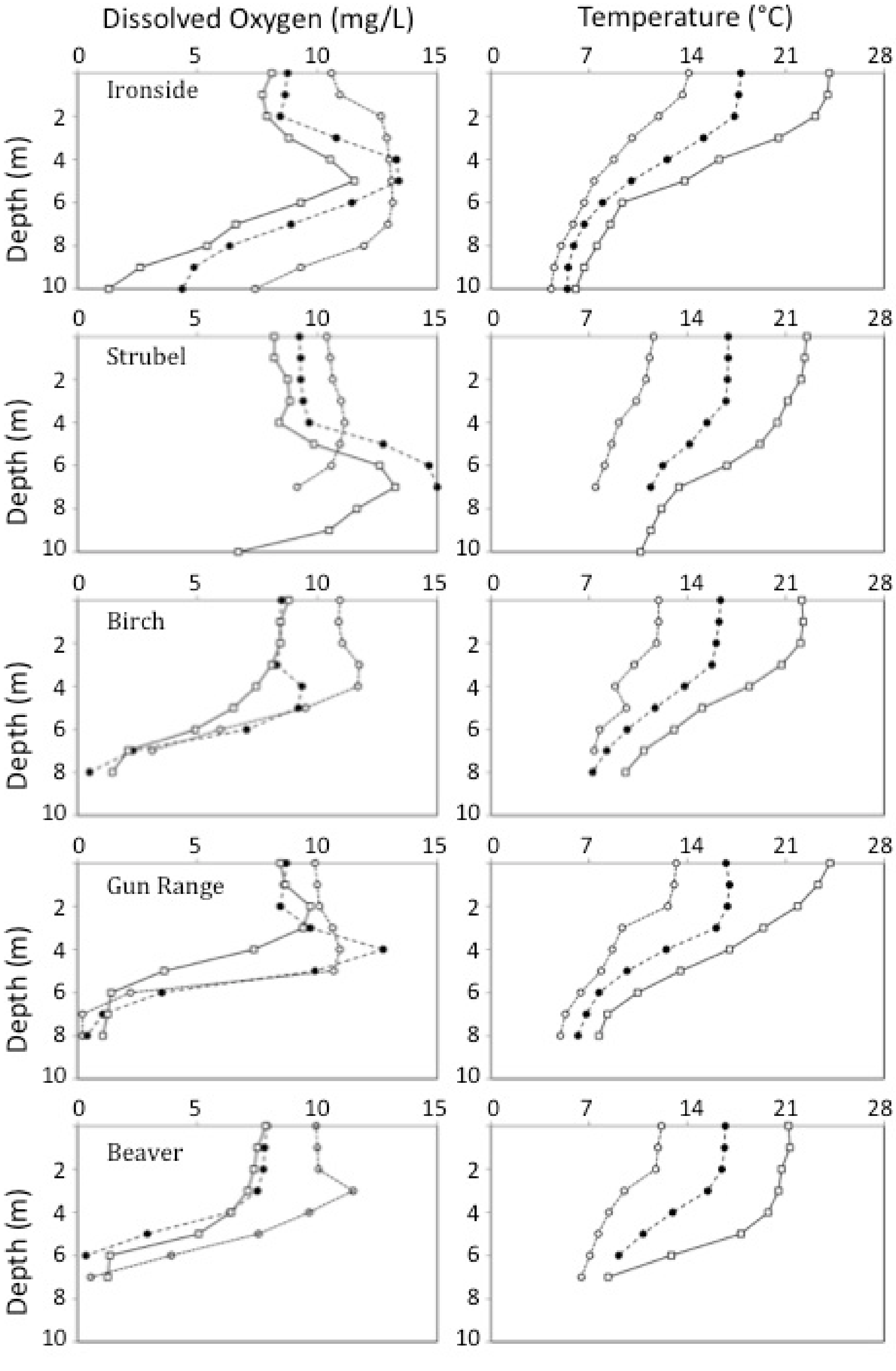
Lake Type/ Lake	TN (µg/L)	TDN (µg/L)	TP (µg/L)	TDP (µg/L)	Chl-a (µg/L)	Conductivity (µS/cm)	Secchi Depth (m)
Stocked							
Beaver	607 ± 7	544 ± 13	34 ± 16	22 ± 11	2.3 ± 1.1	148.9 ± 3.5	3.5 ± 0.5
Birch	683 ± 12	589 ± 14	13 ± 0	6 ± 0	2.4 ± 0.9	84.5 ± 1.6	3.7 ± 0.2
Fiesta	760 ± 27	660 ± 18	25 ± 5	10 ± 0	1.9 ± 0.9	200.4 ± 8.7	2.7 ± 0.4
Ironside	567 ± 13	504 ± 14	11 ± 1	5 ± 0	1.1 ± 0.4	265.3 ± 8.9	4.0 ± 0.3
Mitchell	850 ± 14	752 ± 13	14 ± 1	6 ± 0	1.2 ± 0.2	50.4 ± 1.7	4.2 ± 0.3
Struble	495 ± 10	439 ± 9	9 ± 1	4 ± 1	0.2 ± 0.1	191 ± 7.5	5.9 ± 0.5
Unstocked							
Dog Leg	968 ± 33	824 ± 30	33 ± 4	15 ± 1	4.5 ± 0.5	118.4 ± 2.3	2.2 ± 0.2
Gas Plant	849 ± 19	689 ± 26	39 ± 2	16 ± 2	6.3 ± 1.0	115.0 ± 5.6	1.7 ± 0.2
Gun Range	1018 ± 73	849 ± 72	14 ± 0	7 ± 1	2.6 ± 1.1	224.0 ± 1.2	3.7 ± 0.6
Picard	991 ± 40	898 ± 41	22 ± 3	10 ± 0	1.9 ± 0.6	70.3 ± 2.4	2.9 ± 0.3
Teal	722 ± 34	606 ± 8	24 ± 4	9 ± 1	3.4 ± 1.4	230.0 ± 13.8	2.3 ± 0.3
Fishless							
Conundrum	760 ± 10	712 ± 10	16 ± 1	9 ± 0	0.6 ± 0.2	272.5 ± 0.5	4.0 ± 0.7
Dog Paw	1203 ± 33	1013 ± 49	55 ± 7	28 ± 1	7.9 ± 1.5	37.6 ± 1.0	1.7 ± 0.2
Speedy	699 ± 49	585 ± 62	40 ± 2	18 ± 3	3.8 ± 1.0	61.1 ± 1.7	1.4 ± 0.1

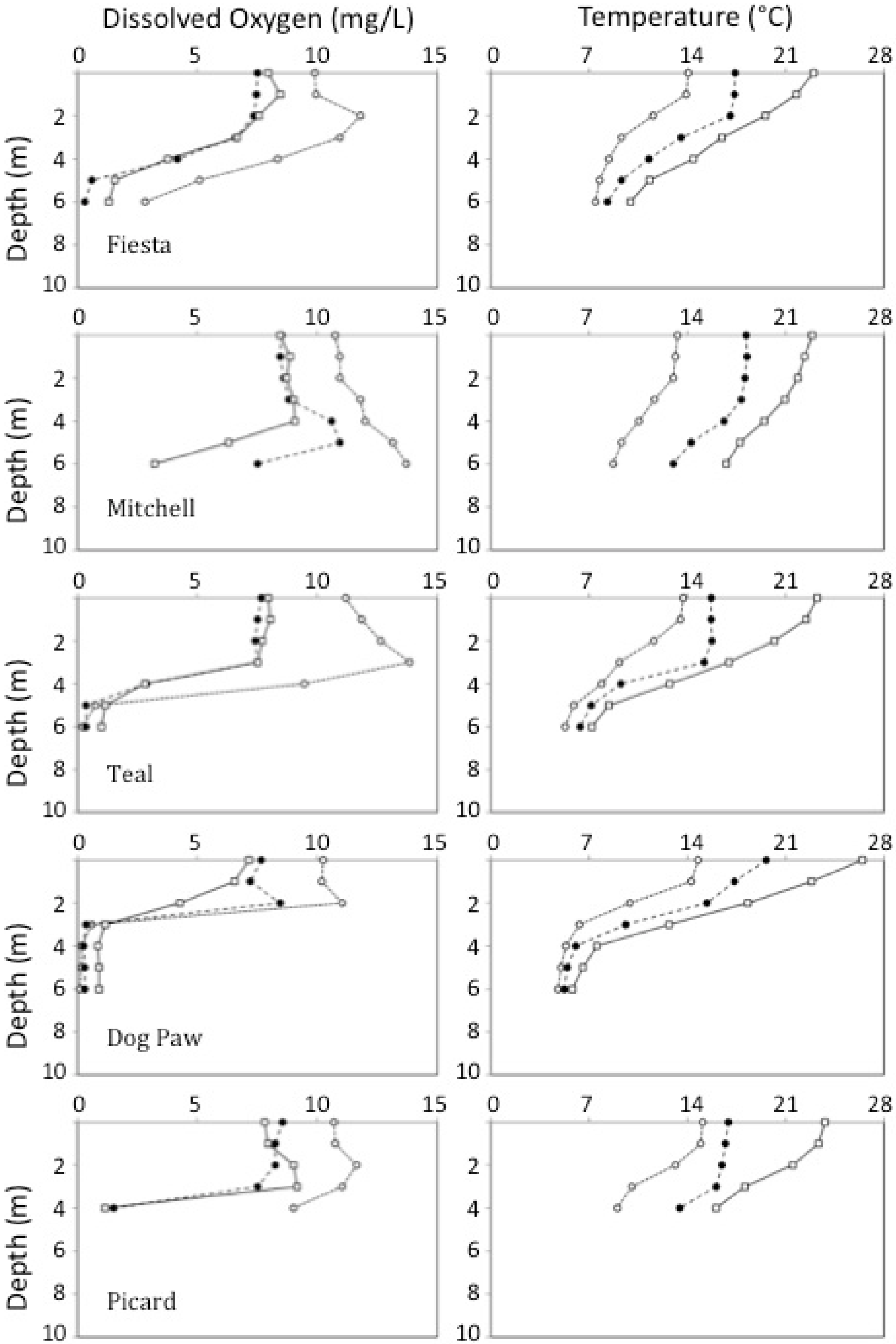
Table A-1 continued

Lake Type/ Lake	Area (ha)	Max. Depth (m)	*Chaoborus* Density	*Chaoborus* Present[1]	Native Fish Present[2]	pH	Surface Temp (°C)	Max. DO (mg/L)	Min. DO (mg/L)
Stocked									
Beaver	31.2	10.0	0.0	None	D, F, S	6.8±0.3	17.1±1.9	8.70±0.94	1.40±0.66
Birch	20.0	9.0	0.8	F	D, F, S	7.9±0.2	17.1±2.1	9.40±0.88	1.80±0.60
Fiesta	7.1	6.6	8.7	F, P	D, F, S	7.8±0.1	18.3±1.8	9.33±0.92	2.45±1.11
Ironside	3.3	13.0	0.7	F, P	D	7.6±0.4	18.4±2.1	11.75±0.99	2.95±1.42
Mitchell	15.0	6.8	0.0	None	D	7.5±0.3	18.7±2.0	10.30±1.35	6.10±1.89
Struble	25.9	12.5	0.0	F	D, S	7.9±0.3	17.3±2.2	11.95±1.60	6.90±1.62
Unstocked									
Dog Leg	6.7	5.0	22.6	F, P, T	D, F, S	7.7±0.2	19.2±2.3	8.10±0.37	1.68±1.15
Gas Plant	17.5	3.9	0.0	None	D, F, S	7.6±0.3	18.8±2.5	9.55±0.60	4.85±1.24
Gun Range	5.9	13.4	8.5	F, T	D, F, S	7.7±0.4	17.9±2.3	10.53±0.90	0.45±0.23
Picard	8.7	4.1	0.0	None	D, F, S	7.8±0.2	19.0±1.9	9.70±0.68	4.05±1.84
Teal	16.6	9.0	5.4	F, P	D, F, S	7.2±0.1	18.3±1.8	9.70±1.43	2.00±1.48
Fishless									
Conundrum	10.0	6.0	15.6	F, T, A	None	8.4±0.5	19.7±1.6	8.79±0.65	4.47±1.46
Dog Paw	3.0	6.0	31.1	F, T, A	None	7.7±0.3	20.1±2.4	8.95±0.81	1.70±1.28
Speedy	1.0	2.5	26.9	F, T, A	None	7.3±0.3	19.9±2.6	6.31±1.07	2.66±0.97

[1] F: *C. flavican; P: C. punctipennis; T: C. trivitatus; A: C. americana.*

[2] D: pearl dace (*Margariscus nachtriebi*) and a dace species complex consisting of northern redbelly dace (*Chrosomus eos*), finescale dace (*Chrosomus neogaeus*) and their parthenogenic hybrid; F: fathead minnow (*Pimephales promelas*); S: brook stickleback (*Culaea inconstans*).


Dissolved Oxygen (mg/L)
Temperature (°C)
Ironside
Strubel
Birch
Gun Range
Beaver
Depth (m)
0
5
10
15
0
7
14
21
28
2
4
6
8
10


Dissolved Oxygen (mg/L)
Temperature (°C)
0
5
10
15
0
7
14
21
28
Depth (m)
2
4
6
8
10
Fiesta
Mitchell
Teal
Dog Paw
Picard

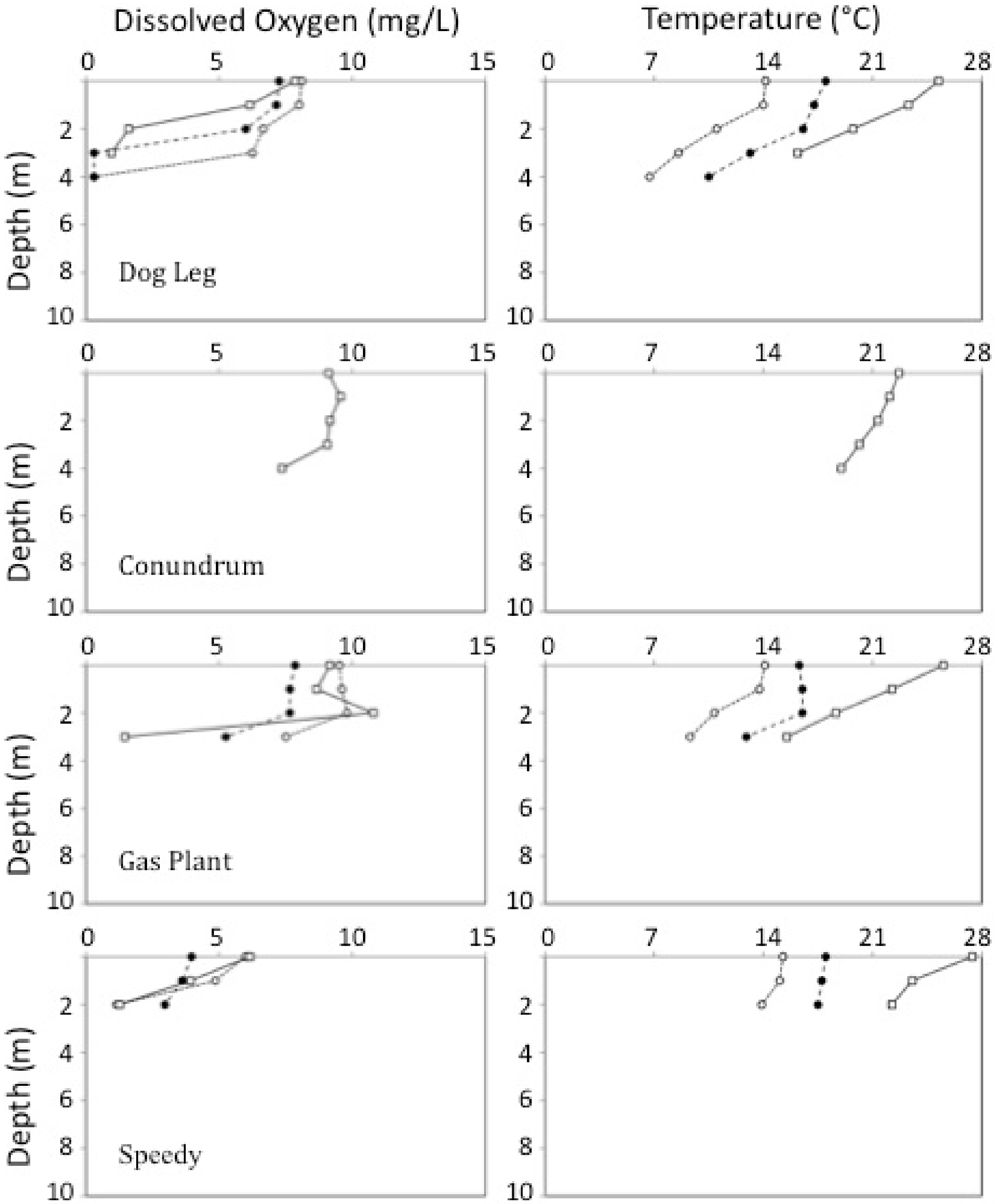


Figure A-1 Dissolved oxygen and temperature profiles taken in the last week of each month, May-July 2009, for all 14 study lakes. May: open circles; June closed circles; July: open squares.

Appendix B: Microcrustacean Communities

Table B-1 Cladoceran abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	11.3	2.2	32.7	56.0
	Birch	6.1	53.0	64.0	58.0
	Fiesta	0.5	62.9	73.3	44.6
	Ironside	0.3	6.7	37.5	11.7
	Mitchell	1.5	20.7	100.7	66.7
	Strubel	2.6	6.5	70.6	57.0
Unstocked	Dog Leg	0.3	13.8	6.2	1.7
	Gas Plant	0.2	40.7	15.5	1.3
	Gun Range	15.1	24.9	28.4	15.3
	Picard	8.4	7.0	45.8	21.3
	Teal	0.1	24.6	83.6	71.4
Fishless	Conundrum	n/a	5.7	19.1	3.6
	Dog Paw	0.04	3.5	26.6	9.7
	Speedy	0.7	11.0	22.1	13.9

Table B-2 Calanoid abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; - : Taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	4.4	20.9	10.3
	Birch	1.8	22.2	46.8	39.5
	Fiesta	0.2	17.3	42.7	39.0
	Ironside	0.2	6.9	5.3	3.4
	Mitchell	1.1	8.1	26.1	22.2
	Strubel	4.9	4.1	34.5	21.1
Unstocked	Dog Leg	0.0	0.9	5.3	13.5
	Gas Plant	-	42.4	21.6	86.6
	Gun Range	1.0	5.1	11.2	9.8
	Picard	0.7	13.6	32.2	33.5
	Teal	0.1	32.0	23.1	34.0
Fishless	Conundrum	n/a	4.2	14.2	2.1
	Dog Paw	0.1	0.1	0.9	0.9
	Speedy	0.1	0.3	14.1	2.7

Table B-3 Cyclopoid abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	64.2	10.8	4.5	19.3
	Birch	16.9	43.9	31.9	23.2
	Fiesta	11.9	8.0	20.7	25.5
	Ironside	2.4	7.7	38.9	14.1
	Mitchell	5.5	14.7	15.8	13.0
	Strubel	23.5	16.2	53.3	28.2
Unstocked	Dog Leg	65.8	0.1	2.2	5.6
	Gas Plant	43.6	48.9	11.2	8.3
	Gun Range	0.6	1.6	0.5	1.5
	Picard	91.5	5.9	26.3	16.8
	Teal	3.4	15.7	24.9	19.0
Fishless	Conundrum	n/a	0.1	5.6	2.0
	Dog Paw	0.1	0.1	0.7	0.2
	Speedy	7.3	0.6	5.4	4.9

Table B-4 Cladoceran biomass (mg/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	46.3	18.0	192.7	464.8
	Birch	20.7	286.3	617.0	254.1
	Fiesta	0.8	199.6	180.5	228.0
	Ironside	1.4	20.6	370.2	90.4
	Mitchell	1.5	39.2	462.0	333.8
	Strubel	6.2	13.5	334.7	344.7
Unstocked	Dog Leg	1.3	189.1	48.3	4.0
	Gas Plant	0.2	34.7	41.1	3.8
	Gun Range	51.0	238.8	637.3	231.9
	Picard	44.1	122.7	128.0	25.0
	Teal	0.2	24.0	147.4	137.9
Fishless	Conundrum	n/a	87.0	72.8	82.0
	Dog Paw	0.2	22.6	230.6	63.5
	Speedy	1.2	28.1	92.6	90.2

Table B-5 Calanoid biomass (mg/L) in each sampling period for each lake in 2009. n/a: lake not sampled; - : Taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	38.4	104.6	29.0
	Birch	16.1	60.7	236.3	237.1
	Fiesta	1.5	119.8	235.8	189.6
	Ironside	2.0	33.5	15.8	11.5
	Mitchell	9.5	23.3	138.0	137.0
	Strubel	27.3	11.6	176.2	121.1
Unstocked	Dog Leg	0.1	8.5	28.3	73.5
	Gas Plant	-	187.0	108.7	503.0
	Gun Range	1.4	30.9	92.2	69.9
	Picard	0.9	48.8	134.8	146.8
	Teal	0.8	89.6	122.7	195.1
Fishless	Conundrum	n/a	69.6	267.2	45.1
	Dog Paw	0.3	2.0	3.6	20.7
	Speedy	0.1	4.4	51.4	30.1

Table B-6 Cyclopoid biomass (mg/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	147.1	43.1	19.7	44.5
	Birch	56.2	72.5	124.4	85.6
	Fiesta	15.7	20.9	51.7	123.5
	Ironside	5.5	17.6	85.0	30.7
	Mitchell	17.8	21.5	55.3	42.9
	Strubel	38.8	27.1	183.7	89.7
Unstocked	Dog Leg	39.7	0.1	1.6	5.3
	Gas Plant	82.9	94.1	11.5	8.7
	Gun Range	0.6	5.1	2.2	4.1
	Picard	81.5	13.4	51.3	35.7
	Teal	6.8	65.6	107.8	90.3
Fishless	Conundrum	n/a	0.8	3.5	1.2
	Dog Paw	0.6	0.1	0.4	2.5
	Speedy	6.9	0.2	6.0	6.6

Table B-7 Mean (n) cladoceran individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.85 (32)	1.05 (33)	0.99 (273)	1.09 (85)
	Birch	0.81 (37)	0.90 (83)	1.05 (533)	0.77 (78)
	Fiesta	0.59 (29)	0.71 (62)	0.59 (358)	0.92 (67)
	Ironside	0.76 (41)	0.60 (48)	1.07 (727)	1.04 (72)
	Mitchell	0.28 (28)	0.53 (67)	0.82 (461)	0.84 (60)
	Strubel	0.70 (28)	0.59 (40)	0.78 (474)	0.98 (67)
Unstocked	Dog Leg	0.73 (8)	1.20 (61)	1.01 (132)	0.50 (24)
	Gas Plant	0.42 (6)	0.30 (47)	0.54 (146)	0.57 (21)
	Gun Range	0.83 (46)	1.22 (32)	1.39 (324)	1.34 (50)
	Picard	0.88 (39)	1.20 (50)	0.57 (193)	0.31 (38)
	Teal	0.55 (8)	0.34 (39)	0.55 (207)	0.55 (75)
Fishless	Conundrum	n/a	1.44 (32)	0.79 (190)	1.30 (45)
	Dog Paw	0.91 (3)	0.82 (40)	1.00 (197)	0.98 (75)
	Speedy	0.65 (10)	0.70 (33)	0.74 (41)	0.95 (41)

Table B-8 Mean (n) calanoid individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled; - : Taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	1.25 (41)	1.04 (187)	0.75 (19)
	Birch	1.22 (15)	0.73 (18)	0.97 (234)	1.06 (30)
	Fiesta	1.26 (15)	1.03 (30)	0.99 (150)	0.88 (30)
	Ironside	1.23 (16)	0.91 (30)	0.64 (201)	0.73 (25)
	Mitchell	1.19 (15)	0.72 (19)	0.96 (159)	1.07 (30)
	Strubel	0.96 (29)	0.64 (30)	0.96 (251)	1.02 (30)
Unstocked	Dog Leg	0.65 (1)	1.29 (23)	0.89 (88)	0.96 (45)
	Gas Plant	-	0.83 (30)	0.80 (90)	1.00 (30)
	Gun Range	0.50 (15)	1.07 (30)	1.38 (192)	1.20 (30)
	Picard	0.46 (14)	0.84 (30)	0.76 (120)	0.86 (30)
	Teal	0.97 (13)	0.69 (30)	0.98 (120)	0.98 (30)
Fishless	Conundrum	n/a	1.47 (30)	1.59 (120)	1.56 (30)
	Dog Paw	0.99 (4)	1.53 (6)	0.76 (31)	1.63 (26)
	Speedy	0.57 (1)	1.24 (5)	0.85 (37)	1.10 (34)

Table B-9 Mean (n) cyclopoid individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	0.63 (45)	0.86 (38)	0.85 (115)	0.65 (33)
	Birch	0.75 (37)	0.61 (17)	0.79 (270)	0.78 (30)
	Fiesta	0.50 (45)	0.71 (25)	0.67 (142)	0.89 (30)
	Ironside	0.64 (35)	0.70 (23)	0.62 (434)	0.61 (37)
	Mitchell	0.75 (31)	0.58 (16)	0.73 (176)	0.77 (30)
	Strubel	0.58 (30)	0.59 (30)	0.77 (286)	0.75 (34)
Unstocked	Dog Leg	0.40 (20)	0.57 (2)	0.44 (15)	0.46 (24)
	Gas Plant	0.55 (45)	0.64 (24)	0.47 (58)	0.50 (20)
	Gun Range	0.44 (17)	0.77 (24)	0.83 (53)	0.66 (16)
	Picard	0.44 (39)	0.59 (29)	0.59 (120)	0.62 (30)
	Teal	0.54 (32)	0.79 (30)	0.87 (141)	0.85 (30)
Fishless	Conundrum	n/a	1.00 (8)	0.43 (60)	0.40 (15)
	Dog Paw	0.78 (11)	0.53 (5)	0.42 (24)	1.30 (15)
	Speedy	0.48 (16)	0.31 (10)	0.49 (19)	0.52 (24)

Table B-10 Mean ±SE (n) cladoceran taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	1.01 ± 0.29 (4)	0.97 ± 0.27 (4)	0.87 ± 0.14 (9)	1.15 ± 0.16 (7)
	Birch	0.64 ± 0.20 (4)	0.90 ± 0.19 (6)	0.86 ± 0.19 (8)	0.69 ± 0.16 (6)
	Fiesta	0.59 ± 0.17 (4)	0.76 ± 0.16 (6)	0.75 ± 0.14 (6)	0.78 ± 0.14 (6)
	Ironside	0.89 ± 0.26 (5)	0.85 ± 0.21 (7)	1.00 ± 0.17 (10)	0.91 ± 0.17 (7)
	Mitchell	0.63 ± 0.26 (4)	0.64 ± 0.16 (7)	0.86 ± 0.17 (9)	0.89 ± 0.18 (4)
	Strubel	0.87 ± 0.17 (5)	0.78 ± 0.17 (4)	0.87 ± 0.17 (6)	0.85 ± 0.23 (5)
Unstocked	Dog Leg	0.68 ± 0.28 (4)	1.20 ± 0.37 (5)	1.21 ± 0.23 (6)	0.53 ± 0.16 (3)
	Gas Plant	0.42 ± 0.19 (2)	0.33 ± 0.05 (4)	0.47 ± 0.13 (4)	0.54 ± 0.15 (3)
	Gun Range	0.91 ± 0.27 (4)	0.73 ± 0.26 (4)	0.94 ± 0.24 (6)	1.12 ± 0.31 (4)
	Picard	0.84 ± 0.37 (3)	1.11 ± 0.31 (8)	0.46 ± 0.14 (4)	0.54 ± 0.17 (3)
	Teal	0.81 ± 0.23 (4)	0.43 ± 0.10 (4)	0.77 ± 0.16 (5)	0.66 ± 0.12 (5)
Fishless	Conundrum	n/a	1.18 ± 0.23 (3)	1.00 ± 0.37 (7)	1.52 ± 0.57 (3)
	Dog Paw	0.85 ± 0.17 (2)	1.31 ± 0.59 (4)	1.53 ± 0.40 (6)	1.14 ± 0.28 (5)
	Speedy	0.67 ± 0.20 (3)	1.28 ± 0.25 (4)	0.95 ± 0.34 (4)	1.06 ± 0.32 (4)

Table B-11 Mean ±SE (n) calanoid taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled; - : Taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	1.35 ± 0.36 (3)	1.21 ± 0.20 (3)	1.02 ± 0.34 (2)
	Birch	1.22 (1)	0.90 ± 0.18 (2)	1.04 ± 0.16 (2)	1.11 ± 0.13 (2)
	Fiesta	1.16 ± 0.15 (2)	0.82 ± 0.38 (2)	1.09 ± 0.22 (2)	1.03 ± 0.31 (2)
	Ironside	1.12 ± 0.12 (2)	0.97 ± 0.21 (2)	0.86 ± 0.37 (2)	0.96 ± 0.35 (2)
	Mitchell	1.19 (1)	0.96 ± 0.28 (2)	1.04 ± 0.19 (2)	1.09 ± 0.12 (2)
	Strubel	0.73 ± 0.33 (2)	0.76 ± 0.32 (2)	1.08 ± 0.23 (2)	1.10 ± 0.17 (2)
Unstocked	Dog Leg	0.65 (1)	1.27 ± 0.38 (3)	1.28 ± 0.35 (3)	1.30 ± 0.38 (3)
	Gas Plant	-	0.91 ± 0.29 (2)	0.93 ± 0.40 (2)	1.11 ± 0.24 (2)
	Gun Range	0.50 (1)	1.31 ± 0.55 (2)	1.30 ± 0.37 (2)	1.27 ± 0.50 (2)
	Picard	0.46 (1)	0.96 ± 0.16 (2)	0.91 ± 0.35 (2)	0.99 ± 0.25 (2)
	Teal	0.87 ± 0.42 (2)	0.91 ± 0.29 (2)	1.03 ± 0.16 (2)	1.07 ± 0.25 (2)
Fishless	Conundrum	n/a	1.52 ± 0.50 (2)	1.31 ± 0.63 (2)	1.39 ± 0.70 (2)
	Dog Paw	0.80 ± 0.38 (2)	1.53 ± 0.86 (2)	1.28 ± 0.59 (2)	1.33 ± 0.67 (2)
	Speedy	0.57 (1)	1.69 ± 0.76 (2)	1.12 ± 0.19 (3)	1.32 ± 0.46 (3)

Table B-12 Mean ±SE (n) cyclopoid taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	1.06 ± 0.30 (3)	0.98 ± 0.11 (3)	0.87 ± 0.15 (3)	0.81 ± 0.15 (3)
	Birch	1.05 ± 0.27 (3)	0.81 ± 0.20 (2)	0.90 ± 0.18 (3)	0.83 ± 0.28 (2)
	Fiesta	1.05 ± 0.32 (3)	0.77 ± 0.18 (2)	0.80 ± 0.25 (2)	0.86 ± 0.28 (2)
	Ironside	0.95 ± 0.26 (3)	0.80 ± 0.06 (3)	0.83 ± 0.16 (3)	0.82 ± 0.18 (3)
	Mitchell	0.94 ± 0.24 (3)	0.87 ± 0.30 (2)	0.87 ± 0.21 (3)	0.82 ± 0.22 (2)
	Strubel	0.71 ± 0.20 (2)	0.74 ± 0.20 (2)	0.99 ± 0.18 (3)	0.85 ± 0.14 (3)
Unstocked	Dog Leg	1.09 ± 0.39 (3)	0.57 (1)	0.44 (1)	0.72 ± 0.29 (2)
	Gas Plant	1.04 ± 0.32 (3)	0.87 ± 0.25 (2)	0.70 ± 0.26 (2)	0.71 ± 0.23 (2)
	Gun Range	0.75 ± 0.27 (3)	0.84 ± 0.19 (2)	0.88 ± 0.26 (2)	0.88 ± 0.35 (2)
	Picard	0.98 ± 0.29 (3)	0.91 ± 0.28 (3)	0.75 ± 0.28 (2)	0.76 ± 0.27 (2)
	Teal	1.06 ± 0.32 (3)	0.95 ± 0.37 (2)	0.92 ± 0.26 (2)	0.91 ± 0.34 (2)
Fishless	Conundrum	n/a	1.11 ± 0.28 (3)	0.43 (1)	0.40 (1)
	Dog Paw	1.09 ± 0.32 (3)	0.53 (1)	0.42 (1)	1.30 (1)
	Speedy	0.84 ± 0.36 (2)	0.31 (1)	0.74 ± 0.29 (2)	0.71 ± 0.25 (2)

Table B-13 Microcrustacean richness at the lowest feasible taxonomic level in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	5	7	11	8
	Birch	6	7	9	6
	Fiesta	6	7	6	6
	Ironside	7	9	11	8
	Mitchell	6	8	10	4
	Strubel	6	5	7	6
Unstocked	Dog Leg	5	6	6	5
	Gas Plant	4	5	5	4
	Gun Range	5	5	7	4
	Picard	4	10	5	4
	Teal	6	5	6	5
Fishless	Conundrum	n/a	5	6	3
	Dog Paw	4	4	5	6
	Speedy	3	4	6	6

Table B-14 Microcrustacean Shannon-Weiner diversity at the lowest feasible taxonomic level in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.85	1.47	1.97	1.70
	Birch	1.30	1.56	1.72	1.54
	Fiesta	1.37	1.45	1.52	1.36
	Ironside	1.21	1.54	1.81	1.62
	Mitchell	1.17	1.50	1.72	1.32
	Strubel	1.02	1.32	1.48	1.44
Unstocked	Dog Leg	1.49	1.16	1.56	1.01
	Gas Plant	0.85	1.14	1.23	0.20
	Gun Range	0.75	0.44	1.12	1.17
	Picard	1.20	1.69	1.39	1.06
	Teal	1.14	1.13	1.35	1.43
Fishless	Conundrum	n/a	0.68	0.83	1.06
	Dog Paw	1.29	0.86	1.03	1.40
	Speedy	1.10	1.01	1.36	1.35

Table B-15 Microcrustacean evenness (%) at the lowest feasible taxonomic level in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	53	76	82	82
	Birch	72	80	78	86
	Fiesta	77	75	85	76
	Ironside	62	70	75	78
	Mitchell	65	72	75	95
	Strubel	57	82	76	80
Unstocked	Dog Leg	93	65	87	62
	Gas Plant	61	71	76	14
	Gun Range	47	27	58	84
	Picard	86	73	86	76
	Teal	64	70	76	89
Fishless	Conundrum	n/a	43	47	96
	Dog Paw	93	62	64	78
	Speedy	100	73	76	75

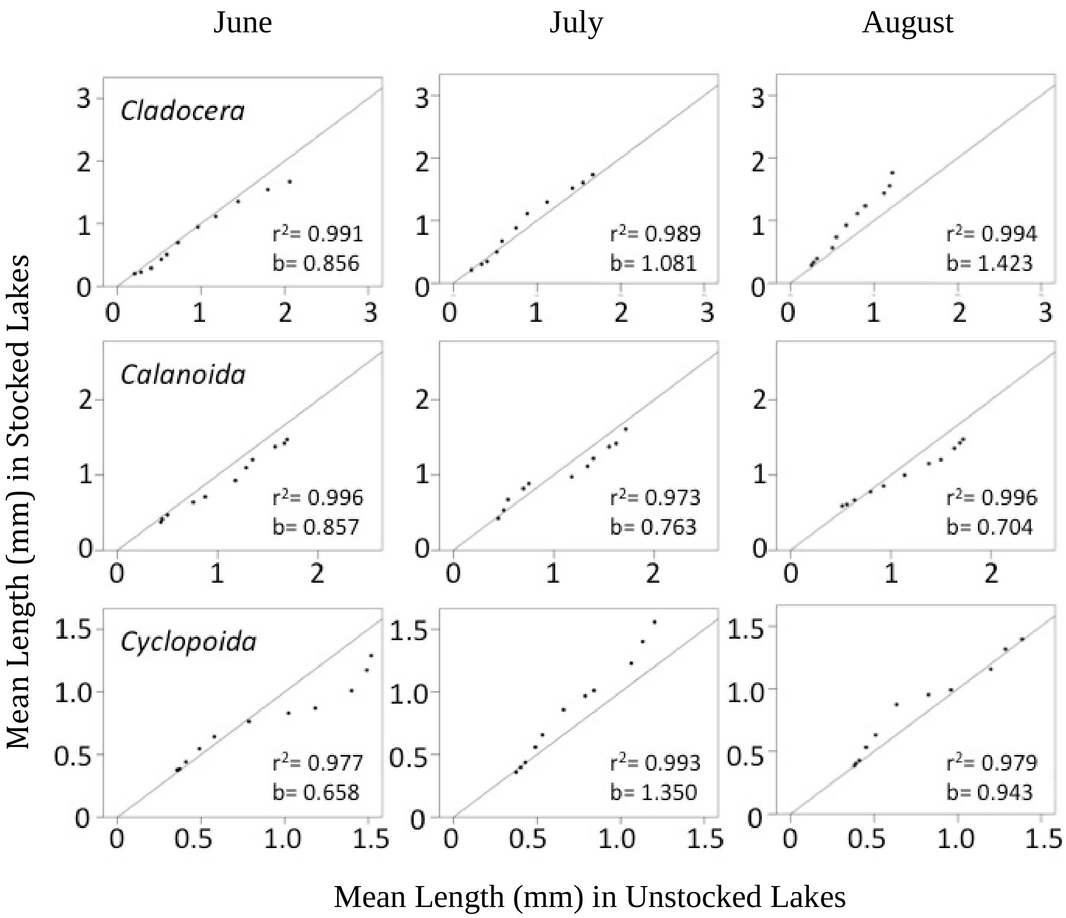


Figure B-1 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between stocked and unstocked lakes for 3 sampling periods in 2009 and 3 taxa. Plots include coefficients of determination (r^2) and slopes (b) from a least squared linear regression. The solid line represents the 1:1 relationship.

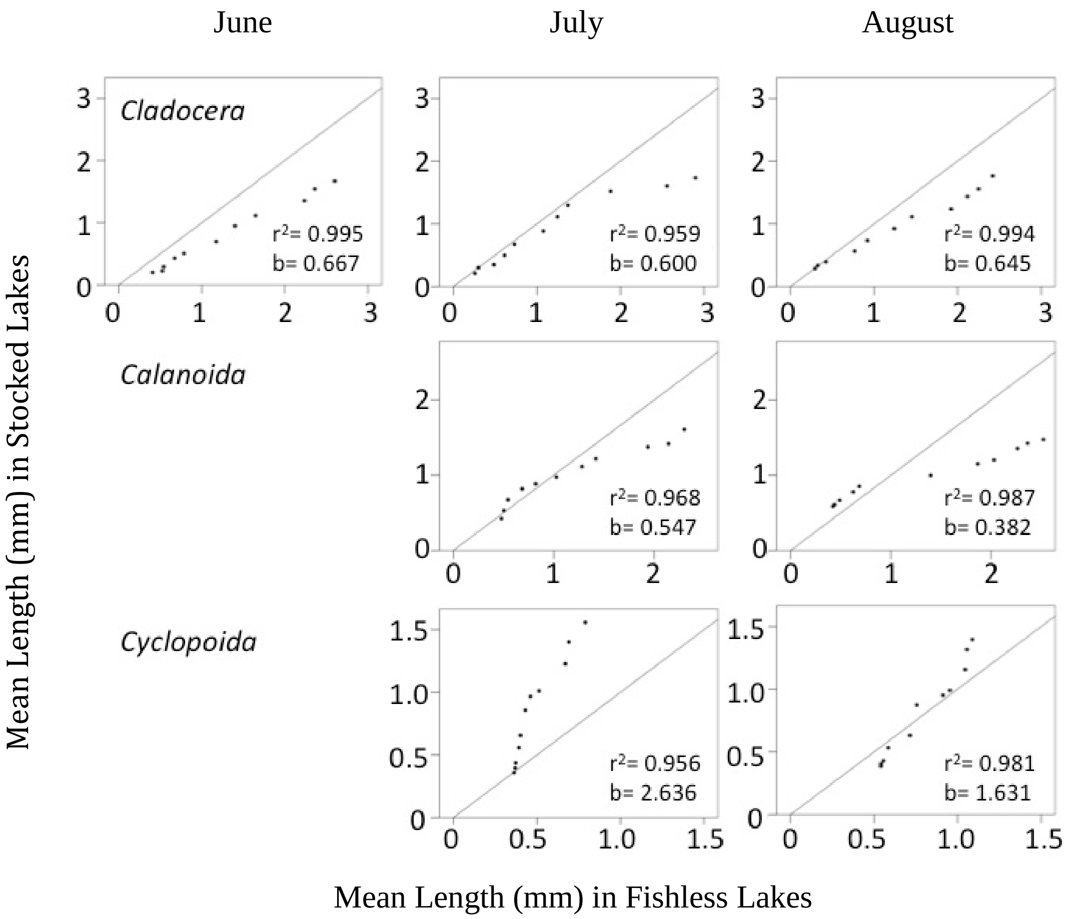


Figure B-2 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between stocked and fishless lakes for three sampling periods in 2009 and three taxa. Plots include coefficients of determination (r^2) and slopes (b) from least squared linear regression. The solid lines represents the 1:1 relationship. Due to the rarity of calanoids and cyclopoids in fishless lakes in June, quantile-quantile plots were not produced.

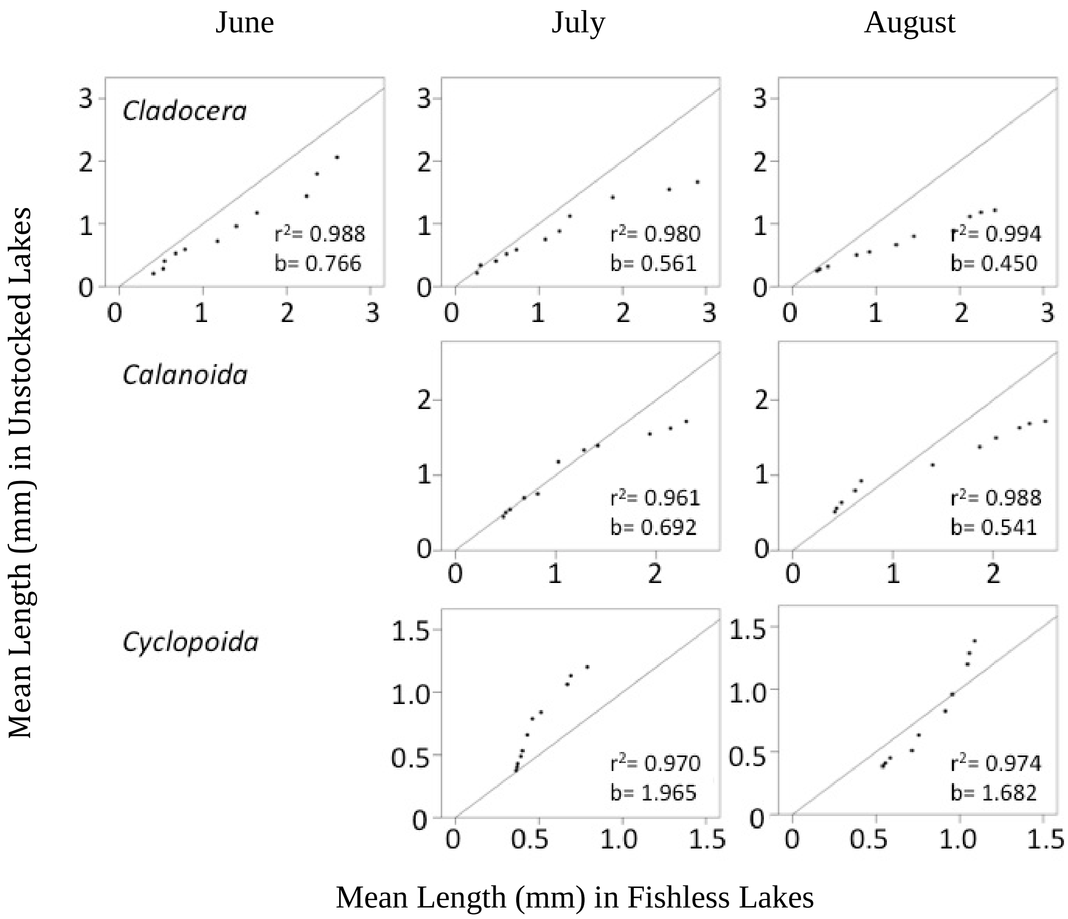


Figure B-3 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between unstocked and fishless lakes for 3 sampling periods in 2009 and 3 taxa. Plots include coefficients of determination (r^2) and slopes (b) from a least squared linear regression. The solid line represents the 1:1 relationship. Due to the rarity of calanoids and cyclopoids in fishless lakes in June, quantile-quantile plots were not produced.

Appendix C: Rotifer Communities

Table C-1 Ploima abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	226.0	46.0	44.2	114.2
	Birch	332.1	943.7	144.2	316.3
	Fiesta	1251.1	760.0	725.6	691.9
	Ironside	478.8	1272.8	805.8	142.3
	Mitchell	659.3	378.1	61.6	181.7
	Strubel	127.9	200.6	48.3	51.8
Unstocked	Dog Leg	521.1	137.0	321.6	475.8
	Gas Plant	119.4	1363.1	2586.1	1721.7
	Gun Range	247.4	78.9	46.7	37.4
	Picard	379.7	333.7	260.3	896.7
	Teal	2382.9	989.7	305.3	490.7
Fishless	Conundrum	n/a	297.4	23.3	144.6
	Dog Paw	22.3	995.9	235.1	40.3
	Speedy	505.5	2290.7	957.8	551.7

Table C-2 Brachionidae abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	48.3	32.6	22.7	22.1
	Birch	139.6	819.3	118.9	248.1
	Fiesta	648.9	614.7	650.2	550.9
	Ironside	233.9	1162.2	762.7	73.2
	Mitchell	526.7	340.0	17.4	112.8
	Strubel	98.0	191.8	33.6	33.6
Unstocked	Dog Leg	101.1	26.2	54.7	343.1
	Gas Plant	80.5	1210.9	2156.2	1582.2
	Gun Range	165.1	60.9	3.8	8.3
	Picard	278.6	318.1	130.8	697.8
	Teal	1499.0	771.0	302.2	433.3
Fishless	Conundrum	n/a	256.5	11.1	81.3
	Dog Paw	18.7	961.4	4.3	1.9
	Speedy	297.6	2124.0	831.4	424.2

Table C-3 Gastropidae abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	2.4	1.6	17.5
	Birch	2.5	83.7	14.5	22.9
	Fiesta	4.4	10.0	66.7	18.7
	Ironside	-	56.4	29.3	67.2
	Mitchell	0.7	4.5	37.6	21.3
	Strubel	0.4	3.6	5.5	8.7
Unstocked	Dog Leg	1.7	0.8	17.2	22.0
	Gas Plant	2.2	2.2	136.2	54.4
	Gun Range	1.3	0.1	37.1	4.6
	Picard	2.9	2.8	32.4	141.5
	Teal	-	17.5	0.8	14.5
Fishless	Conundrum	n/a	-	0.3	1.0
	Dog Paw	-	-	9.2	0.2
	Speedy	-	-	1.9	1.2

Table C-4 Lecanidae abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.5	-	0.1	0.4
	Birch	1.0	-	0.7	2.1
	Fiesta	1.1	0.7	0.5	0.6
	Ironside	-	0.6	0.2	0.1
	Mitchell	2.0	0.5	0.9	0.7
	Strubel	0.1	0.1	0.1	0.3
Unstocked	Dog Leg	1.1	0.2	0.1	-
	Gas Plant	0.4	2.2	3.1	2.2
	Gun Range	0.2	0.5	0.02	0.1
	Picard	2.6	4.8	1.4	0.7
	Teal	-	-	0.3	-
Fishless	Conundrum	n/a	0.1	0.1	0.2
	Dog Paw	0.2	1.1	0.05	-
	Speedy	0.4	1.8	0.8	0.7

Table C-5 Synchaetidae abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	177.1	5.8	4.1	67.5
	Birch	188.5	40.7	9.2	40.6
	Fiesta	596.7	130.7	7.3	113.9
	Ironside	244.8	52.5	7.6	1.3
	Mitchell	129.7	9.9	1.2	6.8
	Strubel	29.3	2.4	0.3	7.8
Unstocked	Dog Leg	417.2	109.2	247.8	108.0
	Gas Plant	35.8	144.2	217.0	70.6
	Gun Range	79.6	16.7	5.7	23.4
	Picard	94.0	5.0	88.9	51.4
	Teal	883.8	182.9	1.6	38.1
Fishless	Conundrum	n/a	40.7	11.1	61.4
	Dog Paw	2.8	32.9	221.5	38.1
	Speedy	200.0	164.9	123.1	123.7

Table C-6 *Ascomorpha* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	2.1	0.0	5.2
	Birch	1.0	4.4	13.4	11.3
	Fiesta	-	3.3	1.9	14.8
	Ironside	-	18.3	19.4	65.3
	Mitchell	-	3.4	5.0	10.7
	Strubel	-	1.2	0.1	4.7
Unstocked	Dog Leg	1.7	0.3	1.4	19.8
	Gas Plant	0.1	0.4	51.4	18.3
	Gun Range	0.4	-	37.1	4.3
	Picard	1.9	2.1	0.0	7.1
	Teal	-	4.6	0.1	14.0
Fishless	Conundrum	n/a	-	0.1	1.0
	Dog Paw	-	-	9.2	0.2
	Speedy	-	-	1.7	1.2

Table C-7 *Kellicottia* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	37.2	6.9	3.9	2.9
	Birch	110.8	237.8	21.4	176.0
	Fiesta	47.8	5.3	1.5	43.0
	Ironside	24.8	40.0	7.0	2.6
	Mitchell	418.0	213.9	1.4	64.3
	Strubel	53.7	100.4	6.7	3.3
Unstocked	Dog Leg	2.2	1.3	0.04	0.9
	Gas Plant	1.0	4.9	138.9	1106.1
	Gun Range	0.2	0.5	0.2	1.1
	Picard	1.7	2.1	0.2	0.3
	Teal	74.3	243.8	102.0	95.0
Fishless	Conundrum	n/a	3.1	0.4	0.3
	Dog Paw	3.1	0.4	0.1	0.6
	Speedy	10.2	1.8	1.1	0.3

Table C-8 *Keratella* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	11.0	25.7	18.8	18.8
	Birch	28.8	581.5	97.5	72.1
	Fiesta	595.6	602.7	648.5	508.0
	Ironside	208.5	1122.2	755.7	70.5
	Mitchell	108.3	126.1	16.0	48.5
	Strubel	44.3	91.4	26.9	30.4
Unstocked	Dog Leg	98.9	24.7	54.6	342.2
	Gas Plant	79.1	1205.1	2017.3	476.1
	Gun Range	165.0	59.5	3.6	7.2
	Picard	276.9	315.8	130.0	696.9
	Teal	1381.0	401.5	198.7	338.1
Fishless	Conundrum	n/a	249.3	10.6	81.0
	Dog Paw	8.9	961.1	4.2	1.3
	Speedy	287.1	2122.2	829.7	423.8

Table C-9 *Polyarthra* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	128.1	5.8	4.1	63.8
	Birch	39.6	39.3	9.2	39.0
	Fiesta	346.7	129.3	4.4	111.5
	Ironside	121.2	51.4	7.0	1.0
	Mitchell	79.0	9.9	1.2	6.8
	Strubel	29.2	2.4	0.3	7.8
Unstocked	Dog Leg	7.8	108.9	226.9	73.8
	Gas Plant	2.0	144.2	214.2	69.4
	Gun Range	36.2	16.7	5.7	23.4
	Picard	84.4	5.0	88.5	51.1
	Teal	760.0	182.9	1.6	37.9
Fishless	Conundrum	n/a	39.6	11.1	60.9
	Dog Paw	1.5	32.9	137.9	35.2
	Speedy	189.4	48.4	88.6	88.4

Table C-10 *K. cochlearis* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	7.1	7.4	3.0	13.5
	Birch	2.7	307.4	12.2	44.8
	Fiesta	57.8	179.3	92.6	105.9
	Ironside	27.3	87.5	93.0	20.3
	Mitchell	51.0	113.5	9.7	27.6
	Strubel	32.3	42.2	15.2	14.4
Unstocked	Dog Leg	76.1	2.5	53.2	336.4
	Gas Plant	74.8	1191.1	1724.1	131.7
	Gun Range	6.5	6.0	0.5	3.0
	Picard	268.9	313.2	48.5	96.5
	Teal	192.4	245.3	81.5	219.3
Fishless	Conundrum	n/a	6.0	7.3	1.4
	Dog Paw	0.7	1.8	3.9	0.6
	Speedy	14.9	5.8	0.3	2.1

Table C-11 *K. crassa* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	5.8	1.1	0.6
	Birch	0.8	8.1	78.4	8.1
	Fiesta	-	238.7	551.0	401.9
	Ironside	-	0.3	2.1	0.6
	Mitchell	-	0.1	1.1	1.9
	Strubel	2.8	1.7	9.2	12.2
Unstocked	Dog Leg	5.0	18.9	0.1	0.2
	Gas Plant	-	1.6	1.0	0.6
	Gun Range	47.4	42.0	1.9	2.9
	Picard	0.2	2.1	23.6	10.1
	Teal	-	57.1	28.2	99.0
Fishless	Conundrum	n/a	228.1	1.3	77.1
	Dog Paw	5.6	949.3	0.3	0.8
	Speedy	56.1	2096.4	828.3	420.1

Table C-12 *K. earlinae* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	-	1.5	14.2	0.8
	Birch	8.1	243.0	6.2	19.2
	Fiesta	26.7	97.3	4.6	-
	Ironside	-	421.7	73.3	5.4
	Mitchell	1.3	11.4	4.9	18.9
	Strubel	-	41.8	1.2	0.3
Unstocked	Dog Leg	-	2.0	-	3.6
	Gas Plant	-	4.4	289.4	342.8
	Gun Range	-	5.0	0.6	0.3
	Picard	-	-	48.1	590.3
	Teal	11.4	93.0	88.8	16.0
Fishless	Conundrum	n/a	1.9	1.8	0.1
	Dog Paw	0.1	3.2	-	-
	Speedy	-	-	0.3	0.1

Table C-13 *K. longispina* abundance (individuals/L) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	37.2	6.9	3.9	2.9
	Birch	108.5	220.7	13.9	1.9
	Fiesta	47.8	5.3	1.4	3.7
	Ironside	24.8	40.0	7.0	2.6
	Mitchell	416.7	213.9	1.1	5.1
	Strubel	53.7	100.4	6.7	2.7
Unstocked	Dog Leg	1.1	1.3	-	-
	Gas Plant	0.9	-	-	-
	Gun Range	0.2	0.5	0.1	0.1
	Picard	0.5	2.0	0.2	
	Teal	72.4	243.0	100.1	42.1
Fishless	Conundrum	n/a	2.8	0.03	-
	Dog Paw	3.1	0.4	-	0.1
	Speedy	9.8	1.8	1.1	0.1

Table C-14 Mean (n) Ploima individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	0.149 (95)	0.151 (121)	0.244 (667)	0.121 (145)
	Birch	0.163 (129)	0.097 (124)	0.115 (1024)	0.117 (144)
	Fiesta	0.123 (115)	0.111 (117)	0.112 (494)	0.117 (143)
	Ironside	0.141 (91)	0.122 (134)	0.128 (1393)	0.144 (130)
	Mitchell	0.128 (108)	0.119 (147)	0.113 (782)	0.158 (154)
	Strubel	0.106 (88)	0.113 (150)	0.125 (929)	0.112 (138)
Unstocked	Dog Leg	0.118 (82)	0.099 (120)	0.108 (281)	0.097 (111)
	Gas Plant	0.106 (110)	0.088 (131)	0.106 (331)	0.109 (121)
	Gun Range	0.130 (105)	0.109 (104)	0.107 (482)	0.116 (132)
	Picard	0.107 (114)	0.090 (126)	0.107 (501)	0.102 (133)
	Teal	0.118 (102)	0.105 (145)	0.110 (297)	0.106 (147)
Fishless	Conundrum	n/a	0.107 (138)	0.106 (409)	0.118 (109)
	Dog Paw	0.125 (122)	0.092 (91)	0.123 (328)	0.123 (50)
	Speedy	0.117 (125)	0.100 (81)	0.109 (68)	0.107 (122)

Table C-15 Mean (n) Brachionidae individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.130 (59)	0.123 (73)	0.106 (400)	0.106 (53)
	Birch	0.121 (80)	0.098 (86)	0.115 (591)	0.111 (69)
	Fiesta	0.113 (80)	0.112 (78)	0.113 (246)	0.112 (62)
	Ironside	0.131 (61)	0.123 (76)	0.125 (704)	0.120 (70)
	Mitchell	0.122 (69)	0.113 (62)	0.098 (358)	0.104 (74)
	Strubel	0.108 (68)	0.113 (87)	0.105 (542)	0.108 (72)
Unstocked	Dog Leg	0.103 (48)	0.097 (80)	0.096 (83)	0.089 (44)
	Gas Plant	0.099 (54)	0.087 (80)	0.095 (107)	0.107 (48)
	Gun Range	0.131 (61)	0.112 (75)	0.109 (323)	0.110 (65)
	Picard	0.100 (43)	0.089 (52)	0.102 (236)	0.100 (51)
	Teal	0.113 (72)	0.104 (84)	0.110 (261)	0.104 (91)
Fishless	Conundrum	n/a	0.107 (114)	0.099 (215)	0.124 (51)
	Dog Paw	0.123 (81)	0.092 (67)	0.094 (111)	0.106 (17)
	Speedy	0.112 (70)	0.099 (47)	0.109 (26)	0.104 (48)

Table C-16 Mean (n) Gastropidae individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled; -: taxa not present.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	-	0.146 (17)	0.110 (63)	0.107 (30)
	Birch	0.134 (12)	0.087 (21)	0.099 (192)	0.099 (30)
	Fiesta	0.119 (4)	0.094 (15)	0.096 (113)	0.100 (30)
	Ironside	-	0.119 (30)	0.135 (328)	0.169 (30)
	Mitchell	0.106 (2)	0.103 (30)	0.098 (180)	0.097 (30)
	Strubel	0.099 (3)	0.110 (25)	0.106 (146)	0.097 (30)
Unstocked	Dog Leg	0.165 (3)	0.107 (11)	0.098 (70)	0.095 (25)
	Gas Plant	0.109 (16)	0.099 (10)	0.096 (72)	0.095 (30)
	Gun Range	0.126 (7)	0.101 (1)	0.106 (36)	0.158 (25)
	Picard	0.125 (17)	0.089 (21)	0.100 (61)	0.099 (30)
	Teal	-	0.091 (22)	0.110 (9)	0.102 (20)
Fishless	Conundrum	n/a	-	0.107 (40)	0.144 (16)
	Dog Paw	-	-	0.153 (60)	0.101 (2)
	Speedy	-	-	0.121 (7)	0.167 (11)

Table C-17 Mean (n) Lecanidae individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled; -: taxa not present.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	0.117 (5)	-	0.123 (13)	0.116 (2)
	Birch	0.117 (5)	-	0.119 (73)	0.116 (10)
	Fiesta	0.101 (1)	0.091 (1)	0.134 (10)	0.130 (4)
	Ironside	-	0.111 (3)	0.109 (28)	0.111 (2)
	Mitchell	0.113 (6)	0.117 (8)	0.123 (76)	0.105 (5)
	Strubel	0.106 (1)	0.121 (1)	0.123 (18)	0.131 (4)
Unstocked	Dog Leg	0.121 (2)	0.093 (3)	0.126 (2)	-
	Gas Plant	0.125 (5)	0.095 (10)	0.116 (9)	0.129 (4)
	Gun Range	0.121 (1)	0.101 (5)	0.109 (5)	0.111 (3)
	Picard	0.123 (15)	0.105 (18)	0.115 (29)	0.123 (5)
	Teal	-	-	0.118 (3)	-
Fishless	Conundrum	n/a	0.087 (1)	0.125 (12)	0.125 (3)
	Dog Paw	0.125 (3)	0.106 (6)	0.105 (4)	-
	Speedy	0.141 (1)	0.101 (4)	0.104 (3)	0.108 (6)

Table C-18 Mean (n) Synchaetidae individual length (mm) in each sampling period for each lake in 2009. Means are calculated as weighted means of individual taxa identified down to the lowest feasible taxonomic level and are weighted according to their relative abundance within a sample. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.154 (30)	0.114 (15)	0.108 (92)	0.110 (30)
	Birch	0.195 (30)	0.096 (17)	0.102 (129)	0.132 (23)
	Fiesta	0.134 (30)	0.108 (17)	0.117 (99)	0.119 (29)
	Ironside	0.151 (30)	0.109 (19)	0.098 (157)	0.123 (20)
	Mitchell	0.153 (30)	0.106 (15)	0.100 (74)	0.104 (15)
	Strubel	0.098 (16)	0.112 (15)	0.100 (38)	0.109 (15)
Unstocked	Dog Leg	0.121 (29)	0.099 (19)	0.111 (90)	0.117 (30)
	Gas Plant	0.121 (30)	0.092 (15)	0.112 (61)	0.118 (17)
	Gun Range	0.127 (30)	0.094 (15)	0.111 (106)	0.099 (16)
	Picard	0.128 (30)	0.093 (15)	0.107 (68)	0.113 (17)
	Teal	0.126 (30)	0.094 (15)	0.108 (18)	0.107 (18)
Fishless	Conundrum	n/a	0.102 (23)	0.102 (62)	0.107 (25)
	Dog Paw	0.143 (30)	0.080 (15)	0.122 (150)	0.124 (30)
	Speedy	0.122 (31)	0.107 (30)	0.110 (30)	0.115 (40)

Table C-19 Mean ±SE (n) Ploima taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	0.145 ± 0.019 (11)	0.151 ± 0.027 (10)	0.169 ± 0.023 (24)	0.164 ± 0.030 (15)
	Birch	0.127 ± 0.008 (15)	0.105 ± 0.008 (10)	0.150 ± 0.019 (26)	0.151 ± 0.039 (12)
	Fiesta	0.119 ± 0.006 (10)	0.150 ± 0.022 (16)	0.148 ± 0.017 (23)	0.154 ± 0.027 (14)
	Ironside	0.128 ± 0.010 (7)	0.162 ± 0.029 (14)	0.136 ± 0.016 (22)	0.155 ± 0.024 (13)
	Mitchell	0.123 ± 0.007 (14)	0.135 ± 0.013 (17)	0.141 ± 0.016 (20)	0.149 ± 0.030 (13)
	Strubel	0.106 ± 0.004 (9)	0.121 ± 0.009 (12)	0.141 ± 0.014 (22)	0.152 ± 0.023 (14)
Unstocked	Dog Leg	0.123 ± 0.006 (10)	0.119 ± 0.011 (17)	0.147 ± 0.022 (13)	0.135 ± 0.028 (10)
	Gas Plant	0.130 ± 0.007 (19)	0.128 ± 0.015 (18)	0.163 ± 0.021 (19)	0.155 ± 0.021 (16)
	Gun Range	0.134 ± 0.009 (12)	0.154 ± 0.032 (16)	0.136 ± 0.011 (21)	0.150 ± 0.023 (16)
	Picard	0.126 ± 0.008 (17)	0.148 ± 0.029 (16)	0.152 ± 0.015 (29)	0.155 ± 0.018 (19)
	Teal	0.126 ± 0.009 (9)	0.131 ± 0.021 (13)	0.136 ± 0.014 (14)	0.151 ± 0.025 (14)
Fishless	Conundrum	n/a	0.116 ± 0.008 (13)	0.154 ± 0.015 (23)	0.152 ± 0.021 (15)
	Dog Paw	0.126 ± 0.007 (14)	0.122 ± 0.018 (11)	0.123 ± 0.008 (14)	0.106 ± 0.008 (8)
	Speedy	0.135 ± 0.006 (14)	0.099 ± 0.004 (8)	0.119 ± 0.008 (15)	0.153 ± 0.021 (18)

Table C-20 Mean ±SE (n) Brachionidae taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.125 ± 0.009 (4)	0.118 ± 0.009 (5)	0.133 ± 0.015 (8)	0.118 ± 0.007 (6)
	Birch	0.114 ± 0.005 (7)	0.101 ± 0.004 (6)	0.117 ± 0.006 (7)	0.109 ± 0.005 (5)
	Fiesta	0.116 ± 0.007 (6)	0.132 ± 0.014 (7)	0.128 ± 0.013 (8)	0.116 ± 0.008 (5)
	Ironside	0.119 ± 0.007 (5)	0.115 ± 0.007 (6)	0.117 ± 0.007 (7)	0.120 ± 0.009 (6)
	Mitchell	0.115 ± 0.006 (7)	0.121 ± 0.008 (6)	0.113 ± 0.006 (6)	0.110 ± 0.006 (5)
	Strubel	0.107 ± 0.006 (5)	0.115 ± 0.008 (6)	0.126 ± 0.013 (7)	0.115 ± 0.007 (6)
Unstocked	Dog Leg	0.118 ± 0.006 (6)	0.111 ± 0.010 (8)	0.109 ± 0.007 (4)	0.106 ± 0.005 (5)
	Gas Plant	0.132 ± 0.013 (7)	0.111 ± 0.010 (7)	0.115 ± 0.007 (6)	0.112 ± 0.008 (5)
	Gun Range	0.118 ± 0.007 (5)	0.126 ± 0.012 (7)	0.132 ± 0.011 (8)	0.117 ± 0.005 (6)
	Picard	0.125 ± 0.007 (6)	0.119 ± 0.013 (6)	0.128 ± 0.011 (8)	0.111 ± 0.006 (5)
	Teal	0.119 ± 0.005 (7)	0.109 ± 0.005 (8)	0.116 ± 0.005 (7)	0.119 ± 0.009 (7)
Fishless	Conundrum	n/a	0.116 ± 0.009 (10)	0.134 ± 0.012 (9)	0.116 ± 0.010 (5)
	Dog Paw	0.115 ± 0.007 (7)	0.102 ± 0.006 (6)	0.127 ± 0.013 (6)	0.108 ± 0.006 (4)
	Speedy	0.122 ± 0.007 (7)	0.097 ± 0.005 (4)	0.130 ± 0.015 (7)	0.114 ± 0.006 (8)

Table C-21 Mean ±SE (n) Gastropidae taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	-	0.128 ± 0.022 (2)	0.115 ± 0.006 (2)	0.110 ± 0.009 (2)
	Birch	0.138 ± 0.027 (2)	0.089 ± 0.002 (2)	0.098 ± 0.001 (2)	0.099 ± 0.001 (2)
	Fiesta	0.119 (1)	0.092 ± 0.006 (2)	0.099 ± 0.003 (2)	0.099 ± 0.000 (2)
	Ironside	-	0.126 ± 0.020 (2)	0.128 ± 0.022 (2)	0.138 ± 0.033 (2)
	Mitchell	0.106 (1)	0.105 ± 0.004 (2)	0.096 ± 0.003 (2)	0.097 ± 0.003 (2)
	Strubel	0.099 (1)	0.110 ± 0.003 (2)	0.112 ± 0.007 (2)	0.097 ± 0.002 (2)
Unstocked	Dog Leg	0.165 (1)	0.111 ± 0.014 (2)	0.112 ± 0.017 (2)	0.094 ± 0.001 (2)
	Gas Plant	0.120 ± 0.011 (2)	0.102 ± 0.004 (2)	0.098 ± 0.005 (2)	0.095 ± 0.000 (2)
	Gun Range	0.136 ± 0.025 (2)	0.101 (1)	0.098 ± 0.008 (2)	0.130 ± 0.031 (2)
	Picard	0.121 ± 0.012 (2)	0.086 ± 0.005 (2)	0.105 ± 0.006 (2)	0.106 ± 0.009 (2)
	Teal	-	0.097 ± 0.011 (2)	0.137 ± 0.035 (2)	0.104 ± 0.003 (2)
Fishless	Conundrum	n/a	-	0.113 ± 0.016 (2)	0.124 ± 0.023 (2)
	Dog Paw	-	-	0.153 (1)	0.101 (1)
	Speedy	-	-	0.109 ± 0.018 (2)	0.167 (1)

Table C-22 Mean ±SE (n) Lecanidae taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled; -: taxa not present.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.114 ± 0.012 (4)	-	0.114 ± 0.009 (7)	0.116 ± 0.005 (2)
	Birch	0.114 ± 0.003 (3)	-	0.124 ± 0.012 (8)	0.123 ± 0.008 (2)
	Fiesta	0.101 (1)	0.091 (1)	0.129 ± 0.008 (5)	0.128 ± 0.007 (2)
	Ironside	-	0.111 (1)	0.115 ± 0.006 (4)	0.111 (1)
	Mitchell	0.113 ± 0.006 (3)	0.120 ± 0.009 (4)	0.118 ± 0.004 (5)	0.108 ± 0.007 (3)
	Strubel	0.106 (1)	0.121 (1)	0.124 ± 0.005 (6)	0.125 ± 0.013 (2)
Unstocked	Dog Leg	0.121 (1)	0.093 (1)	0.126 (1)	-
	Gas Plant	0.126 ± 0.005 (3)	0.089 ± 0.015 (2)	0.117 ± 0.004 (2)	0.136 ± 0.015 (2)
	Gun Range	0.121 (1)	0.099 ± 0.004 (3)	0.111 ± 0.006 (3)	0.111 (1)
	Picard	0.123 ± 0.002 (3)	0.105 ± 0.000 (2)	0.122 ± 0.003 (6)	0.127 ± 0.007 (3)
	Teal	-	-	0.121 ± 0.010 (2)	-
Fishless	Conundrum	n/a	0.087 (1)	0.130 ± 0.013 (4)	0.125 ± 0.003 (3)
	Dog Paw	0.125 ± 0.009 (3)	0.110 ± 0.006 (2)	0.106 ± 0.015 (2)	-
	Speedy	0.141 (1)	0.103 ± 0.003 (2)	0.104 ± 0.012 (3)	0.108 (1)

Table C-23 Mean ±SE (n) Synchaetidae taxon length (mm) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	0.190 (2)	0.114 (1)	0.115 (2)	0.141 (2)
	Birch	0.167 (2)	0.133 (2)	0.139 (3)	0.124 (2)
	Fiesta	0.138 (2)	0.134 (2)	0.120 (2)	0.135 (2)
	Ironside	0.151 (2)	0.140 (2)	0.118 (2)	0.130 (2)
	Mitchell	0.163 (2)	0.106 (1)	0.111 (2)	0.104 (1)
	Strubel	0.107 (2)	0.112 (1)	0.100 (1)	0.109 (1)
Unstocked	Dog Leg	0.116 (2)	0.111 (2)	0.128 (2)	0.124 (2)
	Gas Plant	0.113 (2)	0.092 (1)	0.129 (3)	0.137 (2)
	Gun Range	0.124 (2)	0.094 (1)	0.116 (2)	0.110 (2)
	Picard	0.176 (2)	0.093 (1)	0.198 (3)	0.150 (2)
	Teal	0.152 (2)	0.094 (1)	0.108 (1)	0.131 (2)
Fishless	Conundrum	n/a	0.129 (2)	0.132 (2)	0.129 (2)
	Dog Paw	0.146 (2)	0.080 (1)	0.126 (2)	0.127 (2)
	Speedy	0.140 (3)	0.100 (2)	0.115 (2)	0.131 (3)

Table C-24 Rotifer lowest feasible taxonomic level (often species but sometimes genus) richness in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	12	13	23	17
	Birch	17	13	26	14
	Fiesta	12	19	27	17
	Ironside	7	17	20	15
	Mitchell	16	18	20	14
	Strubel	11	14	20	15
Unstocked	Dog Leg	12	19	14	12
	Gas Plant	19	19	19	17
	Gun Range	14	17	17	18
	Picard	20	19	30	19
	Teal	11	16	16	17
Fishless	Conundrum	n/a	15	27	17
	Dog Paw	15	13	14	9
	Speedy	14	10	17	20

Table C-25 Rotifer lowest feasible taxonomic level (often species but sometimes genus) Shannon-Weiner diversity in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	Lake	May	June	July	August
Stocked	Beaver	1.18	2.05	1.66	1.77
	Birch	1.47	1.76	1.60	1.53
	Fiesta	1.60	1.91	1.08	1.45
	Ironside	1.57	1.57	1.03	1.40
	Mitchell	1.31	1.18	1.59	1.96
	Strubel	1.61	1.51	1.83	1.98
Unstocked	Dog Leg	1.16	1.17	1.09	1.07
	Gas Plant	1.07	0.94	1.44	1.28
	Gun Range	1.55	1.59	0.77	1.68
	Picard	1.06	0.41	1.81	1.11
	Teal	1.47	2.18	1.93	1.76
Fishless	Conundrum	n/a	0.91	1.68	1.21
	Dog Paw	1.94	0.39	0.60	0.20
	Speedy	1.36	0.71	0.58	0.79

Table C-26 Rotifer lowest feasible taxonomic level (often species but sometimes genus) evenness (%) in each sampling period for each lake in 2009. n/a: lake not sampled.

Lake Type	**Lake**	**May**	**June**	**July**	**August**
Stocked	Beaver	47	80	53	62
	Birch	52	69	49	58
	Fiesta	64	65	33	51
	Ironside	81	55	34	52
	Mitchell	47	41	53	74
	Strubel	67	57	61	73
Unstocked	Dog Leg	47	40	41	43
	Gas Plant	36	32	49	45
	Gun Range	59	56	27	58
	Picard	35	14	53	38
	Teal	61	79	70	62
Fishless	Conundrum	n/a	34	51	43
	Dog Paw	72	15	23	9
	Speedy	52	31	20	26

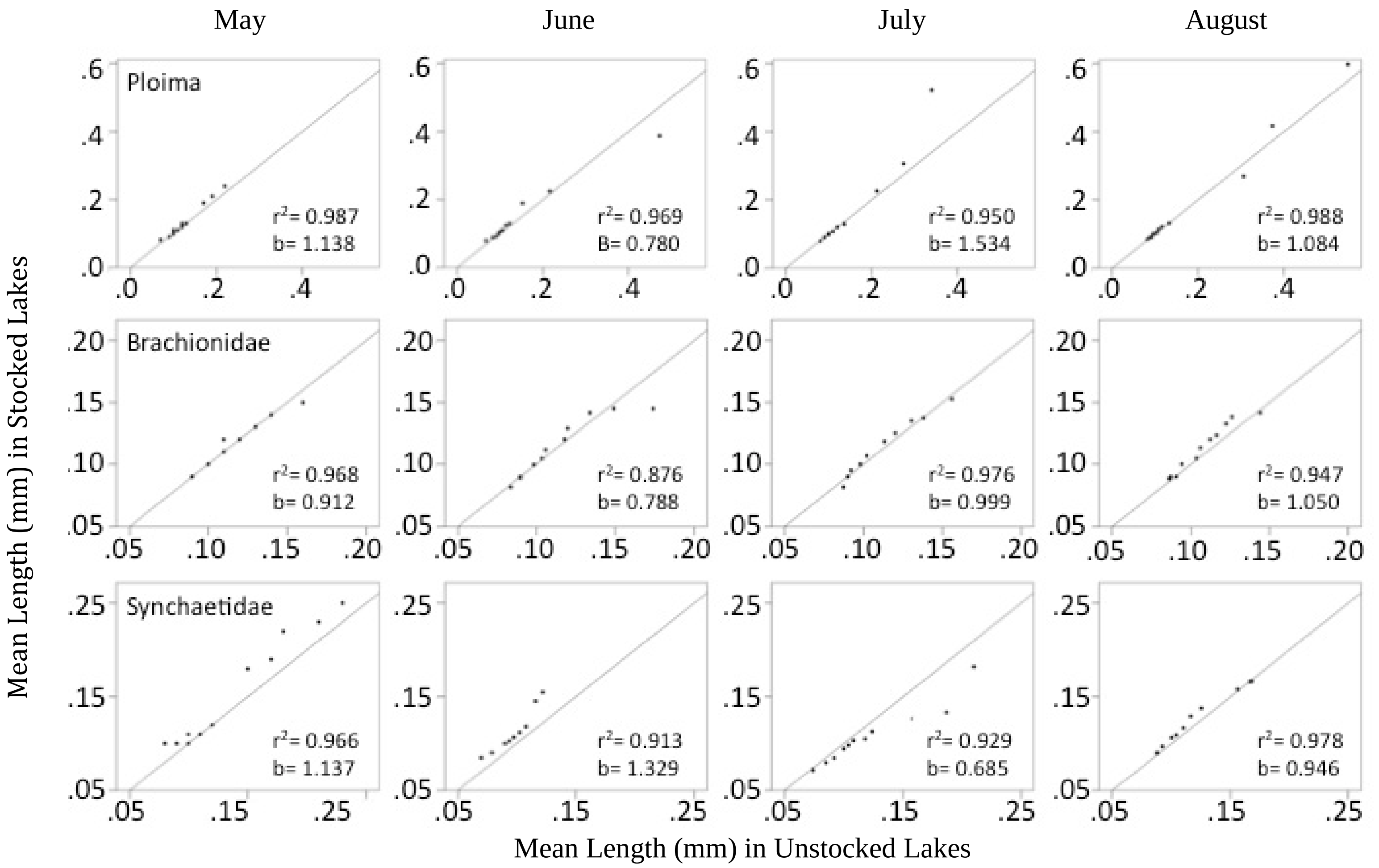


Figure C-1 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between stocked and unstocked lakes for the four sampling periods in 2009 and three taxa. Plots include coefficients of determination (r^2) and slopes (b) from a least squared linear regression. The solid line represents the 1:1 relationship.

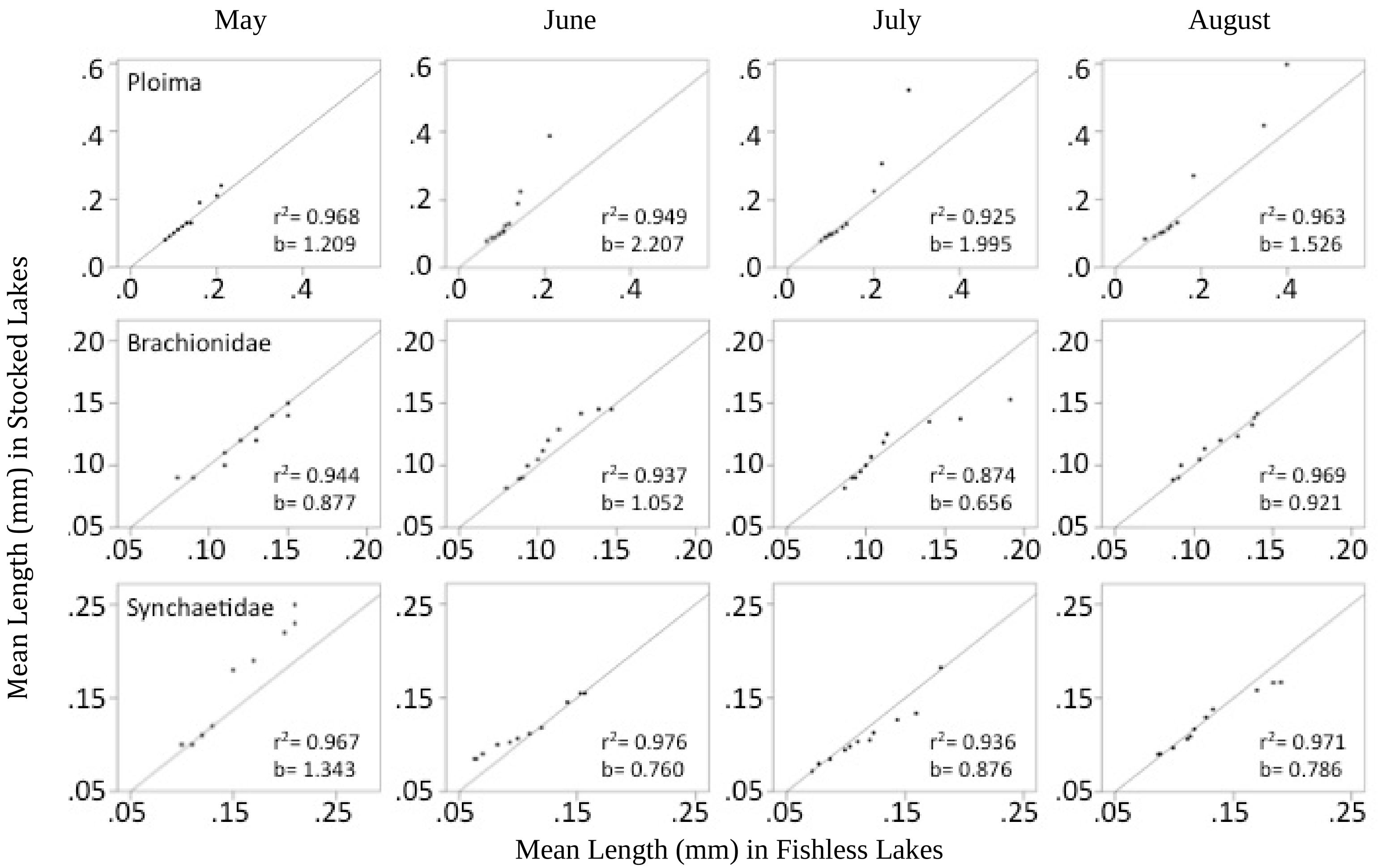


Figure C-2 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between stocked and fishless lakes for the four sampling periods in 2009 and three taxa. Plots include coefficients of determination (r^2) and slopes (b) from a least squared linear regression. The solid line represents the 1:1 relationship.

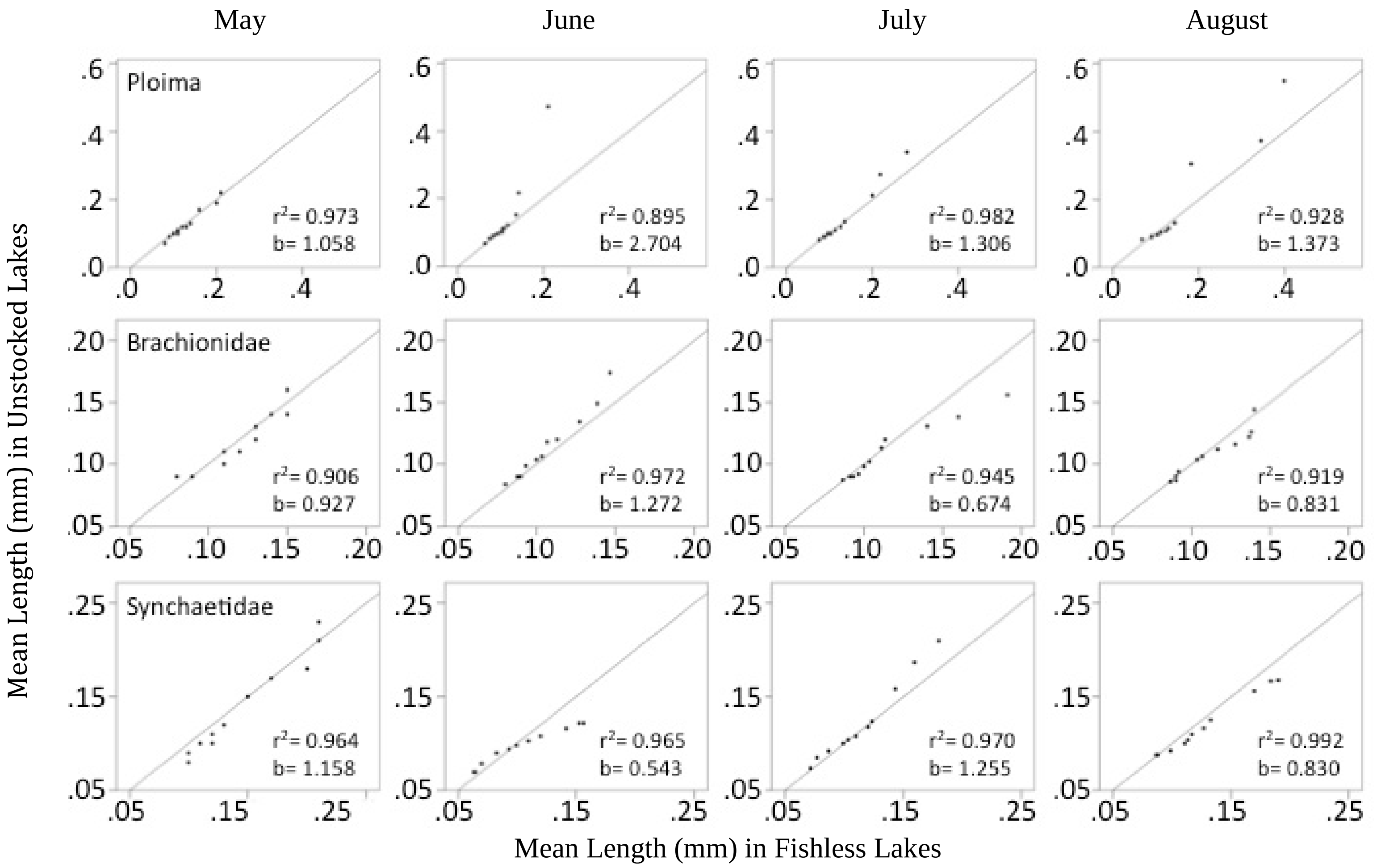


Figure C-3 Quantile-quantile plots comparing mean lengths at 11 quantiles (see text) between unstocked and fishless lakes for the four sampling periods in 2009 and three taxa. Plots include coefficients of determination (r^2) and slopes (b) from a least squared linear regression. The solid line represents the 1:1 relationship.