University of Alberta

Food web interactions of waterbirds and fish in eutrophic wetlands of Alberta's Aspen Parkland

by

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Abstract

Studies on competition between fish and waterbirds have typically involved large-bodied fish and oligotrophic aquatic ecosystems. In eutrophic systems, small-bodied fish such as fathead minnow (*Pimephales promelas*) may also compete with waterbirds for invertebrate prey, thereby reducing the viability of waterbird breeding habitats like Aspen Parkland. Such wetlands are often disturbed by drought and winter hypoxia, making distributions of fish in pothole wetlands highly variable. Relationships between waterbirds, fish and invertebrates in the Aspen Parkland of North America are largely unknown, despite the importance of these regions for breeding waterbirds. My research showed that abiotic factors such as nutrient status of wetlands were important determinants of waterbird and invertebrate assemblage compositions in Aspen Parkland, and that invertebrate assemblages differed among wetlands with and without fish. An observational study showed that low densities of fathead minnow and brook stickleback (*Culaea inconstans*), reduced numbers but not biomasses of some invertebrate prey of two waterbird species, Red-necked Grebe and Blue-winged Teal. Unlike previous studies, birds' foraging activities were unaffected by fish, but Blue-winged Teal were generally less abundant on wetlands with fish than fishless wetlands. Experimental addition of fish, followed by natural winterkill of added fish, induced increases in Blue-winged Teal foraging activities that did not reverse when fish were extirpated. Herbivorous invertebrates (gastropods) were also reduced in the presence of added fish, but increased in biomass when fish were extirpated. Fish had no effect on Red-necked Grebe foraging activities or abundance, but stable isotope analysis revealed that grebes obtained resources for egg production at a higher trophic level in the presence of these

fish than in their absence. Conversely, American Coot, being more herbivorous than Red-necked Grebe, generally obtained egg resources by foraging at a lower trophic level in the presence of fish. Longer-term studies that monitor Aspen Parkland waterbird-fish-invertebrate relationships during wet years would allow managers to make decisions based on knowing the point at which fish become an important biotic factor in determining waterbird habitat quality. Land-use activities that alter the incidence of winterkill of fish, such as wetland consolidation, should be discouraged.

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Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction and Review of Waterbird-Fish Interactions

1.1 Introduction

Competition for food between waterbirds and fishes has been examined extensively under the umbrella of acid precipitation studies in oligotrophic lakes where fish were extirpated or their densities greatly reduced (e.g., Eriksson 1979, Eadie and Keast 1982, Eriksson 1984, Pehrsson 1984, Bendell and McNicol 1995). In these systems many species of waterbird appeared to benefit from fish extirpations if they could exploit nektonic invertebrates such as dytiscids, hemipterans and chaoborids, that increased after the fish disappeared, and did not rely solely on acid-sensitive invertebrates such as molluscs. These findings suggested that waterbirds might also benefit from biomanipulations in hypereutrophic lakes, where fish are removed to try to reduce nuisance algae (Bergman et al. 1999). In hypereutrophic systems, removal of fish results in increased grazing pressure on algae by zooplankton, and decreased turbidity that encourages macrophyte development. Consequent increases in macroinvertebrates can lead to increased use of hypereutrophic lakes by waterbirds (Hanson and Butler 1994, Andersson and Nilsson 1999).

However, not all waterbirds in acidified lakes can switch prey, and the methods used in biomanipulations, such as poisoning lakes with rotenone or toxaphene, can be detrimental to invertebrates that waterbirds might rely upon (Miskimmin and Schindler 1994). Recent studies of fish colonizations and studies that involve adding fish to mesocosms may provide more unequivocal evidence for effects of fish on invertebrates and hence on breeding waterbirds, particularly in poorly studied systems that are rich in waterbirds, such as the wetlands of North America's Aspen Parkland on which my research focuses.

Below, I review our current understanding of waterbird-fish competition as obtained from acid precipitation studies and the more limited information on the outcomes of biomanipulations for waterbirds. As a prelude to my own research on waterbird-fish competition in North America's Aspen Parkland, I suggest different ways of studying waterbird-fish competition based on adding fish to waterbodies instead of removing them. These new methods, which include monitoring waterbird foraging behaviour and invertebrates following additions of fish, may provide more useful baseline information to wetland managers on the effects of fish on waterbirds and their invertebrate prey than traditional diet studies or fish removals, both of which are costly, invasive and labour-intensive.

1.2 Methods

This review is based on a literature search in Cambridge Scientific Abstracts and the Web of Science databases. The literature for acid precipitation and biomanipulations is extensive, and so the focus was almost exclusively on those studies that dealt directly with waterbirds, or those whose findings could be feasibly extrapolated to waterbird-fish competition, particularly for breeding birds and their young that are more likely to compete with fish for invertebrate protein than wintering birds. A search for studies that had been performed in Europe and North America covered as broad a range of biomes as possible. Because biomanipulation was not a widely used or well-developed technique before 1975, and since acid precipitation began to be a serious issue at that point, searches were restricted to 1975 or after. Because there are many studies that repeat the information presented here, this review cites a subset of about 50 references that most comprehensively covered the findings of the 388 studies I found.

1.3 Acid Rain Is Good for Ducks?

The first studies of waterbird-fish competition on oligotrophic, poorly buffered lakes focused purely on the interactions between fish, waterbirds and invertebrates, without really delving into the role of pH in these interactions (Table 1.1). Eriksson (1978, 1979) showed that Common Goldeneye (*Bucephala clangula*) used fishless oligotrophic lakes in southwest Sweden more than oligotrophic lakes with Eurasian perch (*Perca fluviatilis*) or roach (*Rutilus rutilus*). Odonates and dytiscid beetles were less abundant in oligotrophic lakes with fish and Goldeneye increased their use of a lake from which fish were removed (Eriksson 1978, 1979). In eastern Canada, another region that supported many acid precipitation studies, Eadie and Keast (1982) suggested that Goldeneye-perch interactions in oligotrophic lakes were similar over large geographic areas. These authors found 80% diet overlap between Goldeneye ducklings and yellow perch (*P. flavescens*) based on prey size, and 71% overlap for prey types (mostly Ephemeroptera nymphs).

Some of the lakes involved in the above studies had declining fish populations due to acidification and would later be studied in that context (Eriksson 1987). Pehrsson (1984) found that Mallard (*Anas platyrhynchos*) pair densities were higher in Swedish oligotrophic lakes that were losing fish due to acidification. Imprinted ducklings obtained more food when released into fishless lakes than into lakes with fish. Fishless lakes had significantly more and larger invertebrates than lakes with fish. The larger size of these invertebrates in the absence of fish was most likely due to the selection for larger prey items by perch, roach and northern pike (*Esox lucius*) (Pehrsson 1984).

Eriksson (1983) suggested that dabbling ducks such as Mallard and Green-winged Teal (*Anas crecca*) did not compete directly with fish in the lakes of southwest Sweden. Fish predation on invertebrates might even indirectly benefit dabblers, if invertebrates seek refuge from fish on the edges of lakes where the dabbling ducks feed. The inherent assumption of Eriksson's (1983) conclusion is that fish only cause a change in invertebrate distributions/numbers and not in their species composition. However, Pehrsson's (1984) evidence of Mallard-fish competition in the same lakes in southwest Sweden (above) suggested that Eriksson's (1983) assumption was incorrect. Later studies in unrelated systems have also shown that indirect benefits to generalist dabblers from fish would not stem from a change in invertebrate distribution, but from increased invertebrate diversity that is created if fish are eating competitively superior invertebrates, thus allowing dabbling duck prey to coexist with them. For example, Batzer et al. (2000) showed that chironomids, an important prey source for dabbling ducks (Street 1977), are sometimes more abundant in the presence of fish because the fish suppress chironomid competitors, such as gastropods, as well as preying on the chironomids themselves.

The Swedish oligotrophic lakes in which some of the above competition studies had been performed were good candidates for liming to restore fish stocks (Eriksson 1987), but different waterbird species responded differently to both acidification and liming (Eriksson 1984, 1987). Common Goldeneye were thought to benefit from acidification because they could exploit aquatic insects that expanded into the open water following fish extirpation (Eriksson 1984) and were less dense after liming than before (Eriksson 1987). Mallard and Teal were thought to be relatively unaffected since they did not appear to compete with fish (Eriksson 1983, 1984). However, Eriksson (1987) found a negative correlation between Mallard densities and fish densities in limed and unlimed acid lakes. Dabbling ducks were not apparently affected directly by liming. Rather, Eriksson's (1987) study showed that dabblers responded to changes in lake pH via their interactions with fish.

In eastern Canada, DesGranges and Rodrigue (1986) found that Common Goldeneye and Black Duck ducklings (*Anas rubripes*) spent less time feeding and gained weight faster on acidic lakes from which brook trout (*Salvelinus fontinalis*) were extirpated than they did on acidic lakes to which these fish were added. Hunter et al. (1986) showed that Black Duck ducklings grew faster and spent less time searching for food on fishless acidified lakes than on circumneutral lakes with fish. Ducklings on fish lakes showed greater dietary (50-70%) similarity with fish than with ducklings on fishless lakes (38-50%). Bendell and McNicol (1995) found that ducklings of a variety of diving and dabbling species ate significantly more nektonic invertebrates on fishless lakes than on lakes with fish, each species adjusting to the loss of acid-sensitive prey. Similarly to the Swedish systems, these studies implied a positive effect of acidification on waterbirds, mediated by loss of fish, and this was supported by fish-invertebrate studies. For example, Bendell and McNicol (1987) showed that fishless lakes supported nekton-dominant assemblages of invertebrates, including dytiscid beetles, notonectids, corixids and chaoborids, irrespective of pH. Thus, the differences seen in lakes of high and low pH were more closely linked to fish predation on invertebrates than to pH itself, which of course decreased as fish populations declined when pH fell.

This latter conclusion, along with Eriksson's (1987) finding that dabbling ducks responded to pH changes via their interactions with fish rather than lake liming, suggests that direct competition between fish and waterbirds in oligotrophic lakes is so strong that it masks any direct effects of pH change on waterbirds. If the birds respond most directly to changes in fish densities, manipulating fish populations may be a useful method of managing waterbirds. Although Eriksson (1987) did not monitor invertebrates, earlier studies (e.g., Eriksson 1978, 1979, Eadie and Keast 1982; Table 1.1) allow us to suggest that competition with fish for invertebrates is the pivotal biotic factor that mediates the effects of pH changes on waterbirds. Results of long-term studies of restored lakes in Scandinavia indicate that recovery of perch results in reductions of macroinvertebrates and in Goldeneye duckling abundance (e.g., Rask et al. 2001).

However, not all waterbirds benefit from fish extirpations, because not all waterbirds can exploit the nektonic invertebrates that increase when fish are lost (McNicol and Wayland 1992). One critical deleterious effect of acidification in lake systems is the loss of acid-sensitive invertebrates such as clams, snails and crayfish that provide breeding waterfowl and wetland-associated birds with calcium for egg formation (Scheuhammer et al. 1997). Additionally, important waterbird prey such as odonate larvae, notonectids, and gyrinid beetles all had significantly lower calcium content in acid-stressed lakes than in non-stressed lakes (Scheuhammer et al. 1997). Thus, the benefits that acidification might bring via fish extirpation were offset by lowered reproductive successes due to acid-induced calcium deficiencies in waterbird diets.

DesGranges and Rodrigue (1986) also showed that Goldeneye ducklings gained weight faster and spent less time searching for food on circumneutral lakes with fish and fishless acid lakes than on acidic lakes with fish. Thus, increases in nektonic invertebrates following extirpations of fish in acidified lakes (Bendell and McNicol 1987) do not imply that a loss of fish due to acidification is universally good for waterbirds. At some point on the pH scale, the direct negative effects of acidification will replace competition with fish and may outweigh the fish-mediated benefits described above. This change from indirect positive to direct negative effects of acidification on waterbirds occurs most likely below pH 5.3, the point at which molluscs are lost (Scheuhammer et al. 1997). Thus, mitigation techniques such as liming may help restore fish that compete with waterbirds, but this is surely a more favourable outcome than loss of fish and a calcium-deficient prey base for breeding waterbirds.

The study of waterbird-fish interactions in the acid precipitation context demonstrated that competition with fish is detrimental to waterbirds that feed on invertebrates in oligotrophic lakes. Thus, waterbirds might be managed by manipulating fish, particularly since birds appeared to respond more directly to changes in fish densities than to changes in pH induced by mitigation strategies such as liming (Eriksson 1987).

Eadie and Keast's (1982) suggestion that waterbird-fish competition occurs over a broad geographic range was well supported by the above studies. The same general pattern appeared in oligotrophic lakes in Europe and North America (Eriksson 1979, 1984, Eadie and Keast 1982, Pehrsson 1984, Blancher et al. 1992, Bendell and McNicol 1995; Table 1.1) although they supported different fish and waterbird species: fish reduced the abundance of invertebrates such as ephemeropterans and odonates and this was associated with reduced growth rates of ducklings and reduced numbers of waterbirds. The suggestion that loss of fish could benefit waterbirds to some extent could be applied to hypereutrophic systems where fish are often removed in biomanipulations (Bergman et al. 1999). Studies of fish-invertebrate interactions in biomanipulated aquatic ecosystems, and the outcomes for birds that compete with fish in these very productive systems, are reviewed below.

1.4 Biomanipulation and Competition

Anthropogenic nutrient inputs to lakes can lead to eutrophication and toxic algal blooms, and this has prompted removals of planktivorous fish from hypereutrophic lakes in hopes of increasing the grazing rates of large zooplankton on the nuisance algae (see Bergman et al. 1999 and Meijer et al. 1999 for reviews). First developed by Shapiro et al. (1975), biomanipulation takes its rationale from the precursors of trophic cascade theory – removing planktivorous fish reduces predation on grazing zooplankton, allowing these plankters to consume and significantly reduce nuisance algae, which are thus reduced. Removals of benthivorous fish that stir up lake sediments when foraging are also beneficial, resulting in decreased lake turbidity and increased macrophyte development (Scheffer et al. 1993). In shallow lakes, the desired outcome of manipulation is a shift from a turbid, algal-dominated stable state to a clear, macrophyte-dominated stable state (Scheffer et al. 1993) at the same level of primary productivity. This switch results in increased habitat for macroinvertebrates. Although one can extrapolate and suggest that these fish removals, which lead to increases in water clarity, development of macrophyte beds and macroinvertebrate habitat, would benefit waterbirds that rely on macroinvertebrates in eutrophic ecosystems, there have been surprisingly few biomanipulation studies that focus on interactions between fish and waterbirds. A few studies suggest that grazing waterbirds retard macrophyte recovery following biomanipulations (Lauridsen et al. 1993, Van Donk and Otte 1996, Mitchell and Perrow 1998, Marklund et al. 2002), but do not deal with competition between birds and fish for invertebrates.

Gravel pit studies performed in England in the late 1980s and early 1990s are among the few that deal directly with waterbird-fish competition in the biomanipulation context (Table 1.2). Gravel quarries that are flooded after quarrying is completed contribute significantly to the restoration of lost wetlands in the United Kingdom (Giles 1994). Bream (*Abramis brama*), perch, tench (*Tinca tinca*) and other sport fish are often stocked in these gravel pit lakes (Hill et al. 1987). Gut content analyses show that diets of these fish and diets of Mallard and diving waterbirds such as Tufted Duck (*Aythya fuligula*) exhibit some overlap for benthic invertebrates such as chironomids, gastropods and amphipods (Giles 1990, 1994; Giles et al. 1990; Phillips 1992). Fish density in experimental mesocosms in gravel pit lakes was negatively correlated with Mallard duckling growth and chironomid density (Hill et al. 1987). Giles (1990) removed fish from gravel pit lakes and found increased macrophyte abundance, chironomid density and water clarity, with concurrent increases in survival of young Tufted Ducks.

Gravel pit lake studies showed that waterbirds could benefit from biomanipulations and that waterbirds and fish competed in hypereutrophic aquatic systems much as they do in the more oligotrophic systems involved in acid precipitation-based studies. However, these gravel pit studies generally used a combination of imprinted ducklings, diet studies, and experimental mesocosms, rather than natural populations in whole lakes as some of the acid precipitation studies had done (*but see* Giles 1990). Additionally, these studies involved large game fish species (Phillips 1992). Thus, although gravel pit lake studies provided valuable information on the direct and indirect effects of fish on waterbirds in eutrophic systems, they are somewhat limited in scope and difficult to tie to biomanipulations that tend to (1) occur at the whole lake level and (2) involve assemblages of large- and/or small-bodied fish.

There are a few studies at the whole lake level that suggest that biomanipulation can benefit waterbirds in a number of eutrophic and hypereutrophic aquatic systems; i.e., that birds and fish compete for invertebrates in such systems. When Hanson and Butler (1994) used rotenone to remove planktivorous (bluegill sunfish, *Lepomis macrochirus*, and yellow perch) and benthivorous (bullhead catfishes, *Ictalurus* spp.) fishes from a large shallow lake in Minnesota, USA, the biomass of grazing zooplankton, the main prey of the removed planktivores, increased as expected. The fish removal also reduced the turbidity that is often associated with the foraging activities of benthivorous fish. Subsequently, there was increased development of macrophytes and the invertebrates associated with them, and diving waterbirds increased from <5000 to 57,000. Similar effects were seen in biomanipulated lakes in Sweden (e.g., Andersson and Nilsson 1999). Thus, the removal of assemblages of large- and small-bodied fish prompted increases in water clarity and invertebrate densities - characteristics that some of the earlier acidic lake-based studies had shown to be important for waterbirds (Eriksson 1979, Eadie and Keast 1982, Eriksson 1983).

This latter evidence (Hanson and Butler 1994, Andersson and Nilsson 1999) for negative effects of planktivorous or benthivorous fish on waterbirds in productive, biomanipulated lakes is compelling, particularly since it involves whole populations on whole lakes.

However, these results should be interpreted with caution. First, waterbirds in these examples were monitored during fall migration. The need for invertebrate protein in waterbirds is most critical for laying females and young ducklings or chicks earlier in spring and summer (Swanson et al. 1974, Swanson and Meyer 1977, Taylor 1978, Swanson et al. 1985). The birds may have been responding directly to the increased macrophytes available to them following fish removals, since they tend to eat more plant materials in autumn than they do earlier in summer (Owen and Black 1990). Secondly, fish removal methods may have direct negative effects on invertebrates, making the mechanisms of invertebrate change equivocal. Drawdown of water to remove fish (Giles 1990) can eliminate invertebrates such as amphipods, which lack a terrestrial phase in their life cycles and are important prey of some waterbirds (Swanson et al. 1974, 1985). Rotenone causes short-term reductions in some invertebrates (Aldhous 1996). Toxaphene, a polychlorinated camphene once used for fish removals, reduces invertebrate zooplankton predators like *Chaoborus* spp. for up to a decade after application (Miskimmin and Schindler 1994). Thus, removal of *Chaoborus* and similar predators, not fish, may cause the increase in grazing zooplankton. The long-term stability of biomanipulations is also largely unknown, and in some cases large predatory invertebrates can replace the removed fish, or there is a gradual build-up of large inedible algae because the smaller edible forms are being eaten by the more abundant grazing zooplankton. Benndorf et al. (2000) term the functional replacement of small fish by large predatory invertebrates *overbiomanipulation*, and it may be one reason why biomanipulations such as that performed by Hanson and Butler (1994) do not last for more than a decade without maintenance (McQueen 1998, Bergman et al. 1999, Meijer et al. 1999, Benndorf et al. 2000, Sagehashi et al. 2000).

To my knowledge, there are no studies relating long-term consequences of biomanipulations to waterbirds. The vast majority of biomanipulations tend to focus on effects on fish and water quality (e.g., Blindow et al. 1993, Meijer et al. 1999), with only minor attention to the implications for waterbirds. Studies that do incorporate the interactions of planktivorous and/or benthivorous fish with invertebrates and waterbirds tend to use imprinted ducklings, growth rate data, and experimental mesocosms rather than natural systems (Hill et al. 1987, Phillips 1992, Giles 1994, Cox et al. 1998, Sjöberg et al. 2000; Table 1.2).

1.5 Adding fish and monitoring bird foraging behaviour in Aspen Parkland: an alternative approach to studying waterbird-fish competition

Our understanding of waterbird-fish competition for invertebrates in oligotrophic and eutrophic aquatic ecosystems has been well established by acid precipitation and biomanipulation studies. However, there are still two main gaps in our knowledge of the generality of waterbird-fish competition, the first of which is related to methodology and the second of which is related to aquatic ecosystems that have not been studied to date.

Firstly, most of the studies above necessarily involve fish removals, which as indicated by the biomanipulation studies in particular do not always allow us to unequivocally say that changes in macroinvertebrate prey for waterbirds is due to fish removal or extirpation (Benndorf et al. 2000). Fish additions are not a new concept in understanding the foraging ecology of waterbirds, (e.g., Cox et al. 1998), but they have not been widely used to study waterbird-fish competition. Some studies that focus purely on fish and invertebrates have used fish additions to show that fish have negative effects on invertebrates (Gilinksy 1984, Bechara et al. 1993, Batzer 1998). Because some of these studies show negative effects of fish on important waterbird prey such as chironomids (Taylor 1978, Swanson et al. 1985), we can extrapolate and say that adding fish results in reduced food availability for breeding waterbirds (e.g., DesGranges and Rodrigue 1986). However, such extrapolation assumes that birds will not switch prey. Some of the acid precipitation studies used gut content analyses to show that waterbirds could switch prey in the presence of fish (DesGranges and Rodrigue 1986, Bendell and McNicol 1995).

Gut content analyses, although clearly useful in enhancing our understanding of waterbird-fish competition, are invasive, labour-intensive, provide only a snapshot of bird and fish diets, and are not feasible at large scales. One alternative would be to monitor foraging behaviour. DesGranges and Rodrigue (1986) and Giles (1990) both monitored waterbird foraging effort to show that Black Duck ducklings spend more time moving and searching for food than in their absence, and that Tufted Duck ducklings can obtain their daily diet requirements in just 36 minutes of diving for chironomids where they do not have to compete with fish for the largest prey items. Whilst monitoring foraging behaviour does not deal with the issue of prey switching, it can be used on wild birds on whole lakes rather than imprinted ducklings in mesocosms and is somewhat more conducive to replication than gut content analyses. If behavioural data are collected on unmarked individuals, it can, however, produce pseudoreplicated results as multiple behavioural sequences may be recorded from the same individual. Thus, foraging behaviour monitoring should be complemented with dietary analyses such as stable isotope analysis (SIA), which often uses stable isotope ratios of carbon and nitrogen in tissues to determine carbon sources and trophic position (Kelly 2000). SIA has the advantage of providing long-term data on animal diets. Tissues such as eggs and feathers can be used for birds, which is less invasive than using adult muscle tissues (Kelly 2000).

Secondly, an approach to studying waterbird-fish competition for invertebrates that involves fish additions to wetlands is especially useful in ecosystems where natural colonizations of fish are a frequent occurrence. For example, the Aspen Parkland regions of North America contain pothole wetlands that provide high quality habitat for breeding waterbirds (Krapu and Reinecke 1992) and are strongly influenced by a 5-20 year precipitation cycle (Mitsch and Gosselink 2000). Such wetlands are very productive, hypoxic and prone to frequent colonizations and extirpations of small-bodied fishes such as fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) (Nicholson and Vitt 1994, Cox et al. 1998, Zimmer et al. 2001, Danylchuk and Tonn 2003). Waterbird-fish competition has not been well studied in such systems despite their importance as waterbird breeding habitat (but see Cox et al. 1998). Additionally, land-use practices such as wetland consolidation, whereby mosaics of small shallow wetlands are consolidated into larger, deeper, more permanent wetlands that would be less prone to winter hypoxia, could increase the survival of small-bodied fish populations through drought periods in Aspen Parkland wetlands and similar systems. Whilst there is currently very legitimate concern that anthropogenically induced climate change will increase the incidence of winterkill for fish populations in western Canada (Danylchuk and Tonn 2003), land-use practices like wetland consolidation, that decrease the natural occurrence of winterkill, could be detrimental to waterbirds in Aspen Parkland, the Western Boreal Forest and the Prairie Pothole Region if birds are have negative interactions with the fish fauna in these regions.

Advising wetland managers to discourage wetland consolidation and fish introductions into these kinds of wetlands is a reasonable suggestion, but if this advice is based largely on studies that involve removals or extirpations of fish from lakes that breeding waterbirds use then it is somewhat equivocal. With the above considerations in mind, I used a combination of monitoring foraging behaviour, SIA, and fish additions to investigate waterbird-fish competition in Aspen Parkland wetlands. Because Aspen Parkland wetland communities have been relatively poorly documented beyond annual waterfowl counts and a few limnological studies (e.g. Savard et al. 1994, Puchniak 2002; but see Murkin et al. 2000), I began my research by surveying waterbirds, fish and invertebrates in Aspen Parkland waterbodies. These surveys and the patterns established in conducting them are presented in Chapter 2. Using a multivariate approach, I was able to document whether the composition of waterbird and invertebrate assemblages differed between Aspen Parkland waterbodies with and without fish. Underwood et al. (2000) stress the importance of performing such baseline surveys to establish whether the patterns of interest exist before studying the mechanisms behind the patterns. In this case the patterns of interest are the differences in the invertebrate prey base for waterbirds and the birds' use of waterbodies with and without fish.

I then describe differences in the foraging activities and invertebrate prey bases of two species of waterbird that use the same Aspen Parkland wetlands in different ways, Red-necked Grebe (*Podiceps grisegena*) and Blue-winged Teal (*Anas discors*), on wetlands with and without small-bodied fishes. I also document changes in the prey bases and foraging activities of these two species in one wetland that underwent a winterkill and subsequent recovery of fish (Chapter 3). Chapter 4 documents an experiment in which I added brook stickleback and fathead minnow to an Aspen Parkland wetland, monitoring bird foraging activities, invertebrate abundance and invertebrate biomass before, immediately after and one year after fish addition. In Chapter 5, I document my use of stable isotope analysis to document the diets of Red-necked Grebe and American Coot (*Fulica americana*) in Aspen Parkland wetlands with and without fish. Finally, I discuss the implications of these studies for (1) documenting waterbird-fish competition in systems that are strongly influenced by winter hypoxia and (2) the management of breeding waterbird habitats in these productive but poorly studied aquatic ecosystems.

1.6 References

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Table 1.1: The main findings of 10 of the studies of acid precipitation impacts that dealt with waterbird-fish competition. 1= Eriksson 1978, 2 = Eriksson 1979, 3 = Eadie & Keast 1982, 4 = Eriksson 1983, 5 = Pehrsson 1984, 6 = Eriksson 1987, 7 = DesGranges & Rodrigue 1986, 8 = Blancher et al 1992, 9 = McNicol & Wayland 1992, 10 = Bendell & McNicol 1992.

Waterbird species	Fish fauna	Invertebrate prey	Location	Methods	Conclusion	Source
Common Goldeneye	perch, roach	Odonata, Coleoptera	Sweden	fish removal and compared lakes with and without fish	exploitation competition	1,2
Common Goldeneye	yellow perch	Ephemeroptera	Canada	compared lakes with and without fish, duckling and fish gut contents	competition over large geographic areas	3
Mallard, Teal, Common Goldeneye	perch, roach, pike	not sampled	Sweden	duckling abundance correlated with fish densities and some habitat characteristics	competition only diving ducks & fish	4

Table 1.1 continued

Waterbird species	Fish fauna	Invertebrate prey	Location	Methods	Conclusion	Source
Mallard, Teal, Common Goldeneye	perch, roach, pike	Coleoptera, Odonata, Trichoptera, Diptera	Sweden	food availability, feeding success, breeding pair and duckling counts on lakes with and without fish	more food gained in fishless lakes	5,6
Common Goldeneye, Black Duck	brook trout, yellow perch	Coleoptera, Hemiptera, Diptera	Canada	sampling invertebrates, monitoring duckling behaviour and duckling gut contents	ducklings forage more on lakes with fish	7,8,9,10

Table 1.2: The main findings of 10 biomanipulation studies that focused on waterbirds. 1= Giles 1990, 2 = Giles 1994, 3 = Giles et al. 1990, 4 = Hill et al. 1987, 5 = Marklund et al. 2002, 6 = Lauridsen et al. 1993, 7 = Mitchell & Perrow 1998, 8 = Hanson & Butler 1994, 9 = Andersson & Nilsson 1999, 10 = Cox et al. 1998.

Waterbird species	Fish fauna	Invertebrate prey	Location	Methods	Conclusion	Source
Tufted Duck	not sampled	Diptera	England	imprinted duckling dive times	bird foraging effort correlated with food density	1
Tufted Duck	bream, roach, perch, pike	Diptera	England	fish removal, fish gut samples, invertebrate sampling, duckling counts	removing fish increases duckling survival	2
not sampled	bream, perch, roach, tench	Diptera, Bivalvia	England	fish gut samples	fish diets overlap with ducks	3
Mallard	roach, bream	Diptera, Ephemeroptera	England	mesocosms at different fish densities, duckling growth rates	higher survival/weight gain for ducklings at low fish densities	4

Table 1.2 continued

Waterbird species	Fish fauna	Invertebrate prey	Location	Methods	Conclusion	Source
Eurasian Coot, Mute Swan	tench, perch, roach	not sampled	Denmark	fish removed, macrophyte and bird counts, exclosures	grazing waterbirds retard macrophyte recovery	5,6,7
American Coot, Lesser Scaup, Ring-necked Duck	yellow perch, bluegill, bullhead	Diptera, Cladocera, Amphipoda	Minnesota, USA	fish removed, birds and invertebrates counted before and after	birds and their prey increase after fish removal	8
Eurasian Coot, Mute Swan, Mallard, Tufted Duck, Pochard	roach, bream	not sampled	Sweden	fish removed, bird counts before and after	birds increase after fish removal	9
Mallard	fathead minnow	Diptera	North Dakota, USA	fish and ducklings placed in artificial wetlands, invertebrate densities and duckling growth rates measured	duckling body mass & growth rate correlated with invertebrate density	10

Chapter 2: Biotic and Abiotic Factors Determining the Composition of Aquatic Bird Assemblages in Alberta's Aspen Parkland

2.1 Introduction

Approaches to the study of lake ecosystems have grown more inclusive in recent years, moving from a focus largely on plankton and limnology to include macroinvertebrates, planktivorous fish and piscivorous fish (see Bergman et al. 1999 for a review). However, despite the ecosystem concept itself having had some of its origins (e.g. Forbes 1923) and much of its development in lake studies, few of these studies incorporate aquatic birds that are an integral part of many lake ecosystems. Notable examples of ecosystem and community ecology's development in lake studies include development of top-down:bottom-up theory (McQueen et al. 1986), trophic cascade theory (Carpenter et al. 1985, 1987), and multiple stable states (Scheffer et al. 1993). Trophic studies based on these concepts rarely include birds that can import nutrients (Scherer et al. 1995), consume and disperse algae (Atkinson 1980, Wootton 1992, Kristiansen 1996), and forage on macrophytes, invertebrates and fish (e.g., Sjöberg 1973, Eadie and Keast 1982, Hill et al. 1987, Piersma and Van Eerden 1989, Lauridsen et al. 1994, Van Donk and Otte 1996, Cox et al. 1998, Stout and Nuechterlein 1999). Aquatic bird assemblages are themselves often characterized only in terms of the abiotic factors that drive their composition (e.g. Hill et al. 1993, Savard et al. 1994). Studies of biotic interactions between birds and either fish or invertebrates (e.g., competition) tend to focus only on one or a few species of birds rather than whole assemblages of birds (Eriksson 1979, Swanson et al. 1984, Giles 1990, Hanson and Butler 1994).

Because biotic and abiotic factors act in concert to drive community patterns, aquatic bird studies that separate these factors provide only a piecemeal view of the roles of birds in lake communities and the driving forces behind the structure of bird assemblages in lakes (Pöysä 1984). For example, fish presence/absence is a reliable cue to macroinvertebrate abundance (Diehl 1992, Mallory et al. 1994, Tatrai et al. 1994, Dahl 1998, Wong et al. 1998). One might predict that fish presence/absence is also a reliable cue to bird abundance, because birds' use of lakes is correlated with invertebrate diversity in some systems (Elmberg et al. 1994), and competition between breeding waterbirds and fish in oligotrophic and eutrophic environments is well known (e.g., DesGranges and Rodrigue 1986, Giles 1990). This extrapolation assumes a very tight, simplistic relationship between fish, invertebrates and breeding birds. For example, larger deeper lakes provide fish with refugia from winterkill (Barica and Mathias 1979, Tonn and Magnuson 1983, Fox and Keast 1990), and diving ducks, for instance, will forage in deeper water than dabbling ducks (Savard et al. 1994). This does not mean that fish presence/absence and birds' use of the same lakes are directly related. Fish may simply happen to be present in larger, deeper lakes that can accommodate both diving and dabbling ducks more readily than small shallow lakes, without necessarily having clear effects on the birds (Paszkowski and Tonn 2000). Thus, one should be cautious when extrapolating relationships between fish, or any other factor, and bird assemblage composition based on the findings of separate studies of breeding birds and invertebrates or fish and invertebrates.

The lack of truly comprehensive ecological studies that include birds is considered to be a major problem for waterfowl managers (Krapu and Reinecke 1992), particularly in productive but poorly studied bird habitats such as North America's Aspen Parkland, a transitional zone between the prairies and the boreal forest that is rich in aquatic birds (Nicholson and Vitt 1994). The native vegetative cover of the parkland has been anthropogenically reduced by two-thirds (Blyth and Hudson, 1987) and remnants of parkland are surrounded by agricultural and rural residential land, making it an ecoregion of major conservation concern.

In 1999, I surveyed the aquatic birds, fishes, invertebrates and limnological characteristics of waterbodies in the Aspen Parkland of Alberta, Canada. Aquatic birds included nonpasserine species directly feeding on the water surface or along the shore; wetland associated passerines were not included. I determined the relative importance of a range of biotic and abiotic factors for bird assemblage structure in a series of multivariate and univariate analyses. I had two objectives, the first of which was to describe the assemblages of aquatic birds on waterbodies in Aspen Parkland. One might predict that, since the Aspen Parkland is a transitional zone between the boreal forest and the prairies, parkland bird assemblages would contain species that are characteristic of both ecosystems. There is also a need to elucidate the roles of biotic and abiotic drivers of bird assemblage composition. For instance, do small fish affect bird assemblage composition via their effects on the birds' invertebrate prey bases, or do fish simply occur more often in larger lakes that will also support a more species-rich bird assemblage? Thus, my second objective was to determine which combinations of abiotic and biotic factors were the most important determinants of aquatic bird assemblage composition on these waterbodies during the breeding season.

2.2 Methods

2.2.1 Study Area

Aspen Parkland contains permanent and semi-permanent waterbodies in a knob and kettle moraine. These waterbodies are naturally eutrophic to hypereutrophic (*sensu* Wetzel 1975; where eutrophic lakes have TP >30 μg/L and hypereutrophic lakes have TP > 100μg/L). I focused on waterbodies in Elk Island National Park (EINP, Lat 53°N, Long 112°W), a fenced remnant (195 km^2) of Aspen Parkland 45 km east of Edmonton, Alberta. Bisected by a major highway (Appendix 1), EINP is surrounded on three sides by agricultural and rural residential land. I chose 25 waterbodies that represented the broad variety of waterbodies in EINP, which range from small ephemeral wetlands to large permanent lakes.

2.2.2 Bird surveys

In May 1999, I surveyed aquatic birds located on the water surface, the shore and in flight over 25 waterbodies in EINP. Surveys were conducted between 0500-1100 and 1600-1900. For larger waterbodies, this involved surveying using binoculars from a canoe paddled around the perimeter (for up to six hours); smaller waterbodies were censused form shore with binoculars and a 45x spotting scope (for up to one hour). Each site was surveyed once in May. I repeated these surveys in June, when transient species and individuals had departed and the remainder had settled in the area for breeding.

2.2.3 Fish and invertebrate sampling

I sampled fishes at the 25 waterbodies using Gee minnow traps (6 mm mesh) set at 50 m intervals in 100 m transects that lay 2 m from the shore. At least one transect was set in each waterbody, with up to five transects for large lakes. Traps were set for 24 hours and the fishes caught were counted and identified. Fishes were sampled prior to spawning in mid- to late May 1999. In June 1999, I collected, counted and identified invertebrates using activity traps (2 L plastic pop bottles with the tops removed and inverted to create funnels) that were set horizontally in the water for 24 hours at 25 m intervals along the same transects as the fish traps. There were between two and five transects per waterbody, i.e., 10-25 traps. Invertebrates visible to the naked eye were counted, so that smaller microcrustaceans (e.g. calanoid copepods) were excluded from subsequent analyses.

2.2.4 Limnological and morphometric sampling

I collected up to five 1-litre samples of water from each site in late May 1999. These samples were analyzed for total phosphorus (TP), total dissolved nitrogen (TDN), chlorophyll a (chl. a), conductivity and pH. This was done in late May rather than at ice-out for logistical reasons and to coincide as closely as possible with the bird and invertebrate sampling that occurred in May and June. I obtained estimates of waterbody areas from GIS databases in EINP. I used a marked rope to obtain 10 depth measurements from each waterbody, which were then used to estimate average depth. I used a Secchi disk to similarly obtain average Secchi depth estimates for each waterbody. Since most lakes were very shallow, with few deep-water refugia for fish, and there was little variation in the individual depth measurements, I used average depths rather than maximum depths in my analyses.

2.2.5 Data analysis

Following preliminary Correspondence Analysis (CA) and hierarchical cluster analysis to determine the initial patterns in the bird survey data, I used complementary direct and indirect ordinations in CANOCO v4.0 (ter Braak and Šmilauer 1998) to explore the relationships between bird assemblage structure and fish presence, invertebrate community composition and abiotic factors on the 25 waterbodies. I used log (x+1) transformed census data to represent the bird assemblages. Since an initial Detrended Correspondence Analysis on the bird census data showed ordination axis lengths of >2 s.d., the patterns in the bird census data were probably best described using unimodal ordination methods, i.e., CA and CCA (*see* ter Braak 1995 for a full explanation of DCA as a diagnostic tool for choosing ordination methods). Correspondence Analysis (CA) is an indirect, unrestricted unimodal ordination technique, which was used to determine initial patterns in the bird species survey data. Each site was given a score derived from the bird census data by reciprocal averaging; the ordination axes were thus derived from the bird census data. I complemented the CA with Canonical Correspondence Analysis (CCA), in which environmental variables were incorporated directly into the calculation of the site scores from the bird census data in a forward stepwise regression (Palmer 1993). The site scores in a CCA are therefore constrained by the environmental variables so that true assemblage structure may not be fully shown (McCune 1997). Thus, CA and CCA have complementary strengths and weaknesses and are best used together, at least in the initial analysis of community data. In this particular study, the patterns in bird census data seen in the CCA were very similar to those seen in the CA, which suggested that the environmental variables I chose explained the variation in the bird census data quite well (Zimmer et al. 2000). Thus, only the CCA graphs are presented below. The environmental variables were: fish presence/absence (previously described as a good cue to invertebrate diversity and potentially bird diversity; Mallory et al. 1994), the limnological and morphometric factors listed above, and the community composition of the invertebrates encountered, given by the scores of the first and second axes produced in a CA on the invertebrate census data (Figure 2.1). I used forward stepwise selection on the biotic and abiotic environmental variables to determine which of these variables contributed the most to the variability in the bird census data. I used Monte Carlo permutations (1000 permutations) to test the significance of each environmental variable used in the forward stepwise selection.

I initially used all available environmental variables in the CCA, and then performed a subsequent CCA using only those environmental variables that had significant marginal and conditional effects on the model at $\alpha = 0.10$ (ter Braak and Verdonschot 1995, Zimmer et al. 2000). I tested the significance of the axes in this reduced CCA using Monte Carlo tests (1000 permutations). Marginal effects indicate the amount of variation in the data explained by each environmental variable alone, whilst conditional effects indicate the amounts of variation explained by each environmental variable when entered into the model in the forward stepwise selection with all the other variables (ter Braak and Verdonschot 1995, Zimmer et al. 2000). Prior to each ordination, I deleted rare bird species, which had appeared on only one site during May or June 1999, from the data set. Only the ordination results for June 1999 are presented here (Figures 2.1 and 2.2), since there was a strong positive association between the bird species compositions observed in ordinations for May and June (Mantel test, $r = 0.79$, $p < 0.01$, $t = 4.37$). The CCA ordination of all waterbodies surveyed in May 1999 is shown in Appendix 2.3.

Area may appear as an important determinant of bird assemblage composition in this study simply because the sizes of the lakes ranged over several orders of magnitude (<1 ha to 559.5 ha). Therefore, I also performed CCAs on the subset of waterbodies that were less than 20 ha in size, and on the waterbodies that were greater than 20 ha in size (this split the data set approximately in half). If area is truly an important determinant of bird assemblage composition in Aspen Parkland lakes, it should appear significant in the ordinations even within a smaller range of lake areas.

I further explored the relationships between fish, birds and invertebrates with univariate analyses, which complement the ordination results. I conducted t-tests to determine differences in (1) bird species richness and (2) invertebrate taxon richness between waterbodies with and without fishes. For birds, I performed these tests using all bird species and using just those bird species that had been included in the ordinations. To determine any links between bird species richness and invertebrate taxon richness, I performed a linear regression between invertebrate taxon richness and bird species richness in June 1999. These separate analyses did not fully integrate the related effects of fish and invertebrates on bird species richness, and the regression showed that bird species richness and invertebrate taxon richness were strongly related (see below). Therefore, I then determined the effects of fish status on bird species richness using ANCOVA with invertebrate taxon richness as a covariable.

2.3 Results

Fifty-one aquatic bird species were seen on the twenty-five waterbodies in May and June 1999, of which 44 were seen in June (Table 2.1; $\bar{x} = 10.92 \pm 1.33$ species per site in June, minimum 2 species, maximum 26 species). Twenty invertebrate taxa were also encountered across these waterbodies in June ($\bar{x} = 6.88 \pm 3.00$). Twelve of the twenty-five waterbodies contained fathead minnow (*Pimephales promelas*) and/or brook stickleback (*Culaea inconstans*). The other thirteen waterbodies were fishless. All waterbodies were eutrophic to hypereutrophic, with total phosphorus values ranging from 30.20 μg/L to 441.50 μg/L. The pH of waterbodies ranged from 7.17 to 9.43. The sizes of waterbodies ranged from small, shallow ponds (<1 ha) to large, shallow lakes, the largest being 559.5 ha. A full list of the limnological characteristics of each site is given in Appendix 2.1.

In the initial full CCA of all waterbodies, the first four constrained CCA axes explained 54.2% of the total variance (unconstrained eigenvalues) in the bird census data, or 75.2% of the variance in the fitted values (canonical eigenvalues) obtained when all of the environmental variables were used to explain the bird census data. The forward stepwise selection of environmental variables in this full CCA showed that chlorophyll a, total dissolved nitrogen, presence/absence of fish, the type of invertebrate assemblage (as defined by the scores of the first axis for the CA on the invertebrate census data; Figure 2.1) and area were the environmental variables that explained the greatest proportion of the variance in the bird census data. These abiotic and biotic variables all had significant ($\alpha = 0.10$, 1000 Monte Carlo permutations, Table 2.2) conditional effects in the forward stepwise selection process – that is, they were each statistically significant when entered into the model with other variables. Total phosphorus, depth, the invertebrate community composition as defined by the second CA axis and conductivity all had strong marginal effects, but were not significant when considered along with other variables (conditional effects). The remaining environmental variables (Secchi depth, pH) showed no significant marginal or conditional effects, and explained little of the variation in the bird census data.

In the reduced CCA on the bird census data from all waterbodies, using only the five significant environmental variables (Figure 2.2), the first four constrained axes of the reduced CCA explained 50.5% of the total variance (unconstrained eigenvalues) in the bird census data, or 93.7% of the variance in the fitted values (canonical eigenvalues). The axes were significant at $\alpha < 0.01$ (1000 Monte Carlo permutations, Table 2.3). Chlorophyll-a, fish status and TDN were all highly significantly correlated with area, but invertebrate community composition was only correlated with area at $p < 0.10$ (Table 2.4). Thus, many of the effects of the other variables on the bird assemblage composition are linked to lake area. Fish status was also positively associated with TDN ($t_{2,23} = 2.211$, $p = 0.037$), and with scores on CA axis 1 of the invertebrate ordination (Pearson $r = 0.559$, $p = 0.004$). The CCAs of waterbodies smaller than 20ha and waterbodies greater than 20ha showed that TDN, chlorophyll-a and invertebrates were important determinants of bird assemblage composition, but that area and fish status were not (Table 2.5).

Two bird assemblages were distinguishable from the reduced CCA ordination of all waterbodies (Figure 2.2, Table 2.3). Waterbodies with low scores on CCA axis 1 were characterized by facultatively piscivorous birds such as Red-necked Grebe, Horned Grebe, Bonaparte's Gull, Ring-billed Gull and Common Loon, obligate piscivores such as Double-crested Cormorant and American White Pelican, and some dabbling and diving ducks such as Mallard and Common Goldeneye. Blue-winged Teal, Green-winged Teal, Northern Shoveler, Redhead, Canvasback, Lesser Scaup and Gadwall, as well as shorebirds such as Killdeer and Common Snipe, and rails such as American Coot, characterized waterbodies with high scores on CCA axis 1.

The waterbodies characterized by the "grebe-gull" assemblage were richer in species than the "teal-shorebird" assemblage (Appendix 2.1). "Grebe-gull" waterbodies were typically large waterbodies that had fish, the highest chlorophyll a concentrations, and low axis 1 scores on the invertebrate CA. Cladocerans, amphipods, dipteran larvae and glossiphoniid leeches characterized the invertebrate assemblages on waterbodies with low CA axis 1 scores (Figure 2.1). Many of the species in the "grebe-gull" assemblage also occurred in the "teal-shorebird" waterbodies (Gadwall, Green-winged Teal, Northern Shoveler and Common Goldeneye; Table 2.1). Thus, the "teal-shorebird" assemblage was a depauperate subset of the "grebe-gull" assemblage. The waterbodies characterized by the "grebe-gull" assemblage were also larger than the waterbodies characterized by the "teal-shorebird" assemblage. The "teal-shorebird" waterbodies were generally smaller, fishless, with lower chlorophyll a and TDN, and high scores on axis 1 of the invertebrate CA. These high CA scores reflected assemblages characterized by gastropods, large leeches, dytiscid beetles and Trichoptera larvae (Figure 2.1).

T-tests showed that fish waterbodies were significantly richer in bird species than fishless waterbodies. For all bird species encountered in June 1999, $\bar{x} = 13.25 \pm 1.69$ species in fish waterbodies and $\bar{x} = 8.77 \pm 1.90$ species in fishless waterbodies ($t_{2,23} = 1.75$, $p = 0.094$, $\alpha = 0.10$). For the subset of bird species included in the ordinations, $\bar{x} = 12.5$ species in fish waterbodies, and $\bar{x} = 8.08$ species in fishless waterbodies ($t_{2,23} = 2.025$, $p = 0.055$, $\alpha = 0.10$). Fish waterbodies were not significantly richer in invertebrate taxa than fishless waterbodies ($t_{2,23} = 1.14$, $p = 0.266$; $\bar{x} = 6.91 \pm 0.89$ taxa in fish waterbodies, $\bar{x} = 5.69 \pm 0.62$ taxa in fishless waterbodies). Bird species richness and invertebrate taxon richness were strongly correlated with each other (Figure 2.3). The ANCOVA used to compare bird species richness in waterbodies with and without fish, using invertebrate taxon richness as a covariable, showed that bird species richness (using species included in ordinations) was slightly higher in fishless waterbodies ($F_{4,21} = 7.479$, $p = 0.001$). In this analysis there was no significant interaction between fish status and invertebrate taxon richness ($p = 0.884$). Invertebrate taxon richness had a much greater effect on bird species richness than fish: effect size for fish presence/absence was 0.025, and for invertebrate taxon richness the effect size was 0.418. Fish waterbodies were significantly larger than fishless waterbodies ($\bar{x} = 149.55$ ha $\pm$ 50.11 in fish waterbodies, $\bar{x} = 23.84$ ha $\pm$ 13.38 in fishless waterbodies; $t_{2,23} = 2.424$, $p = 0.031$), but bird species richness was not strongly directly correlated with area (Pearson $r = 0.178$; see also Figure 2.4).

2.4 Discussion

The two bird assemblages, associated with different types of waterbodies, showed some overlap in species composition. The species that occurred on both types of waterbodies were a combination of prairie species (Northern Shoveler, Gadwall; Semenchuk 1992) and boreal species (Green-winged Teal, Common Goldeneye; Semenchuk 1992). In general, all the species encountered were typical of either prairies or boreal forests. Thus the prediction the parkland bird assemblages would contain species characteristic of both the prairies and the boreal forest was supported. Waterbodies characterized by the "grebe-gull" assemblage were more species-rich than those characterized by the "teal-shorebird" assemblage, with the "teal-shorebird" assemblage being a depauperate subset of the "grebe-gull" assemblage.

2.4.1 Abiotic determinants of bird assemblage composition

All waterbodies in this study were eutrophic to hypereutrophic, and the "grebe-gull" waterbodies had the highest chlorophyll-a concentrations (i.e., highest phytoplankton concentrations), and the highest TDN concentrations. TDN was strongly correlated with TP (Pearson r = 0.607, p=0.001), and thus may have been an indirect index of other sources of primary productivity that I did not measure directly, such as the aquatic macrophytes that dominate many parkland lakes (C. McParland, *pers. obs.*). Additionally, the CCAs that included all waterbodies indicated that chlorophyll-a and TDN were the two most important drivers of bird assemblage composition (Table 2.2). This is similar to studies in other systems that indicate relationships between productivity or lake nutrient concentrations and bird assemblage composition (Palmgren 1936, Nilsson and Nilsson 1978). Although area appeared as one of the important drivers of bird assemblage composition, it was poorly correlated with species richness and its apparent importance in the ordinations may have been an artefact of the large range of lake sizes in this study. For the two CCAs that involved only waterbodies of less than 20 ha or only waterbodies of greater than 20 ha, area did not explain a significant proportion of the variation in the bird census data (Table 2.5). Species-area plots of all lakes below 20 ha and all those above 20 ha showed almost no correlation between area and species richness (Figure 2.4). Previous studies suggest caution in using area as a predictor of species richness for highly mobile species such as aquatic birds (Savard et al. 1994). Chlorophyll-a and TDN still explained a statistically significant amount of the variation in the bird data for these latter two CCAs (Table 2.5). Thus, the main abiotic drivers of bird assemblage composition in these Aspen Parkland waterbodies were chlorophyll-a and TDN, with area only appearing important as an artefact of my choice of study sites with a broad range of areas (<1 ha to 559.5 ha).

2.4.2 Biotic determinants of bird assemblage composition

Invertebrate taxon richness was positively correlated with bird species richness (Figure 2.3), which indicated that bird assemblage composition was strongly positively influenced by the array of invertebrate prey available to birds. This conclusion was also supported by the significant effect of invertebrates (CA axis 1 scores) on bird assemblage composition in the CCA of all waterbodies. For the CCAs of small (<20 ha) waterbodies and large (>20 ha) waterbodies, invertebrates again appeared as significant drivers of bird assemblage composition (CA axis 2 scores; Table 2.5). Similarly, Elmberg et al. (2000) found strong correlation between waterfowl species richness and dytiscid beetle diversity on Swedish lakes. The dipterans and amphipods that were typical of the waterbodies characterized by the "grebe-gull" assemblage are important prey for the non-piscivorous birds in that assemblage (e.g., Taylor 1978, Austin et al. 1998, Cox et al. 1998), whilst the gastropods and trichopterans typical of the "teal-shorebird" waterbodies are important prey of breeding dabbling ducks that dominated that assemblage, such as Blue-winged Teal, Green-winged Teal and Northern Shoveler (Taylor 1978, Eriksson 1979, Nudds and Bowlby 1984, Hill et al. 1987, Cox et al. 1998).

The presence of small-bodied fish in the waterbodies characterized by the "grebe-gull" assemblage also added to the resource base for birds, and thus may have been a reason for the greater species richness of these waterbodies relative to the waterbodies characterized by the "teal-shorebird" assemblage. Fish presence was most likely due to the greater depth of "grebe-gull" waterbodies, which could provide refugia for fish in highly productive lakes that are prone to winterkill (Tonn and Magnuson 1982, Hall and Ehlinger 1989). Although depth did not appear important in the CCAs, it was positively correlated with area (Pearson r = 0.408, p=0.043), and the t-tests (above) indicated that lakes with fish were generally larger than fishless lakes. Thus, waterbodies characterized by the "grebe-gull" assemblage, being deeper and supporting small fish, could have provided a greater diversity of resources than "teal-shorebird" lakes, thereby supporting a richer assemblage that included piscivores (American White Pelican, Double-crested Cormorant) as well as invertivores like Mallard and Common Goldeneye.

The invertebrates associated with the most phytoplankton-rich, hypereutrophic waterbodies that were characterized by the "grebe-gull" assemblage included benthic forms like dipteran larvae. Similarly, Bais et al. (1992) showed that benthic invertebrates such as dipteran larvae are associated with nutrient enrichment. The invertebrates typical of the less hypereutrophic waterbodies that were characterized by the "teal-shorebird" assemblage, such as gastropods, may tend to avoid extremely productive waterbodies. For example, other molluscan waterfowl prey, such as *Dreissena*, can be associated with eutrophic lakes and avoid hypereutrophic lakes (Suter 1994). Thus, the association of different invertebrates with the two different types of waterbodies in this study suggests that invertebrate assemblage composition in Aspen Parkland lakes is somewhat influenced by lake nutrient status. This does not, however, mean that invertebrate assemblages are more species-rich in more nutrient-rich lakes as others have suggested (e.g., Hargeby et al. 1994) – it simply means that the invertebrate composition differs between parkland lakes of different nutrient status, all of which are eutrophic or hypereutrophic lakes rather than eutrophic or oligotrophic lakes as is the case in other studies.

Invertebrate assemblages also showed patterns consistent with studies of invertebrate communities in lakes with and without fish (Suter 1994, Batzer et al. 2000). Since bird and invertebrate species and taxon density were positively correlated, it appeared that fish could be a reliable cue to bird assemblage composition in the Aspen Parkland. However, the ANCOVA, which tied bird species richness, invertebrate taxon richness, and fish status together, indicated no significant interaction between fish status and invertebrate taxon richness, with invertebrate richness having a greater effect on bird species richness than fish status. Additionally, the CCA indicated that invertebrate assemblages were a more important driver of bird assemblage composition than fish status (Table 2.2). Thus, whilst fish status appeared significant in the CCA of all waterbodies, it may be a less reliable direct cue to bird assemblage composition in the Aspen Parkland than nutrient status (Nilsson and Nilsson 1978) or invertebrate assemblage composition (Elmberg et al. 2000).

In summary, there were two bird assemblages present on Aspen Parkland waterbodies, a richer "grebe-gull" assemblage and a "teal-shorebird" assemblage that appeared to be a depauperate subset of the "grebe-gull" assemblage. The most important driver of bird assemblage composition was nutrient status, in particular chlorophyll-a and TDN concentrations. Nutrient status may have had an influence on invertebrate assemblage composition: the waterbodies characterized by the "grebe-gull" assemblage had an invertebrate resource base of glossiphoniids, dipterans and amphipods and the waterbodies characterized by the "teal-shorebird" assemblage had an invertebrate resource base of gastropods, large leeches and dytiscids. Although differences in productivity in lakes of the Aspen Parkland may result in different invertebrate resource bases for birds, these invertebrate resources are not necessarily more diverse in the more nutrient-rich lakes as suggested by workers in other systems (Nilsson and Nilsson 1978, Hargeby et al. 1994). All the lakes in this study were highly productive, with the least eutrophic lake having a TP concentration of 30.2 μg/L. The greater richness of the "grebe-gull" assemblage most likely occurred because of the presence of fish in those lakes, which tended to be deeper than the waterbodies characterized by the "teal-shorebird" assemblage. Thus, waterbodies characterized by the "grebe-gull" assemblage were more physically heterogeneous and supported a wider array of prey organisms than the shallower, fishless waterbodies characterized by the "teal-shorebird" assemblage.

2.4.3 Conclusions

This study represents the first attempt at documenting relationships among birds, abiotic factors and biotic factors in the Aspen Parkland, one of the most productive ecoregions in North America. Such questions have more usually been addressed in the context of acid rain effects on oligotrophic lakes that contained large fish (e.g., McNicol and Wayland

1992). Other univariate studies of birds, fish, invertebrates and abiotic factors in lakes give wetland managers the impression that a great many variables must be measured in some detail in order to develop useful management protocols for aquatic birds and their habitats (e.g., Eriksson 1979, Swanson et al. 1984, Hill et al. 1993, Savard et al. 1994, Wong et al. 1998). The multivariate approach of this study could be useful to wetland managers in determining which environmental factors could be important drivers of bird assemblage composition, i.e., which factors should be focused on when attempting to simultaneously manage habitats for a wide variety of species. It is also a useful approach for providing baseline data on community patterns (Underwood et al. 2000) in poorly studied ecoregions such as Aspen Parkland prior to conducting more in-depth studies on phenomena such as the waterbird-fish competition that is the focus of Chapter 3, 4 and 5. For Aspen Parkland habitats, this study suggests that managers could complement traditional censuses with some basic monitoring and manipulation of lake nutrients (e.g. oxygenation of sediments to reduce internal phosphorus and nitrogen cycling , control of agricultural runoff) to maintain the desired assemblages of aquatic birds. One could also suggest that parkland diversity is best maintained by having a variety of larger, deeper waterbodies that support fish and smaller, shallower waterbodies that do not support fish.

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Table 2.1: The number of fish and fishless waterbodies in the Aspen Parkland where bird species were seen in June 1999. Species marked with * were deleted from ordinations for June 1999, but observed in May 1999 (continued over...).

symbol	Species		# fishless sites	# fish sites
CL	*Gavia immer*	Common Loon	1	1
RG	*Podiceps grisegena*	Red-necked Grebe	6	9
HG	*Podiceps auritus*	Horned grebe	1	2
EG	*Podiceps nigricollis*	Eared Grebe	2	4
AP	*Pelecanus erythrorhynchos*	American White Pelican	0	2
DC	*Phalacrocorax auritus*	Double-crested Cormorant	0	2
AB	*Botaurus lentiginosus*	American Bittern*	0	0
BH	*Ardea herodias*	Great Blue Heron	1	2
NH	*Nycticorax nycticorax*	Black-crowned Night Heron*	0	1
CG	*Branta canadensis*	Canada Goose	5	2
TrS	*Cygnus buccinator*	Trumpeter Swan	0	2
TuS	*Cygnus columbianus*	Tundra Swan*	0	0
WD	*Aix sponsa*	Wood Duck*	0	0
GD	*Anas strepera*	Gadwall	8	7
WI	*Anas americana*	American Wigeon	3	0

Table 2.1 continued

symbol	Species		# fishless sites	# fish sites
ML	*Anas platyrhynchos*	Mallard	11	11
BT	*Anas discors*	Blue-winged Teal	9	6
CT	*Anas cyanoptera*	Cinnamon Teal*	1	0
NS	*Anas clypeata*	Northern Shoveler	3	3
PI	*Anas acuta*	Northern Pintail*	1	0
GT	*Anas crecca*	Green-winged Teal	4	5
CN	*Aythya valisineria*	Canvasback	1	1
RH	*Aythya americana*	Redhead	2	9
RnD	*Aythya collaris*	Ring-necked Duck	3	3
GS	*Aythya marila*	Greater Scaup*	1	0
LS	*Aythya affinis*	Lesser Scaup	7	11
SS	*Melanitta perspicillata*	Surf Scoter*	0	0
WS	*Melanitta fusca*	White-winged scoter	1	2
BU	*Bucephala albeola*	Bufflehead	9	6
CoG	*Bucephala clangula*	Common Goldeneye	5	8

Table 2.1 continued

symbol	Species		# fishless sites	# fish sites
BaG	*Bucephala islandica*	Barrow's Goldeneye*	0	0
RD	*Oxyura jamaicensis*	Ruddy Duck	2	9
SO	*Porzana carolina*	Sora	1	5
AC	*Fulica americana*	American Coot	7	10
KL	*Charadrius vociferus*	Killdeer	3	2
AA	*Recurvirostra americana*	American Avocet*	0	1
GY	*Tringa melanoleuca*	Greater Yellowlegs*	0	1
LY	*Tringa flavipes*	Lesser Yellowlegs	1	2
SoS	*Tringa solitaria*	Solitary Sandpiper*	0	1
WL	*Catopthrophorus semipalmatus*	Willet*	0	1
SpS	*Actitis macularia*	Spotted Sandpiper*	0	0
BS	*Calidris bairdii*	Baird's Sandpiper*	0	0
CS	*Gallinago gallinago*	Common Snipe	3	6
WP	*Phalaropus tricolor*	Wilson's Phalarope*	0	1
FG	*Larus pipixcan*	Franklin's Gull	1	5

Table 2.1 continued

symbol	Species		# fishless sites	# fish sites
BGu	*Larus philadelphia*	Bonaparte's Gull	1	6
RGu	*Larus delawarensis*	Ring-billed Gull	0	4
CGu	*Larus californicus*	California Gull*	0	1
CTe	*Sterna hirundo*	Common Tern*	0	1
BTe	*Chlidonias niger*	Black Tern	4	10
BK	*Ceryle alcyon*	Belted Kingfisher*	0	0

Table 2.2: Importance of the 5 significant environmental variables from the CCA ordinations of all waterbodies in the Aspen Parkland, based on censuses of aquatic birds in June 1999. Lambda 1 = marginal importance, lambda A = conditional importance with associated F-statistics and p-values.

	Marginal Effects	Conditional Effects			
	Lambda1		LambdaA	P	F
Chlorophyll a	0.32	Chlorophyll a	0.32	0.001	4.42
Invertebrate assemblage CA 1	0.32	TDN	0.3	0.001	4.84
TDN	0.3	Invertebrate assemblage CA 1	0.22	0.001	4.14
Area	0.18	Fish	0.12	0.004	2.31
Fish	0.11	Area	0.07	0.059	1.48

Table 2.3: Summary of reduced CCA on all waterbodies based on bird census data from June 1999, using the 5 environmental variables that had significant conditional effects at $\alpha = 0.10$ in the initial CCA that contained all 11 eleven environmental variables.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.368	0.333	0.172	0.096	1.921
Species-environment correlations	0.959	0.972	0.931	0.857	
Cumulative percentage variance					
of species data	19.1	36.5	45.4	50.5	
of species-environment relation	35.6	67.8	84.5	93.7	
Sum of all unconstrained eigenvalues					1.921
Sum of all canonical eigenvalues					1.034

Table 2.4: Correlations between area and other environmental variables that had significant effects in the reduced CCA of all waterbodies. Data used were log (x + 1) transformed. ** = Significant at $p < 0.01$.

Variable	Pearson correlation with area	p
TDN	0.506	0.01**
Chlorophyll a	0.618	0.001**
Fish presence/absence	0.57	0.003**
invertebrate CA axis 1	0.394	0.051

Table 2.5: Importance of environmental variables for bird assemblage composition from CCAs on waterbodies larger than 20 ha and waterbodies smaller than 20 ha.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.368	0.333	0.172	0.096	1.921
Species-environment correlations	0.959	0.972	0.931	0.857	
Cumulative percentage variance					
of species data	19.1	36.5	45.4	50.5	
of species-environment relation	35.6	67.8	84.5	93.7	
Sum of all unconstrained eigenvalues					1.921
Sum of all canonical eigenvalues					1.034

Waterbodies < 20 ha

Marginal Effects		Conditional Effects			
	Lambda1		Lambda A	P	F
pH	0.37	pH	0.37	0.001	2.26
TP	0.28	Invertebrate assemblage CA 2	0.26	0.031	1.68
Invertebrate assemblage CA 2	0.27	TDN	0.24	0.036	1.67

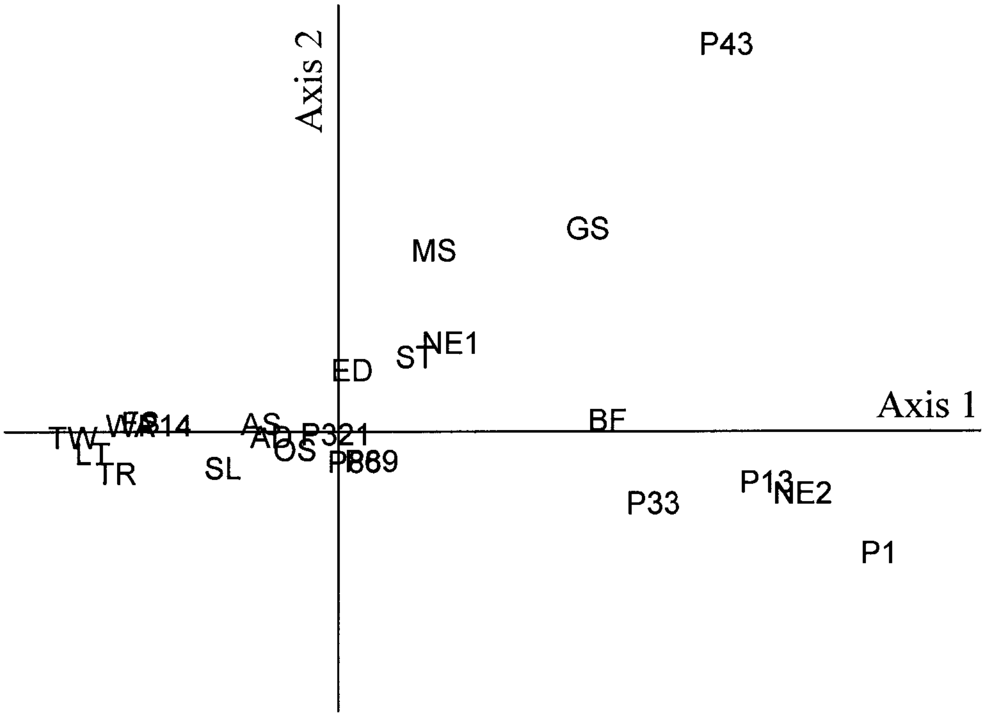

Figure 2.1a: CA ordination of all waterbodies at which invertebrates were collected in June 1999 based on counts of invertebrates in activity traps. Abbreviations are explained in Appendix 2.1.

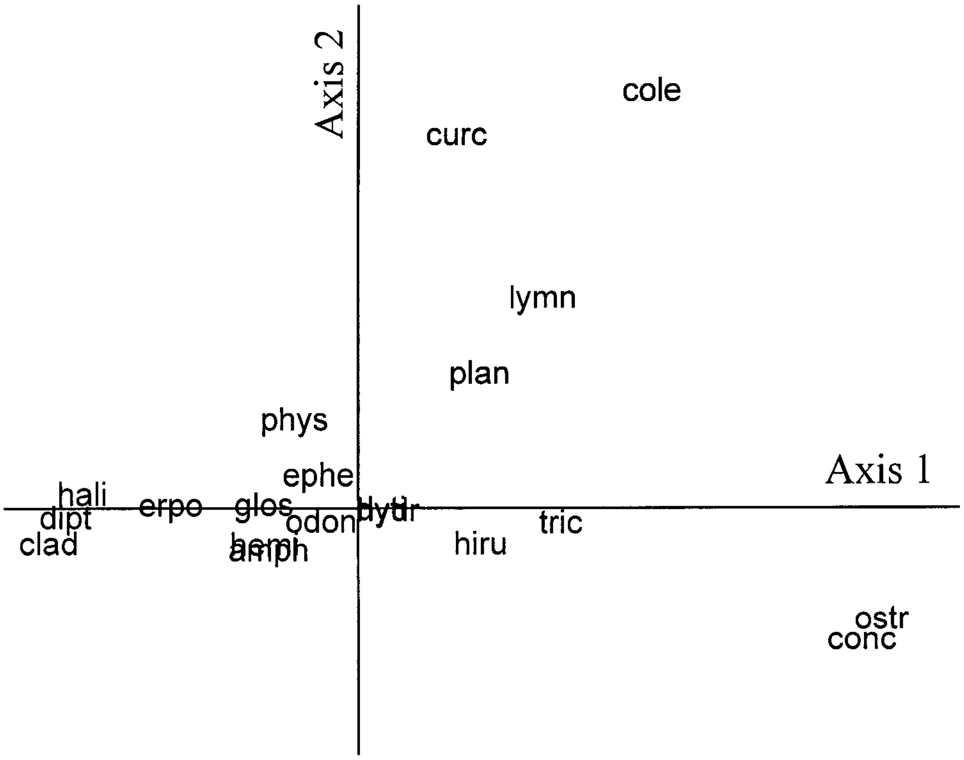

Figure 2.1b: Invertebrate taxa that characterized the waterbodies in Figure 2.1a. Overlaying this plot on Figure 2.1a indicates which taxa characterized which waterbodies. Abbreviations are explained in Appendix 2.2.

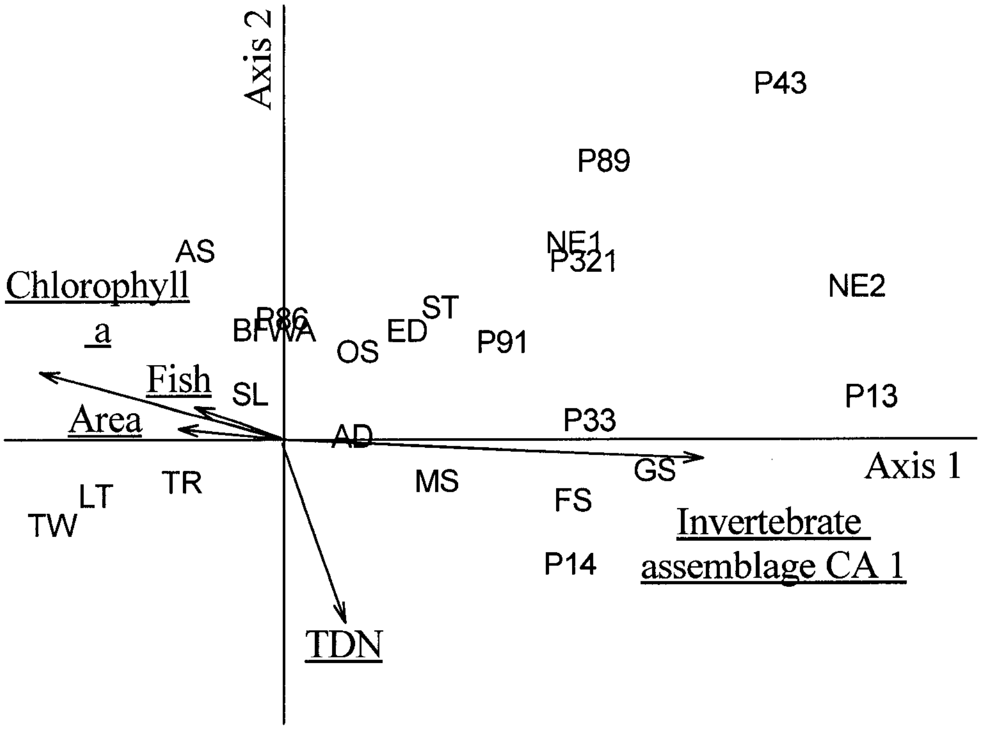

Figure 2.2a: CCA ordination biplot of environmental variables showing 25 waterbodies in EINP at which bird assemblages were surveyed in June 1999. Arrows are vectors that indicate the size of the influence of environmental variables on the bird census data. Arrow length reflects the strength of an environmental influence on the data. TDN = total dissolved nitrogen. Abbreviations for site names are explained in Appendix 2.1.

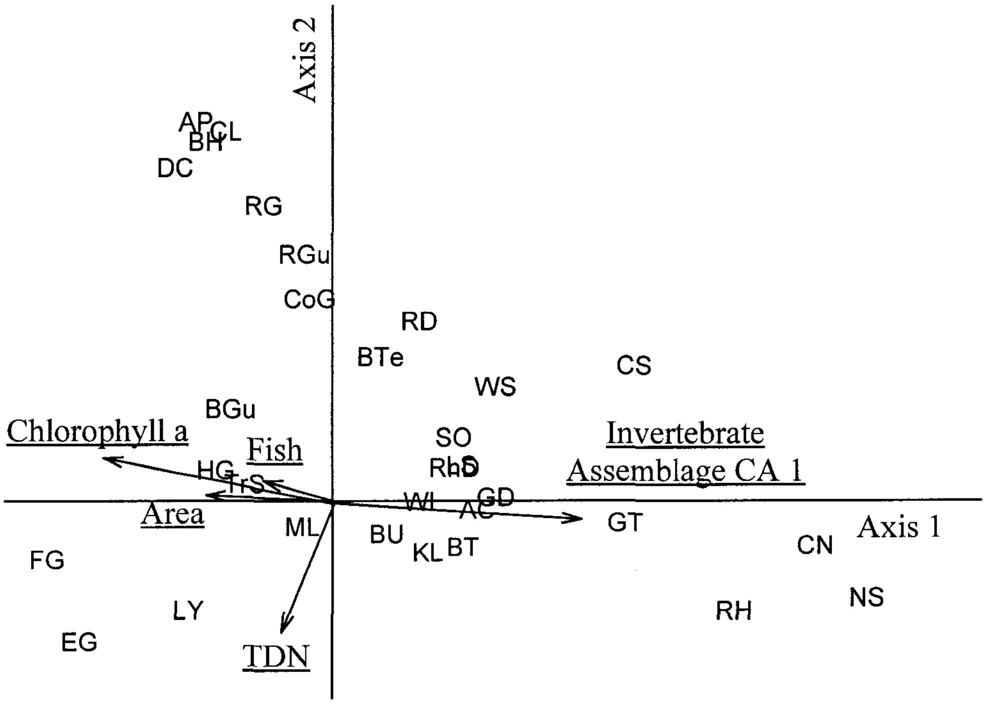

Figure 2.2b: CCA ordination biplot of environmental variables showing bird species that occurred at 25 waterbodies surveyed in EINP in June 1999. Arrows are vectors that indicate the size of the influence of environmental variables on the bird census data. Arrow length reflects the strength of an environmental influence on the data. TDN = total dissolved nitrogen. Abbreviations for species are explained in Table 2.1.

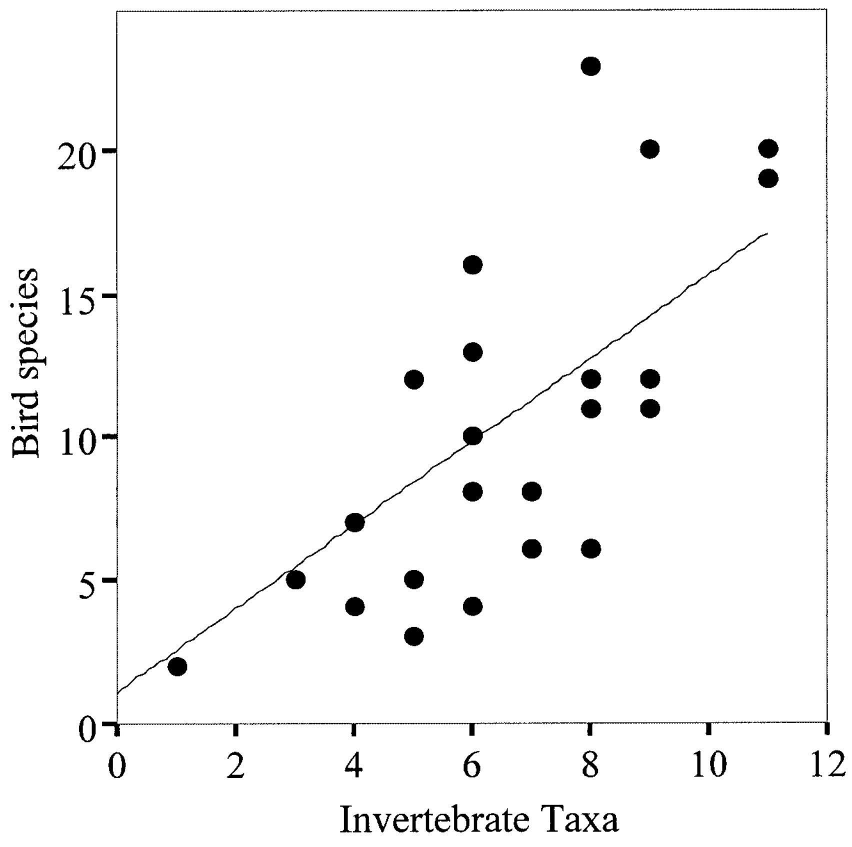

Figure 2.3: Regression between bird species richness and invertebrate taxon richness in Aspen Parkland lakes surveyed in June 1999. $F_{1,23} = 16.57$, $p = 0.0002$, $r^2 = 0.46$. Bird species = 1.03 + 1.46 invertebrate taxa. Only the 32 bird species that appeared on 2 or more lakes were used in this analysis.

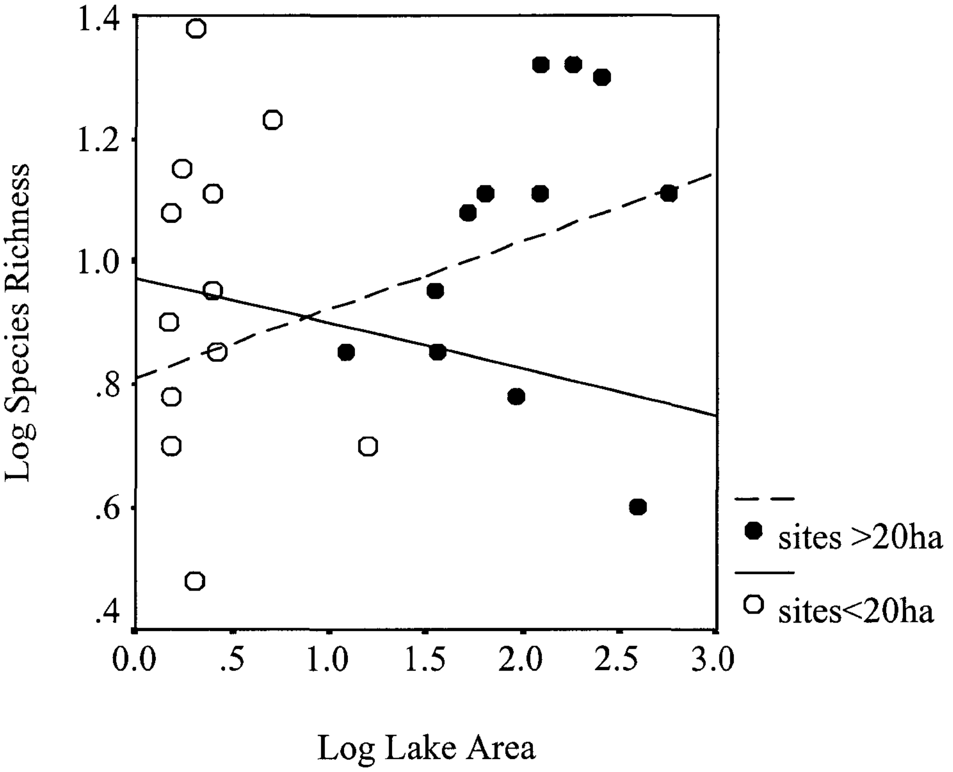

Figure 2.4: Species-area relationships for birds on Aspen Parkland waterbodies less than 20 ha and waterbodies larger than 20 ha. For waterbodies <20 ha, r^2=0.0072. For waterbodies >20 ha, r^2=0.0546. Only the 32 bird species that appeared on 2 or more lakes were used in this analysis.

Chapter 3: Consequences of Fish-Invertebrate Interactions for Foraging Waterbirds in Aspen Parkland: An Observational Approach.

3.1 Introduction

Many highly productive aquatic ecosystems that provide prime habitat for breeding waterbirds in North America (e.g. prairie and parkland potholes, western boreal forest; Krapu and Reinecke 1992, Paszkowski and Tonn 2000) are subject to a high degree of natural disturbance. These ecosystems consist of shallow wetlands (often less than 1 m deep) that are strongly influenced by 5-20 year cycles of precipitation (Mitsch and Gosselink 2000), eutrophic and prone to winter hypoxia. Winter hypoxia in these naturally highly disturbed ecosystems leads to mortality of large-bodied fish species and influences distribution and abundance of small-bodied fishes (Robinson and Tonn 1989, Tonn et al. 1995, Danylchuk and Tonn 2003). Thus, wetlands in productive, naturally disturbed ecosystems tend to be either fishless or contain only small-bodied fishes, which can colonize unoccupied wetlands in wet years when surface flows from large lakes to wetlands are high, and be extirpated in dry years. Colonizing fathead minnow (*Pimephales promelas*) reduce amphipods, chironomids and gastropods in the Prairie Pothole Region (PPR; Zimmer et al. 2001a, b). These invertebrates are important prey of breeding waterbirds (e.g., Taylor 1978). Thus, small-bodied fishes may have negative associations with breeding waterbirds in eutrophic, hypoxia-prone systems. However, there is a general lack of baseline observational data on interactions between waterbirds, fishes and invertebrates in many of these naturally disturbed systems (Krapu and Reinecke 1992). Underwood et al. (2000) have pointed out the need to conduct baseline surveys to establish the existence of patterns in ecosystems before conducting experiments to establish the mechanisms for those patterns. To date, waterbird-fish interactions in hypoxia-prone aquatic systems have been rarely examined in the PPR (e.g., Cox et al. 1998).

This study focused on the roles of fish in North America's Aspen Parkland, a transitional zone between the prairies and the boreal forest (Nicholson and Vitt 1994). Aspen

Parkland contains shallow meso- to hypereutrophic freshwater marshes (~30µg/L to more than 400µg/L total phosphorus; Nicholson 1995, Chapter 2) that are often fishless or contain fathead minnow and brook stickleback (*Culaea inconstans*), which are much more tolerant to low oxygen levels than larger fish species (Nelson and Paetz 1992). Aspen Parkland also supports many species of waterbirds (Chapter 2), and the assemblage composition of invertebrates differs somewhat between waterbodies with and without fish (Chapter 2). Most of the waterbodies in the parkland are rarely more than 1.5 m deep (Chapter 2). There is a lack of baseline observational data on waterbird-fish-invertebrate relationships in Aspen Parkland. Thus, Aspen Parkland is a good candidate system for (1) conducting observational comparisons of invertebrate assemblages and birds in wetlands with and without fishes; and (2) studying whether natural recolonizations and extirpations of small-bodied fishes in wetlands have any effects on invertebrates and consequently on birds that feed on those invertebrates.

With the above in mind, I assessed whether small-bodied Aspen Parkland fishes had measurable impacts on invertebrates and waterbirds in three ways. Firstly, I monitored abundances and biomasses of five guilds of aquatic invertebrates in wetlands with and without fishes, and censused two species of waterbird, Red-necked Grebe (*Podiceps grisegena*) and Blue-winged Teal (*Anas discors*) on the same wetlands in which invertebrates were sampled. Secondly, I monitored the birds' foraging activities on these same wetlands. Red-necked Grebe and Blue-winged Teal were chosen as study species because they were reasonably widespread in the study area and used the same wetlands in quite different ways, the grebe being a diving bird (Stout and Nuechterlein 1999) and the teal being a dabbler (Rohwer et al. 2002). Foraging behaviour is a relevant metric to use to assess effects of fish on breeding waterbirds, because any increase in time invested in foraging by birds, as a result of fish colonization and reduction of invertebrate prey, necessarily means a reduction in time available for activities like incubation. Time available to incubate eggs and successfully fledge young is an important limitation for birds breeding in temperate systems like Aspen Parkland, especially smaller birds that produce precocial young like Blue-winged Teal (Kendeigh 1970, Drent and Daan 1980). Thirdly, I monitored invertebrates and bird foraging patterns in an Aspen Parkland wetland that initially contained fishes, and then underwent a drastic reduction in fish due to winter hypoxia, followed by a natural recovery.

I made the following predictions on the effects of fish on each of the invertebrate guilds I sampled. Amphipods and chironomids (omnivores) would be less abundant in the presence of fish than in their absence in Aspen Parkland, as would planorbids and other gastropods (herbivores). Fathead minnows can reduce the biomass and abundance of planorbid snails, amphipods and chironomids in the PPR, (Cox et al. 1998, Zimmer et al. 2001a, b). Hemipterans, leeches and dytiscids are predators and some tend to be associated with the presence of fathead minnow in PPR wetlands (Zimmer et al. 2001b). They may also attack small-bodied fish (Clifford 1991). Thus, I predicted that these invertebrates would be greater in biomass and abundance in the presence of these fishes. Based on the predictions for invertebrates, I predicted that the abundance of Red-necked Grebe would not differ significantly in the presence or absence of fish, because small fish do not have any negative relationships with the invertebrate prey of Red-necked Grebe, such as predatory invertebrates, and the grebes also eat fish (Stout and Nuechterlein 1999). Conversely, Blue-winged Teal would be less abundant in the presence of small-bodied fish, if fish have negative associations with their invertebrate prey, such as amphipods and chironomids.

For fish effects on bird foraging activities, I predicted that Red-necked Grebe, being opportunistically piscivorous (Stout and Nuechterlein 1999), would spend the same amount of time foraging in the presence/absence of fish, particularly since they eat larger invertebrates that may not be negatively affected by small-bodied fish. Because fish can reduce some of their invertebrate prey (amphipods, chironomids, gastropods; Taylor 1978, Rohwer et al 2002), I predicted that Blue-winged Teal would spend a greater proportion of the observed time foraging in the presence of fish than in their absence. Previous studies have shown that some waterbirds such as Black Duck (*Anas rubripes*) and Tufted Duck (*Aythya fuligula*) spend more time searching for food in the presence of fishes than in their absence (DesGranges and Rodrigue 1986, Giles 1990).

The reductions in amphipods, gastropods and chironomids that followed fathead minnow colonization of a prairie pothole were reversed when Zimmer et al. (2001a) removed the fish. Therefore, when monitoring the wetland that underwent winterkill and recovery of fish, I predicted that rapid increases in these invertebrates would follow a natural loss of fish from the wetland that underwent winterkill, with decreases occurring when they recovered. This prediction, if true, would further complement an experimental study on the effects of colonization and extirpation of fish on invertebrates and birds that is described in Chapter 4, and support the validity of Zimmer et al.'s (2001a) manipulative approach to studying the effects of fish colonization on prairie pothole invertebrates.

3.2 Methods

3.2.1 Study Sites: Fish and Environmental Sampling

I focused on Elk Island National Park (EINP) and Blackfoot Provincial Recreation Area (BPRA), two adjacent reserves that comprise a 292 km^2 remnant of the parkland in east-central Alberta, Canada (Lat 53°N, Long 112°W; Appendix 1). To determine fish status of the wetlands studied, I used standard unbaited activity traps (6mm mesh) to collect fathead minnows and brook sticklebacks. These traps were set for 24 hour periods at 25 m intervals along 100 m transects set within 2 m of shore, where fish were most likely to be found (Danylchuk and Tonn 2003). Fishes were counted and returned to their wetlands. Fish sampling was performed once a month in May-August 2000 and 2001. There was only modest variation in CPUE of fish in any of the wetlands with fish (mean CPUE = 0.39 $\pm$ 0.13fish/trap/hr, range = 0.01-1.80 fish/trap/hr). Thus, I performed most of the subsequent analyses based simply on fish presence/absence (but see 3.2.6). In this way, I established a set of 10 fishless and eight wetlands with fishes on which I monitored invertebrates and birds.

Ten of these wetlands (6 fishless, 4 with fishes) were monitored in 2000 and the remaining eight (4 fishless, 4 with fishes) were monitored in 2001. Previous studies (Chapter 2, Savard et al. 1994) indicate that limnological and morphometric characteristics of Aspen Parkland waterbodies such as total phosphorus, depth and area can be important determinants of invertebrate and bird assemblage composition. Thus, I also collected 1-litre water samples from each wetland in late May/early June 2000 and 2001, and analyzed them for total phosphorus and chlorophyll a content, as well as using a marked rope to measure depth. Depth data were based on the mean of 10 measurements taken in each wetland (Table 3.1).

3.2.2 Invertebrates in wetlands with and without fishes

In 2000 and 2001, I sampled nektonic invertebrates using bottle activity traps placed at 25 m intervals along the same 100 m transects used for fish traps in each wetland. Usually 2-3 transects were set in each wetland, i.e., 10-15 traps. Sampling was conducted four times: early June, late June, mid July and early August. This repeated sampling was intended to account for the (largely unknown) effects of invertebrate life cycles on their abundance and biomasses, and for the changing requirements of waterbirds for invertebrate protein (Taylor 1978). Zooplankton were sampled with a standard 243μm net trawled across the open water where possible (some wetlands were too shallow for this), and benthos were sampled using a combination of Ekman grabs and modified kick-sampling. All invertebrates were identified at least to family level, counted, and some samples were preserved (frozen) for biomass estimation. Frozen samples were: up to five *Dytiscus alaskanus* and 10 smaller dytiscid beetles; up to 10 glossiphoniid leeches per wetland, up to 10 chironomids and up to 10 amphipods. Since birds will select invertebrate prey based on size rather than on taxonomic identity (e.g. Nudds and Bowlby 1984), my emphasis was on sorting invertebrates into guilds rather than on obtaining fine taxonomic resolution. Invertebrates smaller than 250μm were not included in my analyses, since it was unlikely that the birds would consume them. I sorted invertebrates into the following guilds: omnivores (Chironomidae and Amphipoda), larger herbivores (all Gastropoda) and smaller herbivores (grazing zooplankton including Daphnidae and some copepods), small predators (Glossiphoniidae), medium predators (Corixidae, Notonectidae, Dytiscidae except *Dytiscus alaskanus*), and large predators (*Dytiscus alaskanus*, Erpobdellidae and Hirudinidae). I converted counts of invertebrates to catches per unit effort (CPUE, number of individuals per litre per hour) to account for the different types of collection methods. In calculating CPUE as numbers/L/hr, the time for grab and plankton net samples was taken as time to process grab or net contents and time for activity trap samples was taken as the duration the traps were set. For biomass estimates of the preserved invertebrates, I used either direct measurements of wet mass or wet mass data from the literature (Wrona, 1982; Benke et al., 1999). Biomass estimates were thus obtained for all guilds except smaller herbivores.

3.2.3 Abundance of Red-necked Grebe and Blue-winged Teal on wetlands with and without fishes

On the 18 wetlands described above, I counted all teals and grebes present before monitoring the foraging patterns of a subset of the birds (see 3.2.4) present on each wetland. Counts were conducted between 0500 and 1000 in early June, late June, mid July and early August, as closely in time to the invertebrate sampling as possible. I thus obtained counts for grebes and teals four times in each year on the wetlands that were being monitored for invertebrate biomass and foraging activity. In addition, I counted birds in early July and late August, to give a total of six sets of counts of both species on these 18 wetlands. Reproductive status and individual identity of teals observed on the wetlands could not be verified as this species commonly moves among multiple wetlands and nests in upland habitats (Rohwer et al. 2002). In contrast, most of the grebes observed had nests on the study wetlands.

3.2.4 Waterbird foraging patterns in wetlands naturally with and without fishes

In June-August 2000 and 2001, I conducted a series of four activity budgets for Red-necked Grebe and Blue-winged Teal on the eight wetlands with fish and 10 wetlands without fishes. I focused on up to three individuals of each species on each wetland. Each activity budget lasted for 20-25 minutes and was conducted between 0500 and 1000, immediately after the censuses described in 3.2.3. Activities for each individual were recorded every 30 seconds, to allow calculation of the proportion of total observed time spent in each activity. I then calculated the average proportion of observed time spent foraging by each species within each sampling session on each wetland from these data. Data from individuals that displayed no foraging behaviour during a sampling session were not included in any analyses to account for differential use of some sites (e.g., strictly for loafing) by teals in particular.

3.2.5 Waterbird foraging patterns and invertebrates in a wetland that underwent natural loss and natural recolonization of small-bodied fishes

In one of the wetlands that contained fish in 2000 (0.09 ± 0.06 fish/trap/hr), no fish were captured in 2001, but populations recovered in 2002 (0.03 ± 0.02 fish/trap/hr). To assess the responses of invertebrates and birds to these natural fluctuations, I monitored invertebrates and birds throughout the three-year period. I also continued to monitor one of the wetlands that had been fishless in 2000 and remained so in 2001 and 2002, as a reference for the fluctuating wetland. I used the data obtained from these two wetlands to perform Randomized Intervention Analysis (RIA; see 3.2.6) and thus determine whether any changes in birds and invertebrates associated with the loss and recovery of fish were significant.

3.2.6 Data analysis

For the broader surveys of invertebrates and birds on wetlands with and without fishes I used ANOVA with sampling period as a factor to determine whether fish presence/absence had any effect on the numbers (CPUE) or biomass of each invertebrate guild. Repeated measures were based on the sampling of invertebrates in each wetland during the four periods in June-August.

Before proceeding with analyses of bird count data (below), I performed Welch's t-test to determine whether fishless wetlands differed in area from wetlands with fish to ensure that area was not a confounding factor. Area data were obtained from GIS databases in Elk Island National Park. There was no significant difference in area between wetlands with and without fish (Welch's $t_8 = 1.573$, $p=0.153$, mean area fishless = 12.61 ha, mean area fish = 17.38 ha). Additionally, there were no correlations between grebe or teal abundance and area within any of the sampling sessions (Table 3.2). Thus, I was able to use abundance data rather than densities to assess the effects of fish presence/absence on bird abundance.

I used ANOVA that included time of year (sampling period) as a factor on square-root transformed count data to determine if there was any effect of fish on grebe or teal abundance. I used this ANOVA rather than repeated measures ANOVA because I could not be certain that the repeated counts of teals were on the same individuals. Teals move around between wetlands and thus the individuals viewed on a particular wetland at any point in the year may be different (Nudds and Ankney 1982). Although grebes show much greater site fidelity than teals, being highly territorial (Stout and Nuechterlein 1999), I did not use repeated measures ANOVA for counts of grebes because preliminary analyses showed similar results for grebes using both ANOVA models and using ANOVA with time of year as a factor for grebe counts was consistent with my treatment of count data for teals. I also used sampling year as a factor in these ANOVAs on bird counts. This allowed me to address the potential confounding effects of the drought that occurred in 2001 on any comparisons of wetlands with and without fish. Initial analyses of rainfall data from the EINP weather station showed a significantly higher mean rainfall in 2000 than in 2001 (mean daily rainfall for 2000 sampling sessions = 5.20 ± 0.69mm, mean for 2001 = 1.09 ± 0.18mm, Welch's t = 5.728, p = 0.000). This climate effect could confound any fish effects if strong enough, particularly since environmental factors such as lake depth can strongly influence bird community composition in Aspen Parkland (Chapter 2, Savard et al. 1994).

I initially assessed the effects of fish presence/absence on bird foraging activity using Friedman tests on the untransformed behaviour data. I performed ANCOVA on arcsine-transformed behaviour data using fish presence/absence as the main effect to attempt to couple fish effects on invertebrates with fish effects on birds. The covariates in these ANCOVAs were the biomasses of invertebrates, since previous studies (Zimmer et al. 2001b) suggested that this metric best reflects the effects of small-bodied fishes on invertebrate populations. Because the measures of behaviour were taken four times over the summer, I also added time of year as a factor to these ANCOVAs. Additionally, it was possible that fish effects on invertebrate biomasses and bird foraging were related to the numbers of fish present rather than simply fish presence/absence. Thus, for the wetlands with fish, I performed these same ANCOVAs, this time using fish CPUE as a factor rather than just fish presence. I also performed linear regressions between fish CPUE and invertebrate guild CPUE. Finally, since the Aspen Parkland system is highly dynamic, dominated largely by the amount of precipitation and evaporation in wetlands (Mitsch and Gosselink 2000), I used the more powerful but less conservative $\alpha = 0.10$ in these ANCOVAs and the ANOVAs described above.

For the wetland that underwent natural loss and recovery of fish and its fishless reference, I plotted time sequences of invertebrate biomasses to assess whether there were any changes in invertebrate assemblages following fish extirpation and recovery, and also monitored bird foraging patterns. I used Randomized Intervention Analysis (RIA;

Carpenter et al. 1989) to assess changes in bird foraging activity and invertebrate biomass in the winterkill and reference wetlands after fish loss and recovery. Although this technique is generally used for assessing ecosystem change relative to an unchanged reference following experimental manipulation, it could be applied to 'natural experiments' (*sensu* Diamond 1986) such as the winterkill and recovery of fish that occurred in this study. RIA assesses whether there is a non-random change in the average difference between an experimental system and a reference system following manipulation of the experimental system. Series of parallel observations of the data of interest are collected on experimental and reference systems before and after manipulation, and the series of intersystem differences (experimental-reference) is used to calculate average intersystem difference, $\bar{\mathbf{D}}$, pre- and post-manipulation. The absolute value of the change in average intersystem difference following the manipulation, $| \bar{D}\text{pre-}\ \bar{D}\text{post}|$, becomes the test statistic, with a distribution determined by random permutations of the sequence of intersystem differences (Carpenter et al. 1989). Then, $| \bar{D}\text{pre-}\ \bar{D}\text{post}|$ is calculated for each of these permutations to estimate the exact p-value of the test statistic. The goal of this analysis was to assess whether the natural disturbance, treated here as a manipulation, that resulted in loss and then recovery of fish, had any significant effects on invertebrate biomasses and bird foraging patterns.

I predicted that the biomasses of invertebrate omnivores, predators and herbivores would become more similar between the winterkill wetland and the fishless reference in 2001 than they had been in 2000, and that this convergence in biomass would reverse in 2002, when the fish recovered in the winterkill wetland. These changes would be due to an increase in omnivores and herbivores in the winterkill wetland following fish loss, and a decrease in predatory invertebrates (some of which are associated with the presence of fathead minnow; Zimmer et al. 2001a, b), abundance patterns which would reverse when fish returned to the system. I did not expect to see any difference in Red-necked Grebe foraging patterns, regardless of fish presence/absence (see above; Stout and Nuechterlein 1999). I predicted that Blue-winged Teal would spend a decreased proportion of observation time foraging in the winterkill wetland in 2001 than they had in 2000, so that foraging patterns became more similar between the winterkill and reference wetlands. This convergence would reverse when fish reappeared in 2002.

3.3 Results

3.3.1 Invertebrates in the presence or absence of small-bodied fishes

ANOVA (based on measurements made in the four time periods in June-August) showed that the catch per unit effort of large herbivores was unaffected by fish presence/absence. Small predators, large predators and omnivores were less numerous in fish wetlands (Table 3.3). Medium-sized predators were more numerous in the presence of fish. There was no significant difference in the biomasses of any invertebrate guild between wetlands with and without fish, and there were no consistent effects of time of year (sampling period) on the CPUE or biomass of any of the invertebrates (Table 3.3). The small herbivores on which biomass data were not collected were also not significantly more numerous in the absence of fish: mean CPUE was 3215.13 ± 5056.32/L/hr in fishless wetlands and 828.87 ± 4038.73/L/hr in wetlands with fish ($F_{1,3} = 2.995$, $p = 0.182$), although there were generally more of these invertebrates on fishless wetlands.

3.3.2 Abundance of Red-necked Grebe and Blue-winged Teal on wetlands with and without fish

Mean numbers of grebes and teals per wetland are shown in Table 3.4. For Red-necked Grebe, ANOVA on transformed count data did not reveal any effect of fish presence ($F_{1,99} = 1.168$, $p = 0.475$) or year alone ($F_{1,99} = 0.320$, $p= 0.672$), but showed some interaction between the effects of fish presence and year ($F_{1,99} = 3.070$, $p=0.083$). There was also no effect of time of year (sampling period) on grebe numbers ($F_{5,99} = 1.387$, $p=0.236$). The interaction between fish and year effects for grebes did not appear to be directly related to wetland depth, which was on average 1.00 ± 0.41 m in 2000 and 1.37 ± 0.52 m in 2001 ($t_1 = 1.665$, $p= 0.115$; Table 3.1).

For Blue-winged Teal, ANOVA on transformed count data showed that teals were more abundant in fishless wetlands ($F_{1,99} =271.779$, $p= 0.039$) and more abundant in 2000 than in 2001 ($F_{1,99} = 571.903$, $p=0.027$), with no significant interaction between the fish and year effects ($F_{1,99} = 0.01$, $p= 0.972$). There was no effect of time of year on teal numbers ($F_{5,99} = 1.540$, $p=0.184$).

3.3.3 Waterbird foraging patterns in relation to fish presence and invertebrate biomasses

In the 18 wetlands on which invertebrates and bird abundances had been monitored, Friedman tests showed that Red-necked Grebe and Blue-winged Teal did not exhibit a major difference in foraging activity between fish and fishless wetlands ($\chi 2 = 6.00$, $p=0.306$ for grebes; $\chi 2 = 8.00$, $p=0.156$ for teals; Figure 3.1).

ANCOVAs that included the biomasses of invertebrate guilds as covariates and used time of year as a factor showed no effect of fish on Red-necked Grebe foraging activity, although there was a positive association between foraging effort and biomass of omnivores ($F_{1,57} = 3.465$, $p = 0.068$). For Blue-winged Teal there was no effect of fish on foraging effort but there were positive associations between Blue-winged Teal foraging effort and the biomass of omnivores ($F_{1,59} = 3.782$, $p= 0.057$) and small predators ($F_{1,59} = 5.881$, $p = 0.018$). There was no consistent effect of time (sampling period) on bird behaviour for either species.

ANCOVAs that used fish CPUE on the subset of 8 wetlands with fish revealed no effects of fish CPUE on grebe or teal foraging patterns. Pearson correlations between fish CPUE and the foraging activities of grebes and teals were not significant ($r = 0.166$, $p = 0.194$ for grebes and $r = 0.031$, $p = 0.821$ for teals). For linear regression of fish and invertebrate CPUEs, the only significant relationships were between fish CPUE and CPUE of medium-sized predators (positive correlation, $r^2 = 0.126$, $p = 0.046$) and herbivores (negative correlation, $r^2 = 0.09$, $p = 0.098$).

3.3.4 Responses of invertebrates and waterbirds to a natural winterkill and fish colonization

Table 3.5 shows the p-values for the Randomized Intervention Analyses for all invertebrate guilds and bird foraging patterns. RIA showed that for large herbivores and small predators (Figures 3.2a and 3.2b), there was no significant change in the magnitude of intersystem differences between years, i.e., there was no change in the difference in biomass of these two guilds between the winterkill and reference wetlands.

The other invertebrate guilds showed statistically significant changes in intersystem biomass differences, due to large increases in biomass in the winterkill wetland in June 2002 after fish had returned to the system (Figures 3.2c-e). Within the winterkill wetland, for medium-sized predators, the major change appeared to be due to a large increase in the winterkill wetland in 2002, but both wetlands increased in that year (the winterkill wetland increased from 6.35 ± 2.20 mg/L in 2001 to 33.69 ± 26.37 mg/L in 2002, whilst the reference increased from 2.04 ± 0.41mg/L to 110.23 ± 8.02mg/L). Similarly, large predators increased dramatically in the winterkill wetland between 2001and 2002 (from 17.59 ± 1.92 mg/L in 2001 to 162.89 ± 82.53 mg/L in 2002), but there was also a large increase in large predators in the fishless reference wetland between these two years (biomass = 1.05 ± 1.05 mg/L in 2001, 56.10 ± 33.26 mg/L in 2002). Omnivores showed no change in biomass in the reference wetland across years, and no change in the winterkill wetland between 2000 and 2001. However, the biomass of omnivores increased in the winterkill wetland in 2002, rising from a mean of 0.40 ± 0.13 mg/L to 44.48 ± 31.40 mg/L. This increase resulted in a significant increase in intersystem difference between the biomasses of omnivores in the two wetlands.

RIAs showed no significant changes in foraging activities of either bird species in the winterkill wetland relative to the fishless reference in any pair of years (Table 3.5). Red-necked Grebes spent a greater proportion of observation time foraging in the winterkill wetland than in the fishless reference in 2000, more time foraging in the fishless reference in 2001, and similar amounts of time foraging in both wetlands in 2002 (Figure 3.2f). Blue-winged Teals spent a greater proportion of observation time foraging in the winterkill wetland than in the reference in 2000 and 2001, and similar amounts of time foraging in both wetlands in 2002 (Figure 3.2f). This convergence in foraging activities of teals between the two wetlands was about 25%, i.e., there was about a 25% drop in the proportion of observation time spent foraging by teals on the winterkill wetland relative to the reference.

3.4 Discussion

Wetlands of the Aspen Parkland constitute a naturally productive ecosystem that supports many species of breeding waterbird and generally only small-bodied fishes, the latter most likely due to the high incidence of winter hypoxia in wetlands that frequently disturbs north-temperate aquatic systems (Danylchuk and Tonn 2003). The effects of small-bodied fishes on waterbirds and their invertebrate prey in these naturally very disturbed and very productive aquatic systems are poorly known (but see Zimmer et al. 2001a,b), and most studies of waterbird-fish interactions have focused on large-bodied fishes (e.g. DesGranges and Rodrigue 1986, Giles et al. 1990). More generally, baseline observations of patterns in ecosystems are all too often neglected prior to performing experiments (Underwood et al. 2000). Observations of aquatic invertebrate abundance and biomasses, and of Red-necked Grebe and Blue-winged Teal foraging activity and abundance in my study showed only very limited effects of small-bodied fishes on invertebrates and on aquatic birds in Aspen Parkland wetlands. This was potentially because during the course of my study the Aspen Parkland underwent a severe drought, leading to increased winter hypoxia and low fish abundance in wetlands where fish were present.

3.4.1 Invertebrates in the presence or absence of small-bodied fishes

From surveys of 18 wetlands with and without fish, the negative relationship between fish and CPUE of small predators, large predators and omnivores (ANOVA), coupled with the lack of any fish relationship with invertebrate biomasses (ANOVA), suggests that there were fewer, larger individuals of these guilds in the presence of fishes. Thus, small-bodied fishes in Aspen Parkland may have effects on the population structure of these invertebrates, if not on their overall biomass. This is contrary to the effects on biomass seen in PPR wetlands with and without fathead minnow (Zimmer et al. 2001a). Whether wetlands with small fish and fewer, larger invertebrate prey are better or worse feeding sites for breeding Red-necked Grebes and Blue-winged Teals than fishless wetlands with more and smaller invertebrate prey is not known. Additionally, the CPUE of fishes in Aspen Parkland wetlands was quite low compared to other studies: 0.39 ±

0.13fish/trap/hr compared to nearly 30 fish/trap in the Batzer et al. (2000) study of fish-invertebrate interactions in New York marshes (which, since Batzer et al. (2000) set their traps for 24 hours, would be about 1.25 fish/trap/hr). It is possible that small-bodied fishes only have effects on invertebrate biomasses when at high densities (D. Batzer, pers. comm.).

3.4.2 Abundance of Red-necked Grebes and Blue-winged Teals on wetlands with and without fish

There was no effect of either fish status or year on Red-necked Grebe abundance (two-way ANOVA on transformed count data), and this was most likely due to the lack of any effect on invertebrate biomasses (see 3.4.1). This lack of response of grebes to fish presence/absence suggests that, at least when the densities of small-bodied fishes are low, Aspen Parkland wetlands with and without fish are equally viable feeding habitats for this species. Although fish reduce the numbers of some invertebrates, they are also eaten by Red-necked Grebe in North America (Stout and Nuechterlein 1999) and thus their presence does not represent a reduction in resources for Red-necked Grebes as it might for non-piscivorous waterbirds.

Blue-winged Teal also tended to use fishless wetlands more than wetlands with fish (two-way ANOVA). This is consistent with studies in oligotrophic systems that showed reduced lake use by Common Goldeneye, Mallard and Green –winged Teal in the presence of fish (Eriksson 1978, 1979, Pehrsson 1984, Eriksson 1987). In those studies, the proposed mechanism for reduced bird use was a reduction of invertebrate prey by fish. This study showed no differences in biomasses of any invertebrates between wetlands with and without fishes (see 3.4.1). Thus, if the presence of small-bodied fish has a negative effect on the numbers of Blue-winged Teal using Aspen Parkland wetlands, it is not due to any effect of fish on invertebrate biomass. Fish presence was associated with a lowered abundance (CPUE) of amphipods and chironomids, i.e., fewer, larger individuals. These invertebrates are preyed upon by Blue-winged Teals (Taylor 1978, Rohwer et al. 2002). Blue-winged Teals prefer prey in the 2.6 – 12.5mm size range and consume very little above 12.5mm (Nudds and Bowlby 1984). If the presence of fish results in fewer, larger prey items for teals, then this may lead to fewer teals being present on wetlands with fish.

The drought may also have caused a reduction in Blue-winged Teal abundance in 2001 (two-way ANOVA), which was consistent with continent-wide surveys (CWS/USFWS, unpubl. data) for waterfowl. In 2001, these large-scale surveys showed that Blue-winged Teal numbers were reduced by 42% relative to a long term average (based on surveys conducted from 1955 to the present). There was no interaction between fish and year effects in the ANOVA. Thus, the drought did not apparently confound any effects of fish on Blue-winged Teal abundance.

3.4.3 Waterbird foraging patterns in relation to fish presence and invertebrate biomasses

Neither Friedman tests nor the ANCOVAs on foraging activity of Red-necked Grebe and Blue-winged Teal showed any effect of fish on bird foraging patterns. This was the case for the ANCOVAs on all 18 wetlands based on fish presence/absence, and on the 8 wetlands with fish based on fish abundance (CPUE). For both Red-necked Grebe and Blue-winged Teal, the proportions of observed time spent foraging were positively related to the biomasses of some invertebrates: primarily omnivores (amphipods, chironomids) which are prey of Blue-winged Teal (Taylor 1978, Rohwer et al. 2002). Thus, fish appeared to have no effect on waterbird foraging patterns because they had no effect on invertebrate biomass (3.4.1), contrary to other studies of waterbird-fish competition (e.g. Giles 1990, Cox et al. 1998).

For Blue-winged Teal, the lack of effect of fish on foraging activity may at first glance seem contradictory to the effects of fish on Blue-winged Teal abundance. However, if there are fewer teals in the presence of fish than in their absence, due to a change in the size distributions of invertebrate prey (3.4.2), teals on wetlands with and without fish may be distributed in such a way as to spend similar amounts of time foraging. Predicting teal distributions in the presence/absence of fish, however, would require a much more detailed assessment of the size distributions of their invertebrate prey than offered by this study.

3.4.4 Responses of invertebrates and waterbirds to a natural winterkill and fish recovery

The biomasses of five invertebrate guilds showed no change in the winterkill wetland relative to a fishless reference when fish were extirpated in 2001(RIAs). There were, however, large increases in the biomasses of medium and large predators and omnivores in the winterkill wetland following fish recovery in 2002. These increases were significant relative to the biomasses of these guilds in the fishless reference in 2002. Thus, the fish recovery had a positive effect on the biomasses of predatory invertebrates and omnivores (Figure 3.2c-e). This conclusion is consistent with Zimmer et al. (2001a, b) for the medium-sized predators, which were positively associated with prairie potholes that contain fathead minnows. It is also consistent with Batzer et al. (2000) for the omnivores: although marsh fishes prey on omnivores such as chironomids, they can have indirect positive effects on chironomids when added to mesocosms, because they also consume some of their competitors (e.g., gastropods). However, the results of the RIAs should be interpreted with caution (Carpenter et al. 1989) because of the increases in predator and omnivore biomasses that also occurred in the fishless reference in 2002. This result suggested that there are other unknown factors, besides fish recovery from winterkill, which can affect the biomasses of these invertebrates. Possibilities include responses to changes in water levels or oxygen content (e.g., prairie marsh invertebrates show changes in diversity along the course of a wet-dry cycle; Murkin et al. 2000).

As predicted, Red-necked Grebe foraging patterns appeared unaffected by either the fish extirpation or the recovery. The grebes will eat fathead minnow and brook stickleback (Stout and Nuechterlein 1999), and thus, as discussed for the broader wetland survey, are unlikely to change their foraging activity because of changes in these fish. For Blue-winged Teal, there was no relationship between foraging patterns and fish extirpation or recovery, particularly since they foraged more in the winterkill wetland than the reference in 2000 and 2001, despite the winterkill event.

3.4.5 Conclusions

Due to the low densities at which Aspen Parkland fish populations were sampled in this study, their influences on invertebrate prey of waterbirds were much more limited than in other wetlands such as New York marshes, where fish were found at high densities (Batzer et al. 2000). Negative effects of fish on invertebrates and waterbirds were limited to effects on abundance, which suggests that small-bodied fish can only influence the foraging patterns of Red-necked Grebe and Blue-winged Teal if they are at high enough densities to affect the biomasses of the invertebrate prey. The lack of relationship between numbers of fish and invertebrates or birds in this study suggests that none of the ponds had fish at a high enough density to address this question clearly. Studies that monitored waterbird foraging and abundance, and invertebrate abundance and biomass, along marked gradients of fish density would help to determine whether there really is some critical density of fish below which they have no negative effects on birds and invertebrates.

Finally, the RIAs showed that small-bodied fish could have some effect on invertebrate biomasses when they recover from winterkill in Aspen Parkland wetlands. This was consistent with the reductions in invertebrate abundances and biomasses in prairie potholes that occurred with colonization by fathead minnows (Zimmer et al. 2001a). But since teal foraging and invertebrate biomasses were unaffected by fish status of wetlands in the broader scale surveys, this seemed contradictory to the RIA results. A useful way to reconcile this contradiction might be to monitor invertebrates and birds in wetlands at different time intervals after fish colonization: immediately afterwards, one season later, and so on. In short, the baseline observations obtained in this study showed some useful patterns (Underwood et al. 2000) and revealed that the potentially negative effects of fish on waterbirds and their invertebrate prey may be limited by fish density – but these observations could and should be followed up with experiments on the effects of fish colonization on invertebrate biomasses and bird foraging patterns.

3.5 References

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Table 3.1 Limnological characteristics of the ten fishless wetlands and the eight wetlands with fish sampled in 2000 and 2001. Data are based on samples taken in June of each year. Fish status: 0 = fishless, 1 = contains fish. TP = phosphorus, chl. a = chlorophyll a.

Lat/Lng	Area (ha)	TP (μg/L)	Chl. a (μg/L)	Mean depth (± s.d.)	Fish status	Sampling Year
53°40’N 112°52’W	12.77	54.65	4.67	1.19 (0.07)	1	2000
53°29’N 112°46’W	29.36	152.30	15.50	0.68 (0.24)	1	2000
53°35’N 112°47’W	13.20	84.35	13.95	1.40 (0.19)	1	2000
53°34’N 112°52’W	9.64	97.55	18.34	1.30 (0.12)	1	2000
53°42’N 112°50’W	11.90	31.40	10.15	1.41 (0.19)	0	2000
53°40’N 112°50’W	14.78	60.95	1.30	0.40 (0.05)	0	2000
53°34’N 112°48’W	5.46	235.85	45.94	0.86 (0.13)	0	2000
53°34’N 112°54’W	17.62	117.85	15.31	0.34 (0.07)	0	2000
53°30’N 112°56’W	10.88	95.75	21.95	1.06 (0.33)	0	2000
53°32’N 112°46’W	7.69	106.60	13.55	1.41 (0.15)	0	2000
53°29’N 112°45’W	23.44	42.30	7.73	2.48 (0.53)	1	2001
53°33’N 112°58’W	22.23	62.70	17.38	1.03 (0.47)	1	2001
53°42’N 112°49’W	11.86	26.80	9.39	1.51 (0.13)	1	2001
53°36’N 112°55W	89.57	113.40	40.89	1.31 (0.62)	1	2001
53°40’N 112°47’W	14.11	76.55	30.58	1.49 (0.18)	0	2001
53°41’N 112°50’W	16.62	91.85	1.98	1.27 (0.22)	0	2001
53°43’N 112°50’W	13.51	47.95	1.35	0.71 (0.11)	0	2001
53°35’N 112°57’W	11.47	98.65	1.73	1.16 (0.27)	0	2001

Table 3.2: Pearson correlations between wetland area (in ha) and abundance of Red-necked Grebes and Blue-winged Teals in early June, late June, early July, mid July, early

August and late August. Ten of the wetlands were censused in 2000 (4 with and 6 without fish) and eight were censused (4 with and 4 without fish) in 2001. P-values are given in parentheses.

	Red-necked Grebe	**Blue-winged Teal**
Early June	0.266 (0.306)	0.387 (0.125)
Late June	-0.113 (0.665)	0.375 (0.139)
Early July	-0.111 (0.670)	-0.096 (0.713)
Mid July	-0.402 (0.110)	-0.039 (0.883)
Early August	0.037 (0.889)	-0.232 (0.370)
Late August	-0.013 (0.961)	0.268 (0.299)

Table 3.3: Results of ANOVA on the CPUE and biomasses of five invertebrate guilds collected in eight wetlands with fish and ten fishless wetlands in Aspen Parkland wetlands. Boldface = significant at $\alpha = 0.10$.

	CPUE (#/L/hr)			**Biomass (mg/L)**		
Invertebrate Guild	**Mean fish (s.d.)**	**Mean fishless (s.d.)**	**F (p)**	**Mean fish (s.d.)**	**Mean fishless (s.d.)**	**F (p)**
Large herbivores	9.18 (20.32)	2.40 (3.15)	2.751 (0.196)	2.47 (2.39)	2.33 (4.23)	0.019 (0.898)
Small predators	3.53 (7.27)	6.41 (10.16)	**11.973 (0.041)**	0.11 (0.29)	0.10 (0.14)	0.274 (0.637)
Medium predators	25.15 (34.12)	9.97 (13.52)	**5.937 (0.093)**	2.12 (3.98)	4.7 (18.37)	1.278 (0.340)
Large predators	3.94 (6.34)	7.92 (13.76)	**8.442 (0.062)**	11.29 (15.82)	8.23 (16.92)	0.576 (0.503)
Omnivores	19.09 (24.50)	32.84 (42.83)	**11.19 (0.044)**	0.65 (1.11)	0.30 (0.30)	2.909 (0.187)

Table 3.4: The number of Red-necked Grebes and Blue-winged Teals per wetland on Aspen Parkland ponds (1) with and without fish in both years and (2) on all ponds surveyed in 2000 versus 2001. For (1), there were 8 ponds with fish and 10 ponds without fish. For (2), 10 ponds were monitored in 2000 and 8 ponds were monitored in 2001. Six counts were taken throughout the seasons of May-August 2000 and 2001.

(1)

Red-necked Grebe

Count	**1**	**2**	**3**	**4**	**5**	**6**
Fish	4.6	4.3	8.9	5.9	5.0	4.0
Fishless	2.8	5.1	4.9	4.1	2.6	2.0

Blue-winged Teal

Count	**1**	**2**	**3**	**4**	**5**	**6**
Fish	3.4	4.1	3.5	3.3	1.6	6.8
Fishless	2.7	1.8	2.8	4.7	11.2	10.8

(2)

Red-necked Grebe

Count	**1**	**2**	**3**	**4**	**5**	**6**
2000	3.3	5.9	4.7	4.8	3.7	1.2
2001	4.0	3.3	9.1	5.0	4.9	5.0

Blue-winged Teal

Count	**1**	**2**	**3**	**4**	**5**	**6**
2000	2.4	2.8	3.4	4.6	9.0	12.5
2001	3.8	2.9	2.8	3.4	4.4	4.6

Table 3.5: Changes in average intersystem difference, $|\bar{D}pre - \bar{D}post|$, and p-values for Randomized Intervention Analyses on wet biomass (mg/L) of five invertebrate guilds in an Aspen Parkland wetland that underwent winterkill and recovery, compared to a fishless reference wetland. Values for Red-necked Grebe and Blue-winged Teal foraging patterns are also shown. For the biomasses of each invertebrate guild, RIA tested whether there was a non-random change in the difference between the winterkill wetland and its reference following changes in fish status. Significant results are indicated by boldface, p-values are in parentheses. RNGR=Red-necked Grebe, BWTE=Blue-winged Teal

Years Compared	**2000/2001**	**2001/2002**	**2000/2002**
Herbivores	0.63	12.76	13.39
	(0.714)	(0.185)	(0.209)
Small predators	1.32	1.55	2.87
	(0.278)	(0.123)	(0.083)
Medium predators	4.65	19.15	**23.80**
	(0.076)	(0.367)	**(0.019)**
Large predators	0.43	**90.25**	89.82
	(0.968)	**(0.000)**	(0.130)
Omnivores	0.58	**43.71**	**43.13**
	(0.137)	**(0.000)**	**(0.000)**
RNGR	10.05	9.00	1.06
	(0.197)	(0.538)	(0.940)
BWTE	4.48	25.01	29.48
	(0.849)	(0.241)	(0.099)

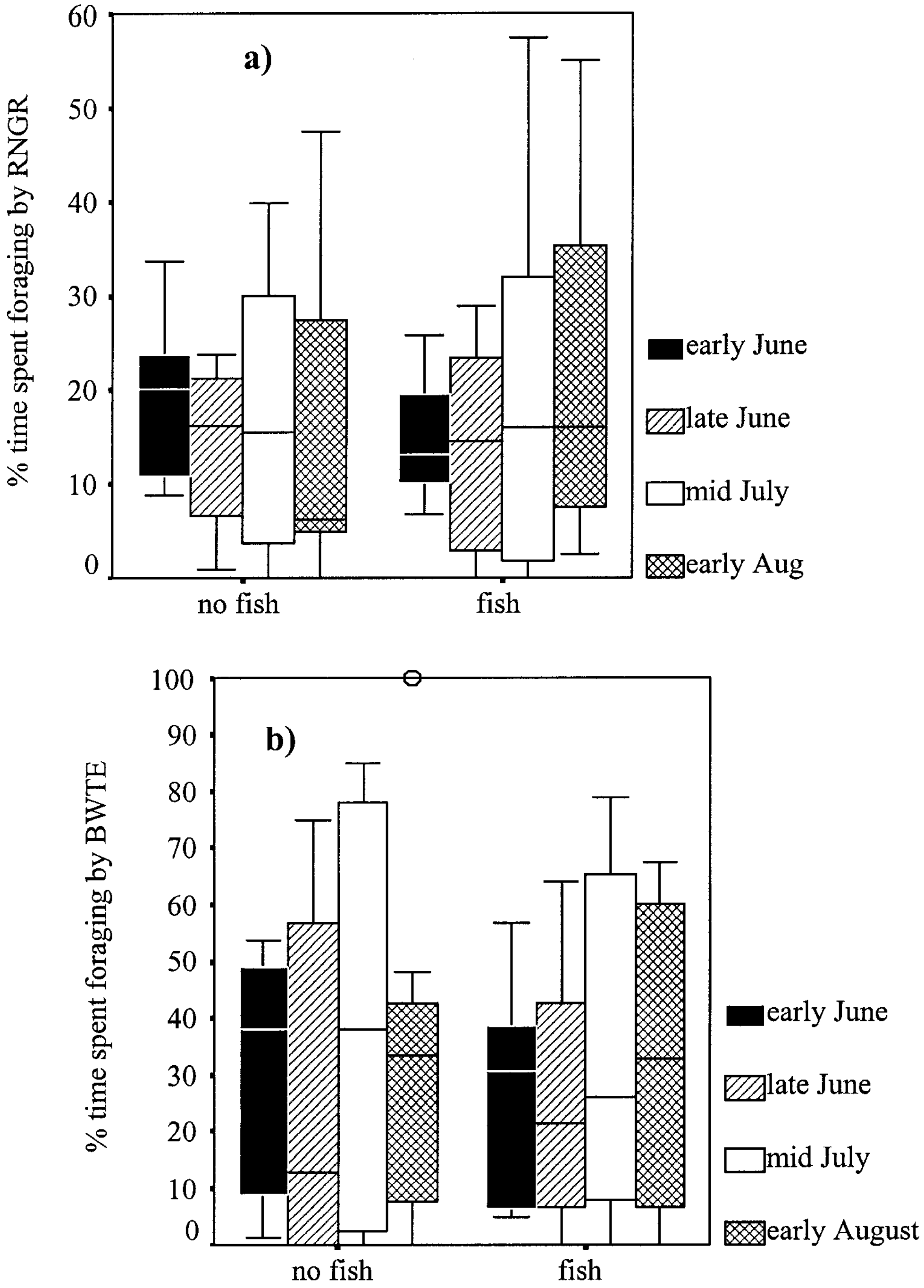
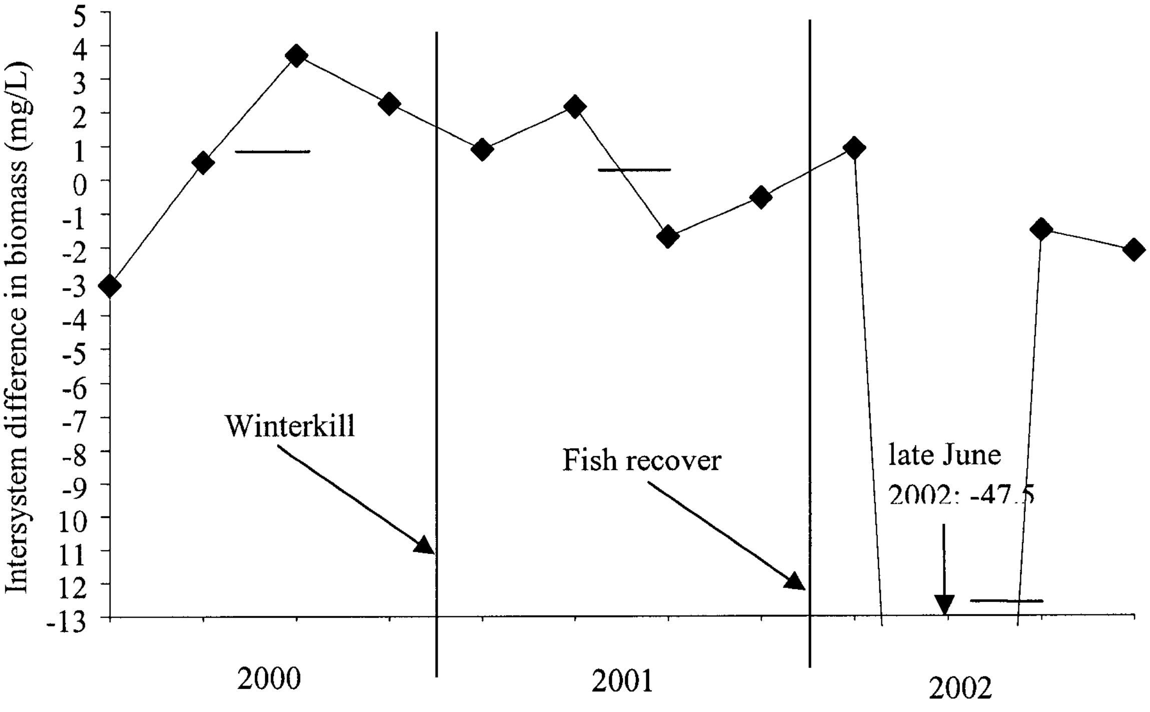
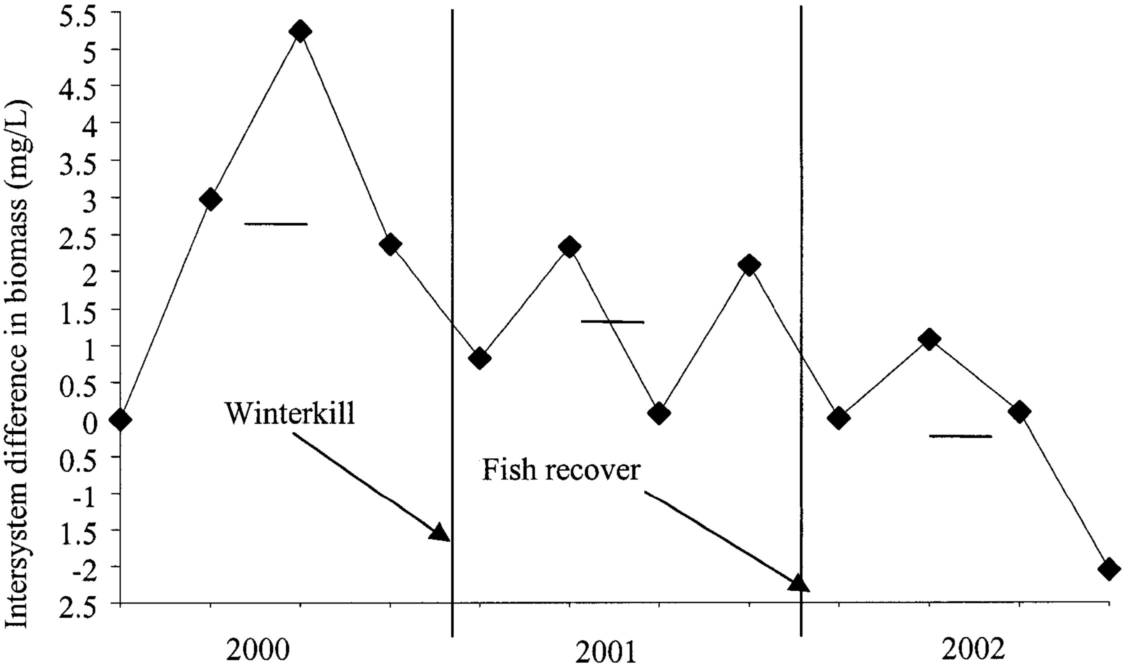


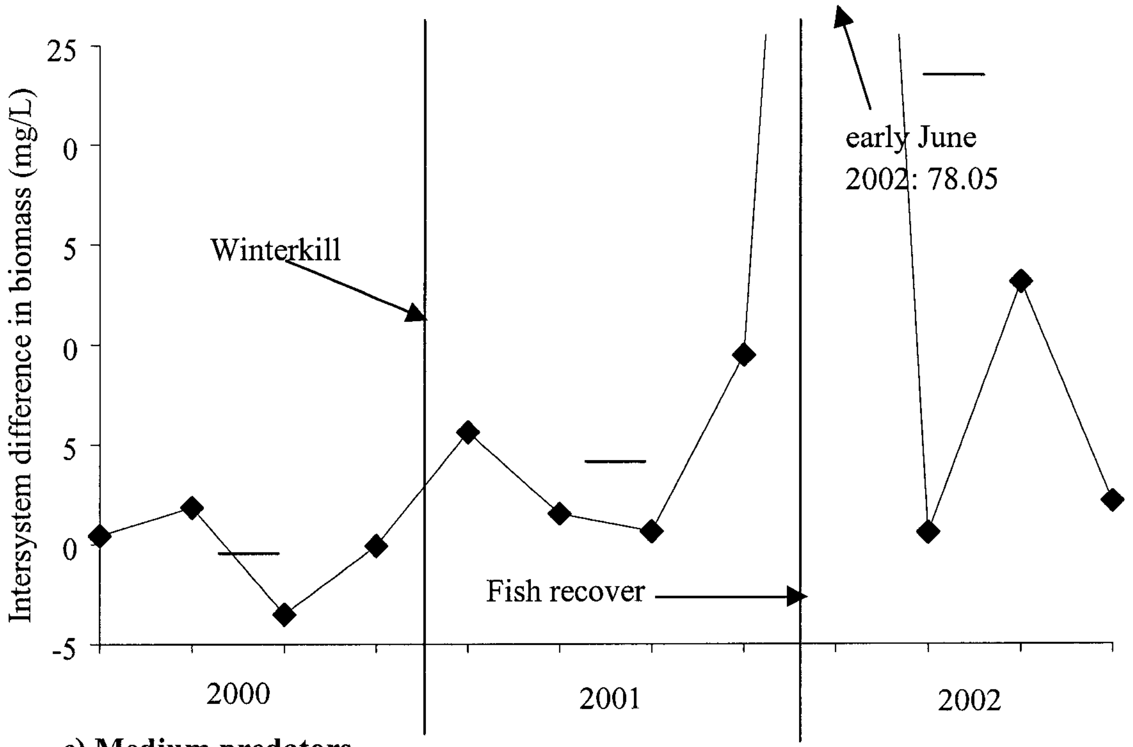
Figure 3.1 Foraging effort of (a) Red-necked Grebes and (b) Blue-winged Teals in ten wetlands without and eight wetlands with fish sampled in 2000 and 2001. Samples from each wetland were based on mean activity budgets of up to three individuals in each sampling period. Six of the fishless wetlands and four of the fish wetlands were sampled in 2000; the remaining 8 wetlands were sampled in 2001. Boxplots show medians for foraging efforts in wetlands with and without fish, with interquartile ranges.



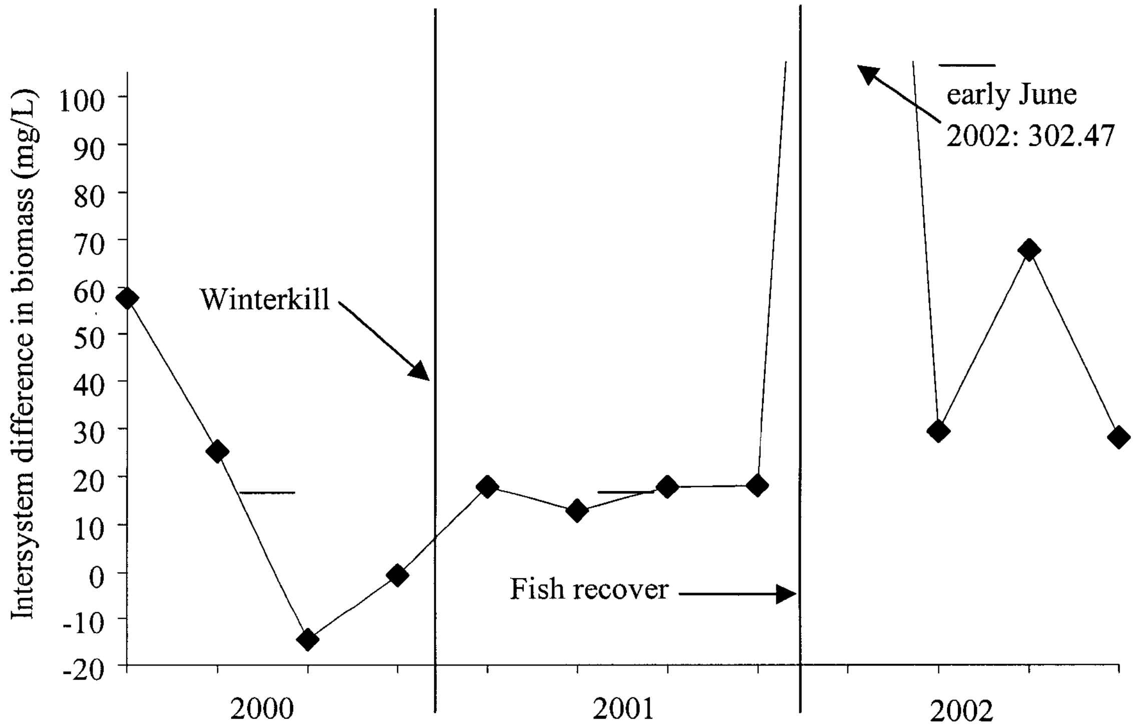
a) Herbivores



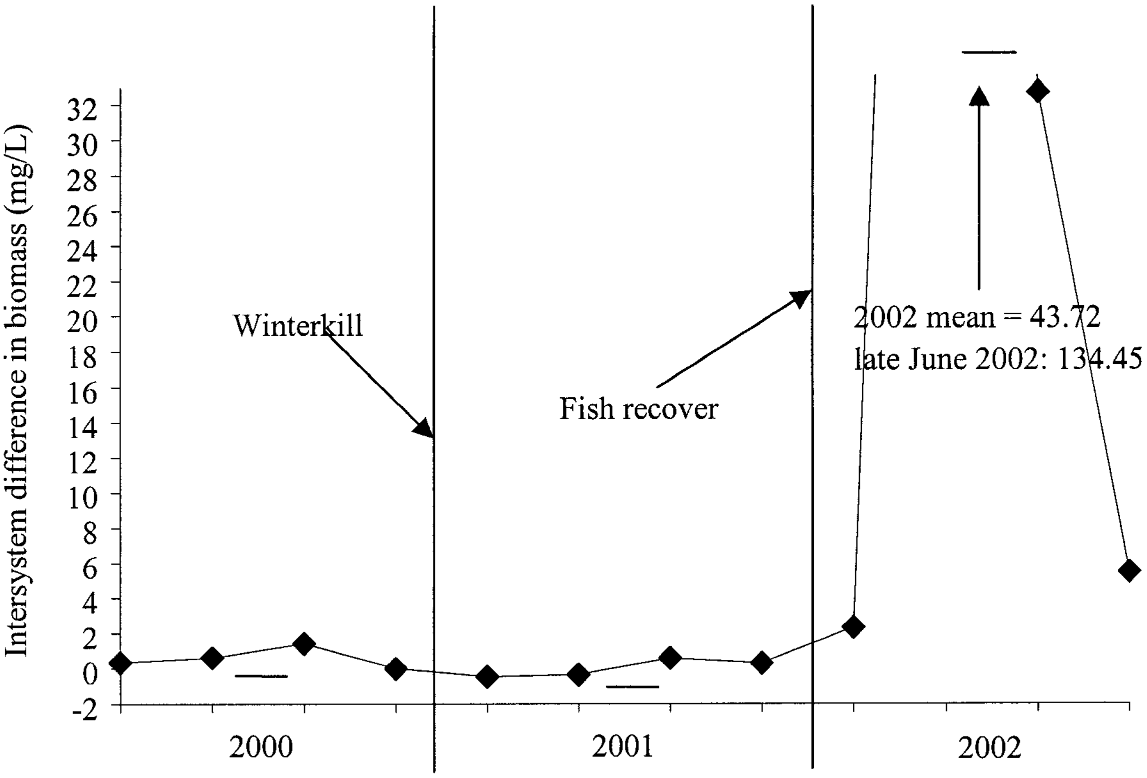
b) Small predators



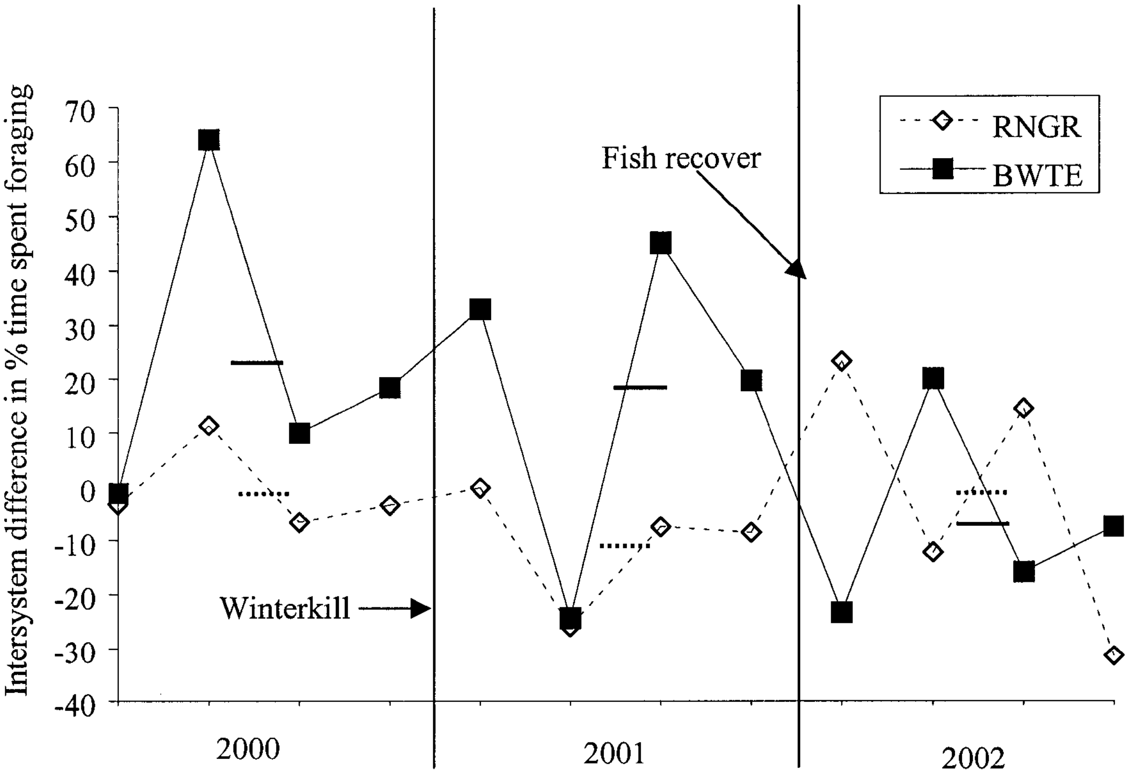
c) Medium predators



d) Large predators



e) Omnivores



f) Birds

Figure 3.2: Randomized Intervention Analysis (RIA) of (a) large herbivore (gastropods), (b) small predator (glossiphoniid leeches), (c) medium predator (hemipterans, small dytiscids), (d) large predator (erpobdellid leeches, *Dytiscus alaskanus*), (e) omnivore (amphipods, chironomids) biomasses and (f) Red-necked Grebe (RNGR) and Blue-winged Teal (BWTE) foraging patterns in an Aspen Parkland wetland in which fish naturally disappeared and recovered compared to a fishless reference. RIA assesses the change in mean *difference* between two systems before and after a manipulation. Horizontal bars = mean intersystem differences in each year.

Chapter 4: Consequences of Fish-Invertebrate Interactions for Foraging Waterbirds in Aspen Parkland: An Experimental Approach.

4.1 Introduction

Competition between large-bodied fish and waterbirds for invertebrate prey is well documented in North American and European oligotrophic lake systems. Eurasian perch (*Perca fluviatilis*), yellow perch (*Perca flavescens*), and roach (*Rutilus rutilus*) show substantial diet overlap with Common Goldeneye (*Bucephala clangula*), American Black Duck (*Anas rubripes*), Mallard (*Anas platyrhynchos*) and Green-winged Teal (*Anas crecca*; Eriksson 1978, Eadie and Keast 1982, DesGranges and Rodrigue 1986). However, waterbird-fish competition is poorly understood in shallow eutrophic systems (*but see* Giles et al., 1990), such as the prairie potholes or Aspen Parkland potholes of North America. These systems often experience winter hypoxia that leads to mortality ("winterkill") of intolerant, often large-bodied fish species (Robinson and Tonn 1989, Tonn et al. 1995).

Fishes reduce invertebrates even in eutrophic, hypoxia-prone systems like prairie potholes that only support small-bodied fishes (Zimmer et al. 2001). Waterbirds' use of eutrophic wetlands can also increase when fishes are removed in biomanipulations (Hanson and Butler 1994, Andersson and Nilsson 1999). It may therefore benefit breeding waterbirds that rely on invertebrates if small fishes are removed or excluded from such systems. But fish removals do not always result in an increase in invertebrate prey for waterbirds, because the methods used can kill invertebrates (e.g., toxaphene; Miskimmin and Schindler 1994). Predatory invertebrates such as *Chaoborus obscuripes* can also occupy the trophic positions of small fishes after removals (Benndorf et al. 2000). Small-bodied fishes also frequently colonize and disappear from eutrophic hypoxia-prone wetlands in wet and dry years, respectively (Mitsch and Gosselink 2000). Thus, simply removing fish to enhance habitat for waterbirds may not be the most appropriate management action for systems like Aspen Parkland or prairie potholes that are strongly influenced by precipitation and evapotranspiration and undergo a 5-20 year wet-dry cycle (Mitsch and Gosselink 2000). Where small wetlands are anthropogenically consolidated into larger, deeper, more permanent waterbodies, colonizing fish are more likely to survive drought years than they would in the original configuration of small, shallow wetlands – thus reducing the invertebrates available to waterbirds. Thus, it might be useful to complement the findings of the aforementioned fish removal/extirpation-based studies by studying the effects on invertebrates and waterbirds of colonization of eutrophic, hypoxia-prone wetlands by small-bodied fishes.

The effects of colonization of such wetlands by small-bodied fishes have only been studied in prairie potholes. Cox et al. (1998) found that chironomid densities and Mallard duckling growth rates were lower in prairie pothole mesocosms with high fish densities. Zimmer et al. (2001) observed reductions in amphipods and planorbid snails following a natural colonization of prairie potholes by fathead minnow (*Pimephales promelas*). It is not clear whether these reductions are limited to highly omnivorous fish species such as the fathead minnow (Keast 1985), or can be exerted by species of a more restricted diet, such as brook stickleback (*Culaea inconstans*). The objective of this study, therefore, was to document changes in invertebrate assemblages and waterbird foraging activities after a simulated colonization by small-bodied fishes of eutrophic pothole wetlands of a previously poorly studied ecoregion: North America's Aspen Parkland.

I added fathead minnows and brook sticklebacks to two fishless Aspen Parkland wetlands, monitoring invertebrates and foraging activities of Blue-winged Teal (*Anas discors*) and Red-Necked Grebe (*Podiceps grisegena*) before and after that addition. These two species are common in Aspen Parkland and use the same wetlands in different ways, the grebe being a diver and the teal being a dabbler. Foraging behaviour is a relevant metric to use to assess effects of fish on breeding waterbirds, because any increase in time invested in foraging by birds, as a result of fish colonization and reduction of invertebrate prey, necessarily means a reduction in time available for activities like incubation. Time available to incubate eggs and successfully fledge young is an important limitation for birds breeding in temperate systems like Aspen Parkland, especially smaller birds that produce precocial young like Blue-winged Teal (Kendeigh 1970, Drent and Daan 1980). Based on previous studies of bird foraging in the presence/absence of fishes (DesGranges and Rodrigue 1986, Giles 1990), I predicted that Blue-winged Teals would spend a greater proportion of observed time foraging after fish addition than before, due to a reduction in the availability of their invertebrate prey. Red-necked Grebes, being opportunistically piscivorous (Stout and Nuechterlein 1999), would spend the same amount of time foraging before and after fish addition, particularly since they eat larger invertebrates that may not be negatively affected by small-bodied fish. This prediction is especially valid if the added fish reduce some of the invertebrate prey available to grebes, effectively replacing them as a food source for grebes (see below). Since fathead minnows reduce the biomass of planorbid snails, amphipods and chironomids (Cox et al. 1998, Zimmer et al. 2001), I predicted that amphipods and chironomids (omnivores) would be reduced following fish addition, as would planorbids and other gastropods (herbivores). Corixids, notonectids and dytiscids are predators, some of which can attack adult fish or at least eat fry (Clifford 1991) would increase in biomass following the addition of these fishes since their prey base has been added to. Finally, I predicted that if the introduced fishes failed to overwinter due to hypoxic conditions, their effects on invertebrates and birds would be reversed.

4.2 Methods

4.2.1 Study Area

North America's Aspen Parkland, a transitional zone between prairies and boreal forest (Nicholson and Vitt, 1994), contains many shallow meso- to hypereutrophic freshwater potholes (~30μg/L to >400μg/L total phosphorus; Nicholson 1995, Chapter 2) that support many species of waterbird (Savard et al. 1994). Most wetlands in the parkland are rarely deeper than 1.5 m (Savard et al. 1994, Chapter 2). The fish fauna often consists only of fathead minnow and brook stickleback, which are very tolerant to low oxygen levels (Nelson and Paetz 1992). I focused on Elk Island National Park (EINP) and Blackfoot Provincial Recreation Area (BPRA), two adjacent reserves that comprise a 292 km^2 remnant of the Aspen Parkland in central Alberta, Canada (Lat 53°N, Long 112°W; Appendix 1).

In June-August 2000, I monitored invertebrates and foraging activity of Red-necked Grebes and Blue-winged Teals on two wetlands with fishes and four fishless wetlands in the Aspen Parkland. I measured average depth using a marked rope, total phosphorus and chlorophyll *a* (Table 4.1) in each of these wetlands in June 2000, since earlier studies of Aspen Parkland wetlands showed that these factors were important determinants of waterbird assemblage composition (Chapter 2, Savard et al. 1994). Pearson correlations showed no relationships between these factors and bird foraging activity in this particular set of six wetlands.

4.2.2 Invertebrate sampling

In early June, late June, mid July and early August, I sampled nektonic invertebrates using bottle activity traps placed at 25 m intervals along 100 m transect within 2 m of shore in the six wetlands described above. Benthos were sampled using a combination of Ekman grabs and kick-sampling along shore with a D-net. Since birds select invertebrate prey based on size rather than on taxonomic identity, my emphasis was on sorting invertebrates into guilds rather than on obtaining fine taxonomic resolution. Invertebrates smaller than 250 μm were excluded from my analyses, since it was unlikely that the birds would consume them (Nudds and Bowlby 1984, Stout and Nuechterlein 1999). I sorted invertebrates as follows: omnivores (Chironomidae, Amphipoda), herbivores (Gastropoda), small predators (Glossiphoniidae), medium predators (Corixidae, Notonectidae, Dytiscidae except *Dytiscus alaskanus*), and large predators (*Dytiscus alaskanus*, Erpobdellidae and Hirudinidae). Zooplankton were not sampled as some wetlands were too shallow at times to trawl a plankton net. All invertebrates were identified at least to family, counted, and some samples were preserved (frozen) for biomass estimation. Frozen samples were of beetles: up to five *D. alaskanus* and 10 smaller dytiscids per wetland; up to 10 glossiphoniid leeches per wetland, up to 10 chironomids and up to 10 amphipods per wetland. I converted counts of invertebrates to catch per unit effort (CPUE, number of individuals per litre of sampling device per hour; time for grab samples was taken as time to process grab contents; Chapter 3) to account for the different types of collection methods, and then used either direct measurement of wet mass or wet mass data from the literature (Wrona 1982, Benke et al. 1999) to convert numbers of invertebrates to biomass for all guilds.

4.2.3 Bird behaviour monitoring

During the same four periods described above, I collected activity data on teal and grebe from all wetlands. I focused on up to three individuals of each species on each wetland per sampling session. Each activity budget lasted for 20-25 minutes and was conducted between 0500 and 1000, waiting about 5 minutes after arrival at each wetland before beginning recordings, to account for any disturbance caused by observers. Activities for each individual were recorded every 30 seconds, to allow calculation of the proportion of total observed time spent in each activity. I then calculated the average proportion of observed time spent foraging (dabbling for teals, diving for grebes) by grebes and teals on each wetland from these data. In the two wetlands with fishes, I used standard wire mesh traps (6mm mesh) to collect fathead minnow and brook stickleback. Since the study area entered a severe drought period in 2000, I wished to ensure that fish did not disappear from these wetlands early on in the study. These traps were set at 25m intervals along the same 100m transects used for the invertebrate activity traps. Fishes were counted and returned to their wetlands. Fish sampling was performed once a month in May-August 2000.

4.2.4 Fish addition to fishless wetlands

In late May 2001, I collected 8000 brook stickleback and fathead minnow (about 4000 of each species) from a lake in the same watershed as the study wetlands. I added 2000 individuals of each species to two of the wetlands that had been fishless in 2000. These two wetlands, both of which were about 10 ha in area, were designated Experimental Wetland 1 (EW1; Lat 53°30’N, Long 112°56’W) and Experimental Wetland 2 (EW2; Lat 53°32’N, Long 112°46’W). Fishes were fin-clipped (pelvic fin) and treated with Furan-2 antibiotic before introduction into experimental wetlands. The other four wetlands from 2000 were used as references: two fishless references [NF1 (53°40’N/112°50’W) and NF2 (53°42’N/112°50’W)] and two fish references [F1 (53°34’N/112°52’W) and F2 53°29’N/112°46’W)]. I sampled bird activity, fishes and invertebrates in the six wetlands according to the protocol described for 2000, and repeated the sampling in 2002. I did not find fish in the two experimental ponds in 2002. Thus, I could determine whether any changes in invertebrates and birds’ foraging effort that followed fish introduction in 2001 were reversed when fish were eliminated, presumably due to winterkill.

4.2.5 Data analysis

I used Randomized Intervention Analysis (RIA; Carpenter et al. 1989) to assess changes in bird foraging activity and invertebrate biomass in the experimental wetlands after fish addition. RIA assesses whether there is a non-random change in the average difference between an experimental system and a reference system following manipulation of the experimental system. Series of parallel observations of the data of interest are collected on experimental and reference systems before and after manipulation, and the series of intersystem differences (experimental-reference) is used to calculate average intersystem difference, $\bar{D}$, pre- and post-manipulation. The absolute value of the change in average intersystem difference following the manipulation, $|\bar{D}\text{pre-}\ \bar{D}\text{post}|$, becomes the test statistic, with a distribution determined by random permutations of the sequence of intersystem differences (Carpenter et al. 1989). Then, $|\bar{D}\text{pre-}\ \bar{D}\text{post}|$ is calculated for each of these permutations to estimate the exact p-value of the test statistic. For clarity, and since in many cases the patterns of response were similar, I present only analyses of comparisons of EW1 with the references NF1 and F1, as these demonstrated the patterns of response most clearly.

4.3 Results

4.3.1 Invertebrate responses to fish addition

The wet biomass of herbivores (gastropods) and small predators (glossiphoniids) decreased following addition of fish to Experimental Wetland 1. Herbivores increased in 2002 after the winterkill, whilst small predators continued to decrease. Medium-sized predators (hemipterans and dytiscids except *Dytiscus alaskanus*) remained at almost the same biomass after fish addition in 2001, but increased in 2002 (Table 4.2). The biomass of large predators (*D. alaskanus*, large leeches) and omnivores (amphipods/chironomids) increased in 2001 and remained at similar levels in 2002. Catch per unit effort of all guilds except large predators increased in EW1 across the period 2000-2002 (Table 4.2).

4.3.2 Invertebrate wet biomass in Experimental Wetland 1 compared to Fish Reference 1

For Randomized Intervention Analysis (RIA) of invertebrate wet biomasses that compared EW1 to F1 or NF1, the absolute values of the changes in intersystem differences, $| \bar{D}\mathrm{pre} - \bar{D}\mathrm{post}|$, and their associated p-values, are shown in Table 4.3. RIA showed that wet biomass of all invertebrate guilds was similar between EW1 and F1 in 2000, the year before fish addition, and did not change significantly following manipulation in 2001. Wet biomasses of herbivores (Figure 4.1) and small predators (Figure 4.2) became slightly more similar between EW1 and F1 in 2001. Between 2000 and 2001, the greatest observed change in intersystem difference between EW1 and F1 in wet biomass of invertebrates was for medium predators.

Between 2001 and 2002, average intersystem difference between EW1 and F1 in wet biomass of herbivores, small predators and omnivores changed significantly, after the winterkill events in both wetlands (Table 4.3). For herbivores and small predators, intersystem differences between EW1 and F1 in 2002 converged with the original differences in 2000. Medium and large predator biomasses became less similar between EW1 and F1 over the period 2001/2002, and the intersystem differences in biomass of these guilds diverged significantly from 2000 values (Figures 4.3 and 4.4). For medium predators, the change in intersystem difference in biomass post-winterkill was driven by a massive increase in the biomass of this guild in F1 during 2002 (from 3.5 mg/L in 2001 to 14.4 mg/L; Figure 4.3). Intersystem differences in omnivore biomass (Figure 4.5) in 2002 diverged from both 2000 and 2001.

4.3.3 Invertebrate wet biomass in Experimental Wetland 1 compared to Fishless Reference 1

Wet biomass of all five guilds was similar between EW1 and NF1 in the pre-treatment year, 2000. Unlike the relationships between EW1 and the fish reference, F1, none of the changes in intersystem difference between EW1 and NF1 in wet biomass of herbivores, large predators or omnivores were statistically significant across any pair of years. For small predators, the increase in intersystem difference in wet biomass between EW1 and NF1 was significant for 2001 vs. 2002, when the added fish were lost from EW1, and for 2000 vs. 2002 (Figure 4.2). This change was due to an increase in NF1 biomass of small predators and a decrease in EW1 biomass in 2002. Wet biomass of medium predators between EW1 and NF1 became more similar in 2001 and diverged again in 2002. These changes were primarily driven by a large increase in biomass of this guild in NF1 during 2001and 2002 (Figure 4.3).

4.3.4 Bird responses to fish addition

In EW1, the proportion of observed time spent foraging by Blue-winged Teals and Red-necked Grebes increased after addition of fish in 2001. The values in Table 4.4 are the averages of the four measures of foraging activity calculated in early June, late June, mid July and early August for EW1 and the references in each year. There was no consistent period in which teals or grebes foraged most or least; the peak of foraging activity was different in each year.

RIA showed that the intersystem difference in teal foraging effort between EW1 and F1 increased between 2000 and 2001 ($|\bar{D}\text{pre}- \bar{D}\text{post}| = 28\%$, p = 0.105), decreased by nearly 14% between 2001 and 2002 (p=0.684), and decreased by approximately 15% when comparing 2000 to 2002 (p=0.662). Thus, teal foraging effort tended to be less similar between EW1 and F1 after fish addition than it was before fish addition or after fish extirpation (Figure 4.6). The largest change in the intersystem difference in Red-necked Grebe foraging effort between EW1 and F1 (Figure 4.6) occurred when comparing 2000 to 2002 ($|\bar{D}\text{pre} - \bar{D}\text{post}| = 25\%$, $p=0.184$), but the change in intersystem difference in foraging effort for grebes was only 5% between 2000 and 2001, the year when fish were present in EW1 ($p=0.678$).

Average intersystem difference in teal foraging effort between EW1 and fishless reference NF1 increased significantly between 2000 and 2001 (the change in difference, $|\bar{D}\text{pre} - \bar{D}\text{post}|$, was 27%; $p=0.000$), so that Blue-winged Teals spent a greater proportion of the observed time foraging in EW1 than in NF1 after fish were added to EW1 (Figure 4.7). This difference changed very little between 2001 and 2002, when fish in EW1 were extirpated ($|\bar{D}\text{pre} - \bar{D}\text{post}| = 7\%$, $p = 0.727$). Comparing 2000 to 2002, the years in which the fish status of EW1 and NF1 were the same, $|\bar{D}\text{pre} - D\text{post}|$ was 20% ($p=0.290$). For Red-necked Grebes, foraging effort was always very similar between EW1 and NF1 (Figure 4.7), the largest value of $|\bar{D}\text{pre} - \bar{D}\text{post}|$ being less than 8% ($p=0.950$) for 2000 vs. 2001.

4.4 Discussion

Overall I observed mixed results when I added fish to fishless Aspen Parkland wetlands. I predicted that adding fish would result in decreased biomass of omnivores (amphipods, chironomids) and herbivores (gastropods), and that predatory invertebrates would increase, based on Cox et al. (1998) and Zimmer et al. (2001). I predicted that, since Blue-winged Teals consume a large amount of herbivorous and omnivorous invertebrates (Taylor 1978, Swanson et al. 1979), the presence of fish would mean increased foraging effort by Blue-winged Teals. Thus, if they were to maintain similar levels of food intake, teal foraging effort in EW1 would be expected to become more similar to F1 and diverge from NF1. A similar response has been seen in Black Ducks foraging in lakes with and without fish in eastern Canada (DesGranges and Rodrigue 1986). I predicted that Red-necked Grebes would not change their foraging effort since they eat the fish species added, fathead minnow and brook stickleback, and breed successfully on North American wetlands with or without fish (Stout and Nuechterlein 1999).

Only herbivores responded as predicted within EW1 itself, decreasing (although not significantly) after fish addition and increasing significantly after fishes were extirpated (Table 4.2). Comparing EW1 to F1, only herbivore and small predator biomasses in the two wetlands converged in 2001 and diverged in 2002 as expected, and the convergence in 2001 was not statistically significant. None of the invertebrate biomass values in EW1 converged on those of NF1 in 2002 (post-winterkill); in fact, biomass of large predators and herbivores in EW1 diverged from NF1 in 2002. The herbivores' response is consistent with Zimmer et al.'s (2001) study of invertebrate communities in prairie pothole wetlands colonized by fathead minnow. Zimmer et al. (2001) also removed the colonizing fish with rotenone and found a reversal in the decreases in invertebrates that occurred when the fish colonized, similar to the response of herbivores to a natural "removal" (via winter hypoxia) of fathead minnow and brook stickleback in my study.

The responses of omnivores (amphipods, chironomids) to fish addition within EW1 and relative to the references are more consistent with the findings of Batzer (1998) and

Batzer et al. (2000), in which chironomids were more abundant in the presence of fishes in New York marsh systems – pumpkinseed sunfish (*Lepomis gibbosus*) and brown bullhead (*Ictalurus nebulosus*) consumed chironomids but they also suppress invertebrates that compete with chironomids for food, e.g., planorbid snails and other gastropods. This effect may outweigh the negative effect of predation on omnivores by colonizing fish and may be beneficial to Blue-winged Teals and other dabbling ducks since it results in an increase in biomass of important prey. As for the predatory guilds, the largest of these attack small-bodied fish (Clifford 1991), whilst medium-sized predators (hemipterans, smaller dytiscids) may consume amphipods, copepods, cladocerans and chironomids (Scudder 1976, Clifford 1991). Thus, large and medium predators may occupy the same or higher trophic positions as the fish in my study (Benndorf et al. 2000). If the fishes are only one of the range of prey items taken by the largest predators, their addition would not necessarily lead to an increase in large predator biomass. Competition between the added fishes and the medium-sized predators for omnivores and zooplankton may also inhibit any potential increases in biomass of that guild in the presence of fish, despite reports of positive associations between hemipterans and the presence of fathead minnow in prairie potholes (Zimmer et al. 2001).

CPUE data showed that numbers of individuals of all guilds of invertebrates in EW1 except large predators increased over the period 2000-2002 (Table 4.2), so that any decreases in biomass of a particular guild, such as the herbivores in this study, would mean that that guild was composed of more and smaller individuals. Brook stickleback are very gape-limited even for small fish (Tompkins and Gee 1986) and would be expected to consume smaller prey, leaving larger individuals in the invertebrate populations sampled. The main fish effect may therefore have been due to fathead minnows, which can take a wide variety of invertebrates (Price et al. 1991, Cox et al. 1998; Zimmer et al. 2001) and may thus affect abundance and population characteristics of invertebrates. Pehrsson (1984) found more and larger invertebrates in the absence of larger fish such as perch (i.e., fewer and smaller in their presence).

RIA on bird foraging effort data (Table 4.4, Figures 4.6 and 4.7) supported my prediction that Blue-winged Teals' foraging effort in EW1 became less like NF1 when fish were added. However, when fish were extirpated from EW1, there was no reversal in teal foraging patterns. This suggests that the effect of fish colonization on teal feeding patterns may be longer-term than I expected, even in a dynamic system like Aspen Parkland (Nicholson and Vitt 1994), where fish colonizations and extirpations are frequent events. Currently, there is little documentation of long-term effects of fish removals on birds in eutrophic systems (Bergman et al. 1999), and none at all on the long-term effects of fish colonizations. The response of teals in EW1 relative to NF1 is consistent with oligotrophic systems in which Ephemeroptera were reduced in lakes with fish and Black Duck and Common Goldeneye ducklings showed greater foraging effort than they did in lakes from which fish were extirpated due to acidification (DesGranges and Rodrigue 1986, Hunter et al. 1986). In my study, increased teal foraging effort in 2001 appeared to be due to a decrease in biomass of herbivores (gastropods), an important food of breeding Blue-winged Teals and other ducks (e.g., Lesser Scaup *Aythya affinis*, Bufflehead *Bucephala albeola*) of the Prairie Pothole Region and Aspen Parkland of North America (Taylor 1978, Austin et al. 1998). Teal foraging effort did not, however, reflect the rebound in herbivore biomass in 2002. This suggests that Blue-winged Teal, being fairly generalist despite their heavy reliance on gastropods (Taylor 1978), may be responding to changes in the overall invertebrate community that I was unable to detect by examining the guilds I chose. This kind of undocumented variation in the system is a factor that Carpenter et al. (1989) urge us to incorporate when interpreting Randomized Intervention Analyses. Although not all my RIA results were statistically significant for Blue-winged Teals, if we consider that laying females can spend 66% of their time feeding when off the nest (Krapu and Reinecke 1992), the increase in foraging effort within EW1 between 2000 and 2001 (Table 4.4) and in EW1 relative to F1 and NF1 was substantial.

Red-necked Grebes behaved as predicted, with no major change in foraging effort in EW1 relative to either F1 or NF1 in any year. This supports the suggestion that adult Red-necked Grebes in Aspen Parkland treat fish and invertebrates as equivalent prey.

Although young grebe chicks rely mostly on invertebrates even in lakes with fish (Stout and Nuechterlein 1999), this may be due to gape limitation. For example, young Black-throated Diver (*Gavia arctica*) chicks reject items above a certain size (Jackson 2003), but eat a more 'adult' diet (including fish) when older. Energetically, invertebrate prey of Red-necked Grebes are similar to fathead minnow: 22.14 J/mg dry weight for *Dytiscus* nymphs and 22.37 J/mg dry weight for large leech *Nephelopsis obscura* (Driver 1981; data converted from calories/g), compared to 25.04 J/mg dry weight for fathead minnow (Gingras 1997).

4.4.1 Conclusions

My study suggests that small-bodied fish can reduce some invertebrate prey and change the foraging effort of Blue-winged Teals in meso- to eutrophic systems, much as large-bodied fish reduce invertebrates for waterbirds in oligotrophic systems. Additionally, some responses of invertebrates to fish addition and extirpation relative to reference wetlands with and without fish suggest that fish are not the only factor that influences on invertebrates, and hence on birds. This suggestion fits well with the findings of Chapter 2, which highlighted the importance of biotic and abiotic factors in determining bird and invertebrate assemblage compositions. Although not all my results for Blue-winged Teals were statistically significant, Carpenter et al. (1989) emphasize the importance of interpreting the results of RIA in terms of their ecological significance rather than solely relying on their statistical significance – particularly since studies such as this one deal with very low sample sizes and thus lack power. Jennions and Møller (2003) recently suggested that meta-analyses of studies in behavioral ecology might be a useful way to address these problems. This approach depends on the existence of a sufficient number of studies available for meta-analysis. Using foraging effort to document waterbird-fish competition is a simple, non-invasive method, unlike traditional analyses of oesophageal or gut content. For Aspen Parkland, a poorly studied ecosystem that provides prime breeding habitat for many of North America's breeding waterbirds (Ducks Unlimited Canada's Institute for Wetland and Waterfowl Research, *unpubl. data*; Puchniak 2002), more studies of foraging patterns are needed to determine if other waterbirds besides Blue-winged Teal exhibit changes in foraging behaviour in the presence of small-bodied fishes. My results suggest that land management practices such as consolidation of small wetlands in larger wetlands, which may enhance survival of colonizing fish through drought years and thus reduce invertebrates available to birds, should be discouraged.

4.5 References

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Table 4.1: Some limnological features of the experimental wetland and references, as sampled each of the three years of the experiment. EW1 = Experimental Wetland 1, F1 = Fish Reference 1, NF1 = Fishless Reference 1.

Pond	**Year**	**Area (ha)**	**Avg Depth (m)**	**Chlorophyll a (μg/L)**	**Total phosphorus (μg/L)**
EW1	2000	10.88	1.0±0.07	22.0	104
EW1	2001	-	0.59±0.11	71.6	147.1
EW1	2002	-	0.63±0.09	2.3	95.2
F1	2000	9.64	1.22±0.12	18.3	133
F1	2001	-	0.81±0.23	3.0	100.8
F1	2002	-	0.87±0.17	2.8	84.1
NF1	2000	14.78	1.53±0.05	10.2	37
NF1	2001	-	1.06±0.2	2.4	34.0
NF1	2002	-	0.94±0.25	1.6	38.0

Table 4.2: Biomass (mg/L) and CPUE (#/L/hr) of invertebrate omnivores, larger herbivores, and predators in Experimental Wetland 1 before (2000), immediately after (2001) and one year after (2002) the fish addition. Values are averages (± s.d.) based on sampling in early June, late June, mid-July and early August of each year.

Wet Biomass	2000	2001	2002	CPUE	2000	2001	2002
herbivores	1.4 (1.5)	0.7 (1.0)	1.1 (1.7)	herbivores	3.4 (2.8)	14.2 (24.1)	392 (279)
small predators	1.3 (1.6)	0.6 (1.0)	0.10 (0.03)	small predators	4.8 (4.8)	21.3 (42.5)	69.5 (127)
medium predators	1.2 (1.7)	1.2 (1.2)	5.6 (10.4)	medium predators	9 (4.2)	10.6 (18.6)	98.9 (64.5)
large predators	1.3 (1.0)	14.1 (16.8)	23.6 (37.7)	large predators	23.5 (30.0)	5.7 (7.6)	259 (200.8)
omnivores	0.1 (0.1)	0.6 (1.1)	0.6 (0.6)	omnivores	9.1 (13.8)	21.4 (24.1)	561.7 (466)

Table 4.3: The absolute values of the changes in average intersystem differences, $|\bar{D}\mathrm{pre} - \bar{D}\mathrm{post}|$, between Experimental Wetland 1 (EW1) and references for RIA on wet biomass (mg/L) of five invertebrate guilds. Comparisons with Fish Reference 1 (F1) and Fishless Reference 1 (NF1) are shown. P-values are shown in parentheses. A significant result (boldface) indicates a non-random change in the difference between the experimental and reference system.

Comparison	**EW1/F1**			**EW1/NF1**		
Years	**2000/2001**	**2001/2002**	**2000/2002**	**2000/2001**	**2001/2002**	**2000/2002**
herbivores	2.4	**5.3**	2.9	0.04	13.5	13.5
	(0.648)	**(0.044)**	(0.462)	(0.971)	(0.561)	(0.619)
small predators	0.03	**3.1**	3.0	0.7	**1.7**	**2.4**
	(0.790)	**(0.000)**	(0.120)	(0.384)	**(0.000)**	**(0.000)**
medium predators	3.3	6.5	**9.7**	**1.1**	3.7	4.8
	(0.100)	(0.137)	**(0.000)**	**(0.000)**	(0.158)	(0.113)
large predators	2.3	59.5	**61.8**	16.7	45.5	28.8
	(0.975)	(0.147)	**(0.000)**	(0.193)	(0.150)	(0.382)
omnivores	1.0	**4.5**	**3.5**	0.1	0.4	0.3
	(0.224)	**(0.000)**	**(0.000)**	(0.969)	(0.680)	(0.673)

Table 4.4: Average foraging effort (± s.d.) of Red-necked Grebe (RNGR) and Blue-winged Teal (BWTE) within the experimental and reference wetlands EW1, F1 and NF1. Values are average % of observed time spent foraging over the period early June – early August each year.

BWTE	**2000**	**2001**	**2002**
EW1	3.80±4.39	51.37±8.23	53.34±29.86
F1	11.26±14.95	34.48±29.23	50.14±28.08
NF1	0.31±0.63	20.66±17.90	29.84±14.52

RNGR	**2000**	**2001**	**2002**
EW1	13.96±6.14	21.08±14.86	28.73±42.22
F1	6.80±8.14	19.29±18.21	46.95±24.03
NF1	15.90±6.63	30.89±20.02	36.09±13.21

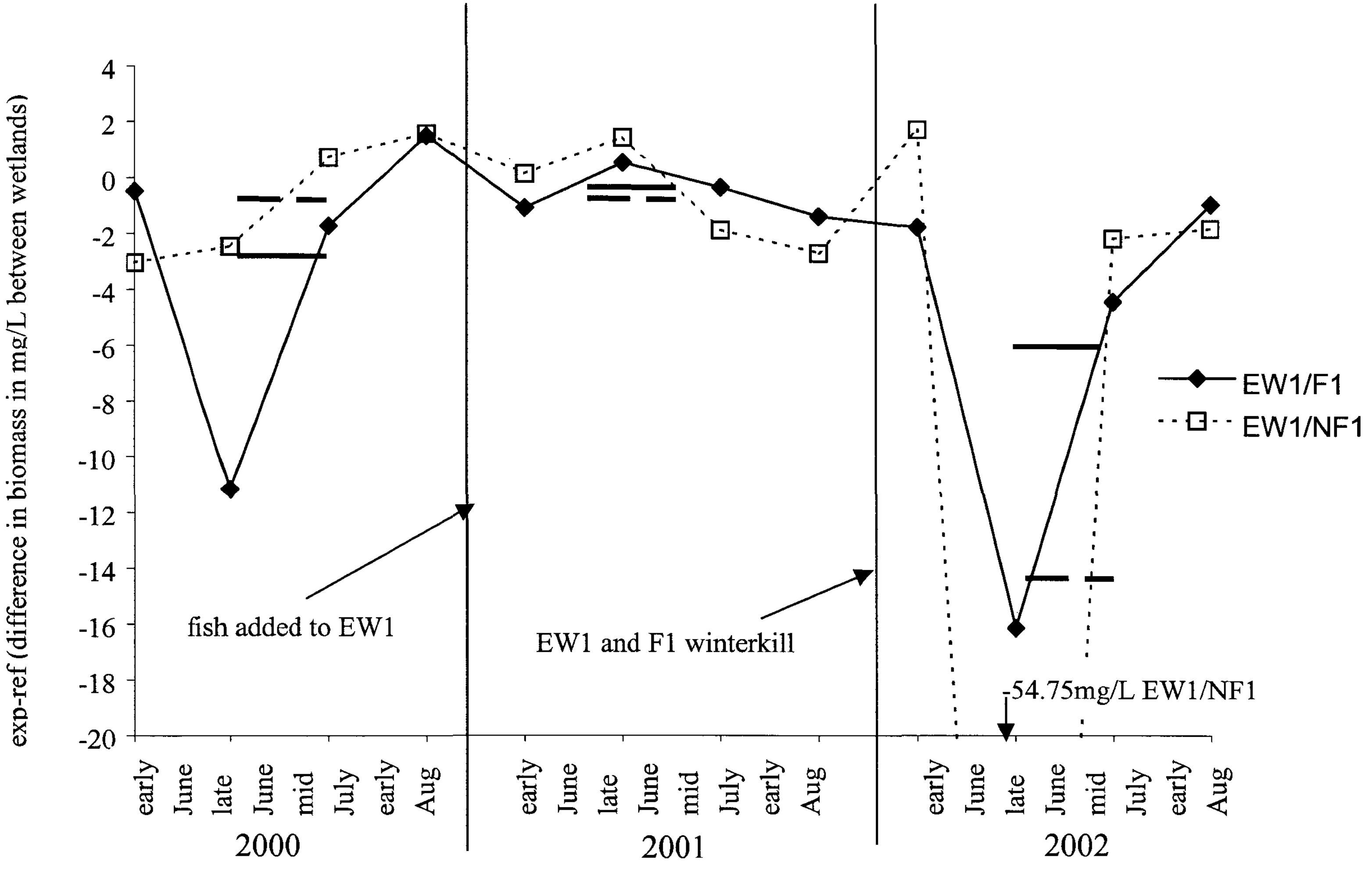

Figure 4.1: Intersystem differences in herbivore biomasses

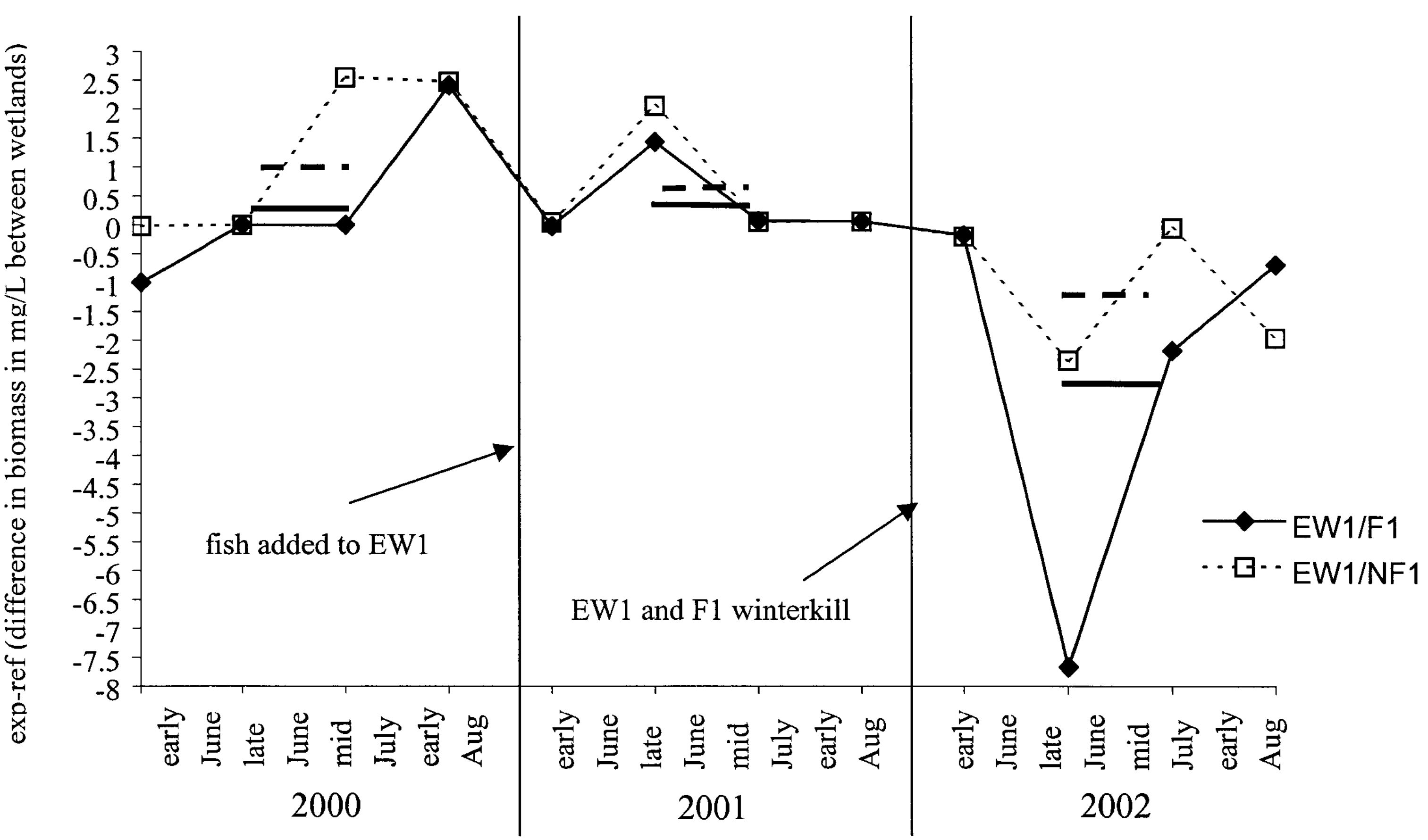

Figure 4.2: Intersystem differences in small predator biomasses

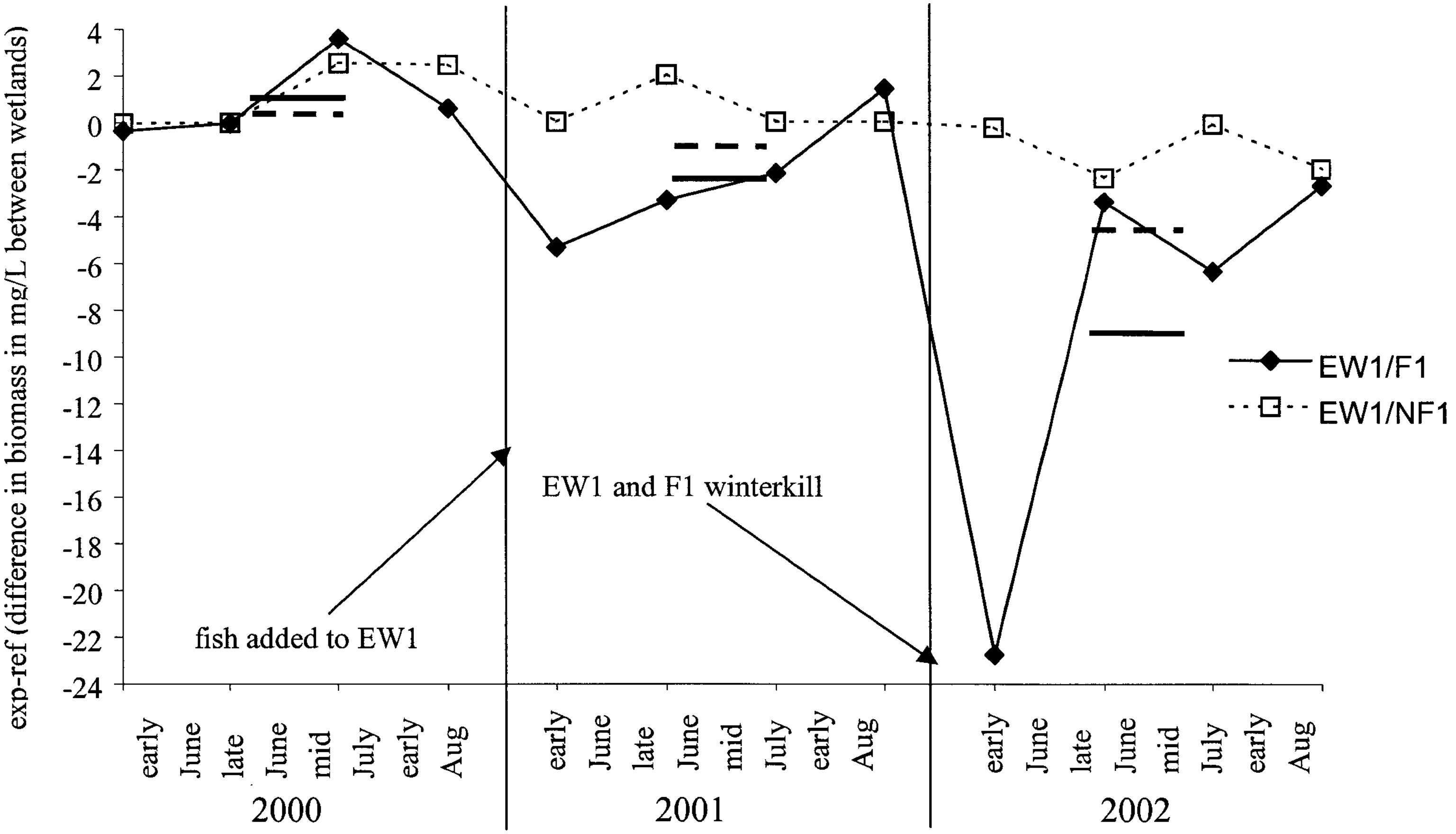

Figure 4.3: Intersystem differences in medium predator biomasses

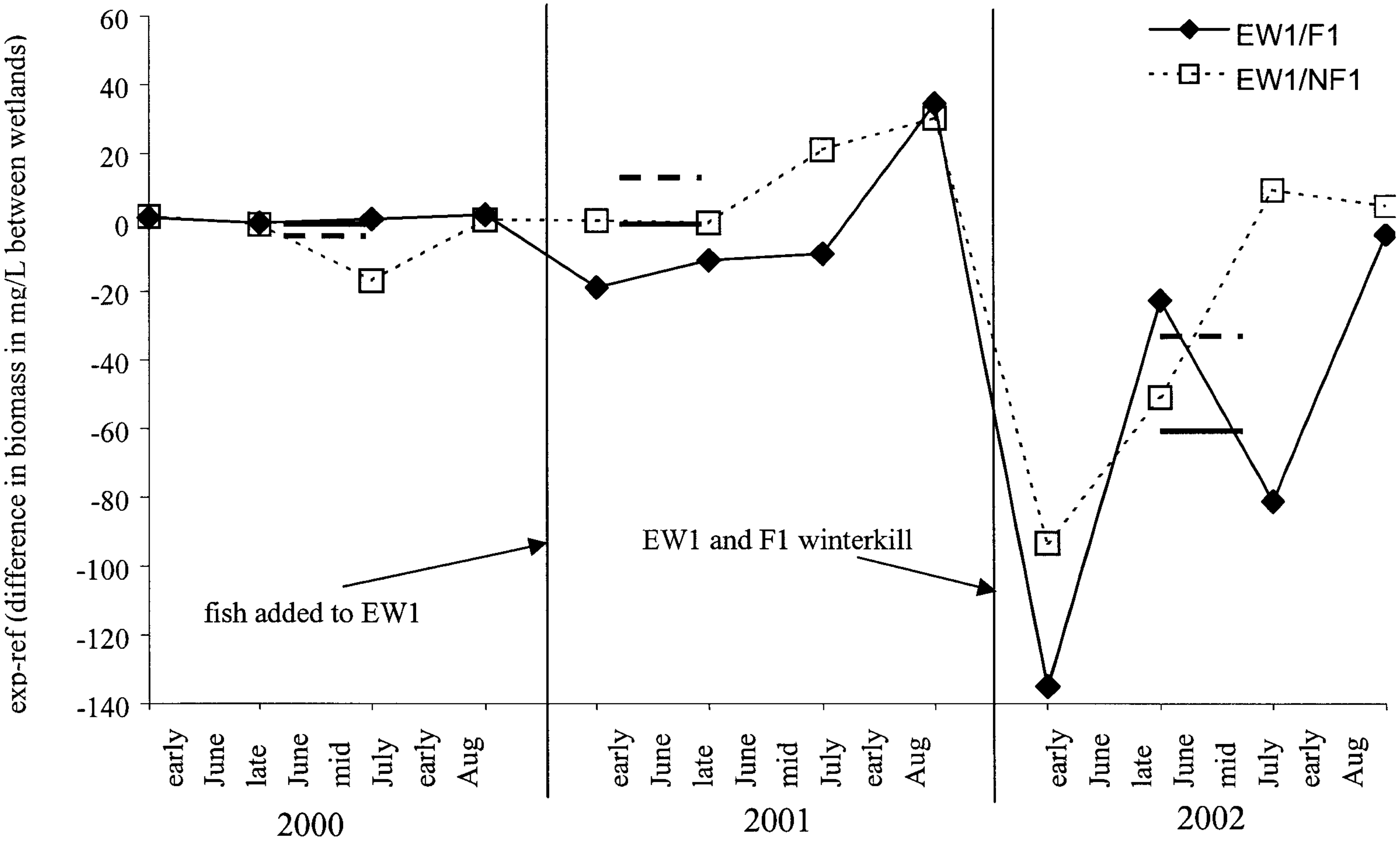

Figure 4.4: Intersystem differences in large predator biomasses

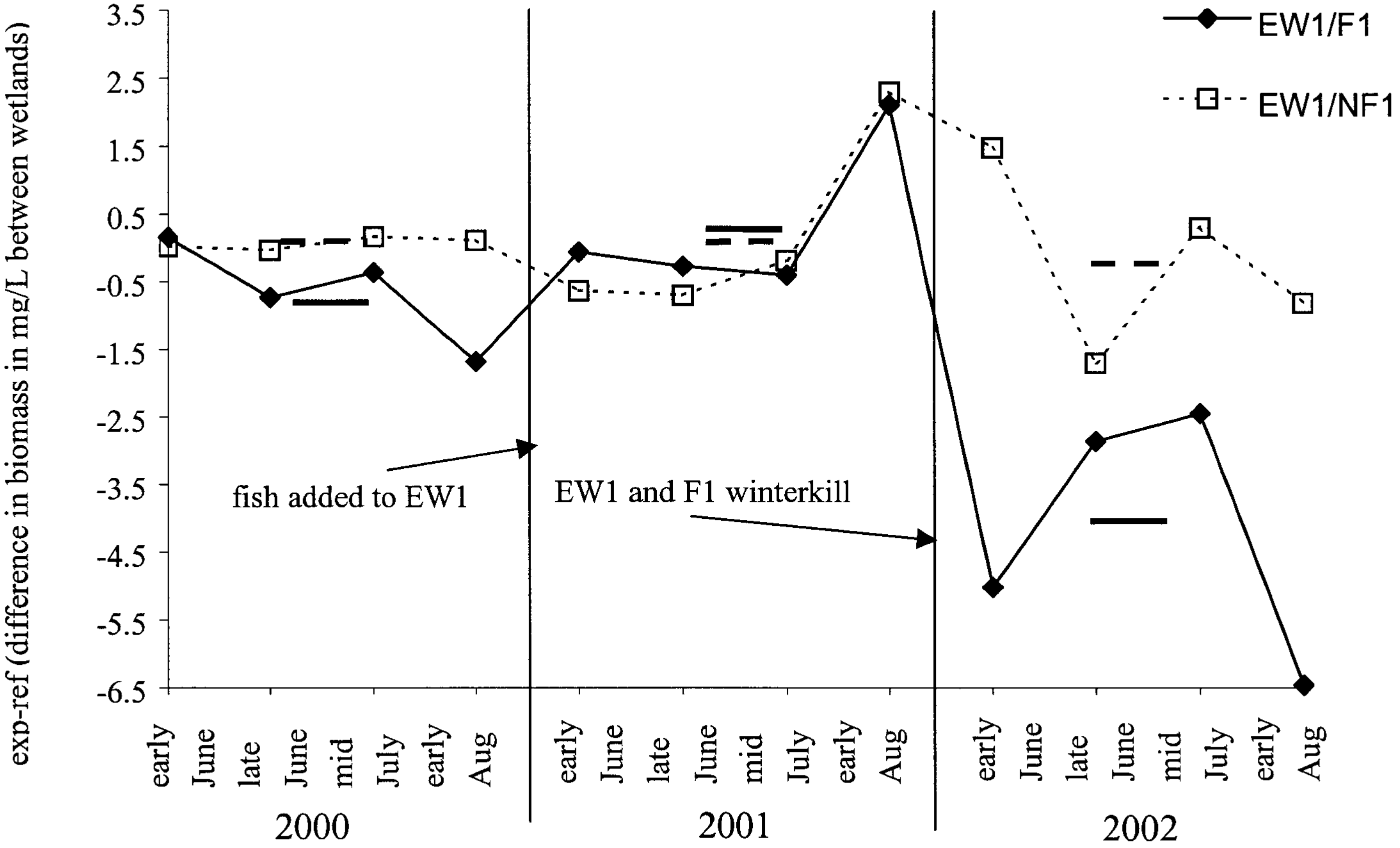

Figure 4.5: Intersystem differences in omnivore biomasses

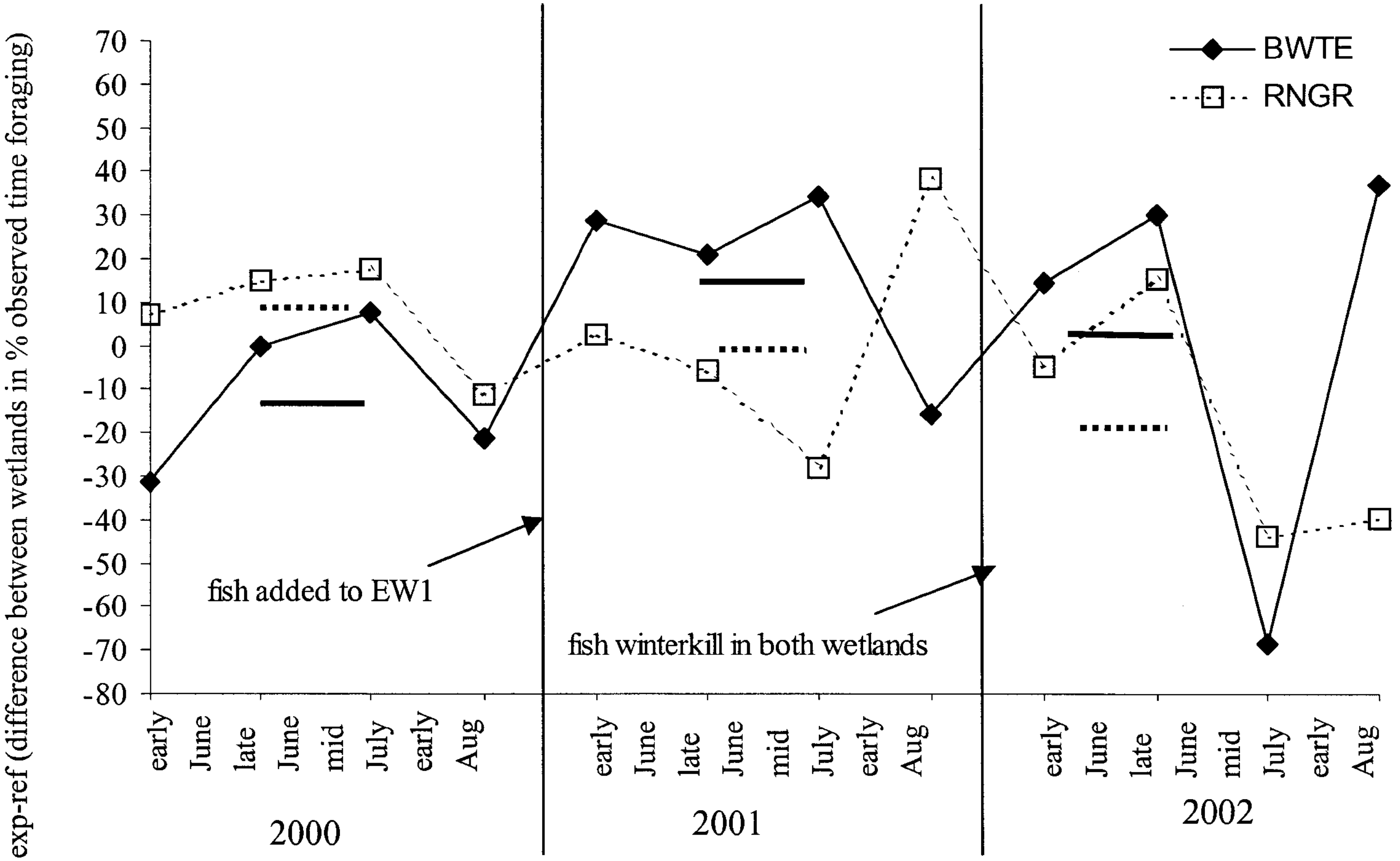

Figure 4.6: Bird foraging on Experimental Wetland 1 compared to Fish Reference 1

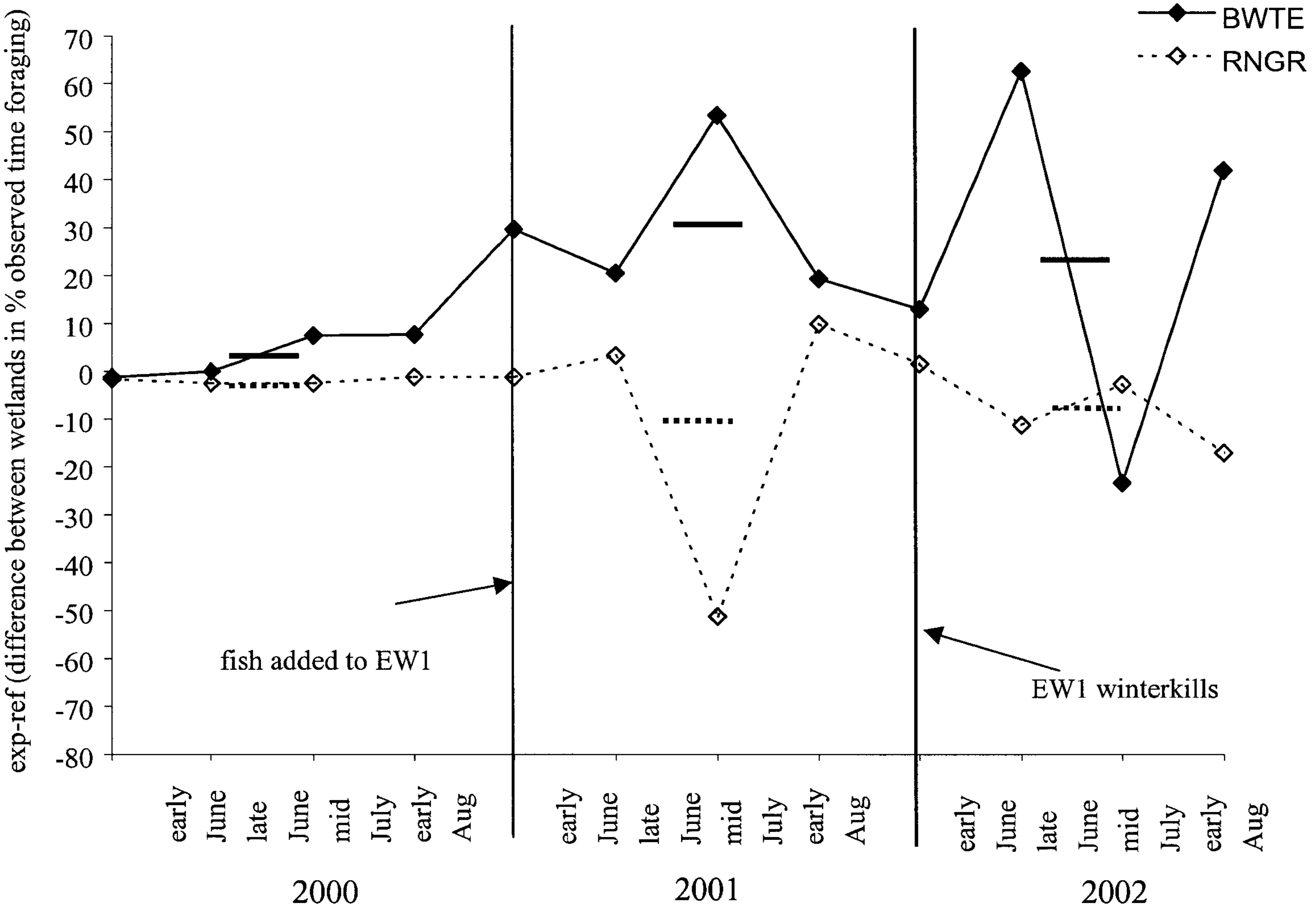

Figure 4.7: Bird foraging on Experimental Wetland 1 compared to Fishless Reference 1

Figure 4.1: RIA of larger herbivore (gastropod) biomass in EW1 vs. fish (F1) and fishless (NF1) references. Solid horizontal bars = mean difference in biomass (mg/L) between EW1 and F1, dashed horizontal bars = mean difference between EW1 and NF1, which is calculated from the series of intersystem differences (exp-ref) in each year.

Figure 4.2: RIA of small predator (glossiphoniid leeches) biomass in EW1 vs. fish (F1) and fishless (NF1) references. Solid horizontal bars = mean difference in biomass (mg/L) between EW1 and F1, dashed horizontal bars = mean difference between EW1 and NF1, which is calculated from the series of intersystem differences (exp-ref) in each year.

Figure 4.3: RIA of medium-sized predator (hemipterans, beetles except *D. alaskanus*) biomass in EW1 vs. fish (F1) and fishless (NF1) references. Solid horizontal bars = mean difference in biomass (mg/L) between EW1 and F1, dashed horizontal bars = mean difference between EW1 and NF1, which is calculated from the series of intersystem differences (exp-ref) in each year.

Figure 4.4: RIA of large predator (large leeches, *D. alaskanus*) biomass in EW1 vs. fish (F1) and fishless (NF1) references. Solid horizontal bars = mean difference in biomass (mg/L) between EW1 and F1, dashed horizontal bars = mean difference between EW1 and NF1, which is calculated from the series of intersystem differences (exp-ref) in each year.

Figure 4.5: RIA of omnivore (amphipods, chironomids) biomass in EW1 vs. fish (F1) and fishless (NF1) references. Solid horizontal bars = mean difference in biomass (mg/L) between EW1 and F1, dashed horizontal bars = mean difference between EW1 and NF1, which is calculated from the series of intersystem differences (exp-ref) in each year.

Figure 4.6: Randomized Intervention Analysis of EW1 compared to Fish Reference 1 (F1). The solid horizontal bars represent the average intersystem difference, for Blue-winged Teal foraging in each year, which is calculated from the series of intersystem differences (exp-ref). The dashed horizontal bars represent the average intersystem difference for Red-necked Grebe foraging in each year. RIA tests the change in these average intersystem differences (| $\bar{D}$pre- $\bar{D}$post|) between years.

Figure 4.7: Randomized Intervention Analysis of EW1 compared to Fishless Reference 1 (NF1). The solid horizontal bars represent the average intersystem difference, for Blue-winged Teal foraging in each year, which is calculated from the series of intersystem differences (exp-ref). The dashed horizontal bars represent the average intersystem difference for Red-necked Grebe foraging in each year. RIA tests the change in these average intersystem differences (| $\bar{D}$pre- $\bar{D}$post|) between years.

Chapter 5: Stable Isotope Analysis of Aspen Parkland Food Webs Associated with Red-necked Grebe and American Coot.

5.1 Introduction

Waterbird-fish competition has often been studied in oligotrophic and eutrophic systems using analyses of bird and fish gut contents. These techniques have documented diet overlap between waterbirds and fish in England's gravel pit lakes (e.g., Hill et al. 1987, Giles et al. 1990), or have suggested that restoration and restocking of acidified lakes may reduce the invertebrate prey available to some breeding waterbirds (e.g., Eadie and Keast 1982, Hunter et al. 1986, Eriksson 1987). Other workers have monitored foraging behaviour of waterbirds to show that ducklings of Black Ducks (*Anas rubripes*) and Tufted Ducks (*Aythya fuligula*) spend more time searching for food in the presence of fish (DesGranges and Rodrigue 1986, Giles 1990). Monitoring bird foraging behaviour is much less invasive and labour-intensive than gut content analyses and is somewhat more conducive to replication. However, monitoring behaviour does not necessarily take account of the fact that many waterbirds switch prey in the presence of competing fishes (DesGranges and Rodrigue 1986, Bendell and McNicol 1995). Therefore, in studying waterbird-fish competition, researchers need to strike some balance between non-invasive techniques such as monitoring foraging behaviour and detailed 'snapshot' techniques such as gut content analysis.

One increasingly popular method of dietary study is stable isotope analysis (SIA, see Kelly 2000 for a review), whereby trophic position is determined by the ratios of ^{15}N: ^{14}N in an organism's tissues. Because there is a greater net loss of ^{14}N relative to ^{15}N during nitrogen metabolism, top predators are more enriched in ^{15}N than primary consumers (Kelly 2000). The carbon source at the base of the food web to which an organism belongs is determined using ^{13}C:^{12}C ratios, which do not change substantially between trophic levels. C3, C4, marine and freshwater primary producers all process ^{13}C and ^{12}C isotopes differently during photosynthesis (Kelly 2000), with C3 plants being the most depleted in ^{13}C and C4 plants being the least depleted. These ^{15}N: ^{14}N and ^{13}C:^{12}C ratios are usually shown in delta notation and expressed as parts per thousand, ‰:

$$\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$$

where δX is the isotope of interest, R_{sample} is the ratio of the sample of interest and is given relative to the isotope ratio ($R_{standard}$) of an accepted standard (air for nitrogen, PeeDee Belemnite (PDB) limestone for carbon; Craig 1957, Ehleringer and Rundel 1989). SIA of some tissues such as muscle (Kelly 2000) has the advantage of providing longer-term dietary information than the snapshot measurements represented by gut content analyses. SIA can also be used on tissues such as feathers and on bird eggs (e.g., Hebert et al. 1999, 2000), thereby being less invasive to breeding adult birds than blood sampling or muscle tissue collection (Hobson and Clark 1992a, 1992b, Gloutney et al. 1999). Since the carbon analysis gives an indication of the food web a given study organism is a member of, it can be used to determine migration patterns in wildlife, or whether birds obtain resources for eggs from breeding or wintering areas (Hobson 1987, Hobson et al. 1997b, Marra et al. 1998, Hobson 1999). Different tissues can be used to provide shorter - or longer - term indices of diet; for example bone collagen, which has a very slow turnover rate, gives an indication of lifetime diets, whilst egg albumen would indicate the sources of protein obtained during egg formation by breeding female birds (Hobson and Clark 1992a, 1992b).

I used SIA of eggs to document the trophic relations of adult Red-necked Grebe (*Podiceps grisegena*) breeding on wetlands of North America's Aspen Parkland as part of a larger study involving foraging behaviour surveys on waterbirds in wetlands with and without fishes. Red-necked Grebes have been shown to avoid seemingly appropriate breeding habitat in northern Europe due to competition with fish (Wagner and Hansson 1998), but feed and breed on wetlands with and without fish in North America (Stout and Nuechterlein 1999), including the shallow, meso- to hypereutrophic potholes (Nicholson and Vitt 1994) in Aspen Parkland. Aspen Parkland wetlands are poorly studied but support many breeding waterbirds (Chapter 2), including Red-necked Grebe. These wetlands are also commonly fishless or support small-bodied fishes capable of surviving the winter hypoxia that frequently occurs in shallow eutrophic wetlands: fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*). Despite their small size, these two fish species are capable of consuming a wide variety of aquatic invertebrates (Tompkins and Gee 1986, Price et al. 1991, Zimmer et al. 2001). Thus, Aspen Parkland wetlands made good candidates for a stable isotope analysis study that took the unique approach of documenting the interaction between fish presence/absence and the trophic relations of invertebrates and breeding birds on a number of wetlands.

Red-necked Grebe breeding in wetlands with small-bodied fishes likely eat a combination of invertebrates and small fishes, whilst those in fishless wetlands eat only invertebrates (Stout and Nuechterlein 1999, Paszkowski et al. in review). Thus, I predicted that Red-necked Grebe in Aspen Parkland wetlands that contain fishes would be more enriched in $\delta^{15}N$ relative to invertebrate prey and thus occupy a higher trophic position than on fishless wetlands, due to their consumption of fishes that also eat aquatic invertebrates. Hobson (1995) reports that for carnivorous birds (which would include Red-necked Grebe feeding on invertebrates and/or fish), $\delta^{15}N$ fractionation is about 3.4‰ between consumers and prey. Thus, it is reasonable to predict enrichment in $\delta^{15}N$ of about 3.4‰ between Red-necked Grebe tissues and that of their prey. For this study, I used eggs as the source of grebe tissues, to provide an index of grebe diets at a time when their need for invertebrate protein would be high, i.e., during egg formation. A recent study of boreal-lake food webs in Alberta that combined gut-content analysis and SIA showed good agreement between the $\delta^{13}C$ and $\delta^{15}N$ signals of Red-necked Grebe eggs and isotopic signals of their freshwater prey of invertebrates and fishes versus more enriched values expected from marine-based food sources (Paszkowski et al. in review). Thus, Red-necked Grebe obtain the nutrients for egg production from exogenous sources (breeding wetlands), and eggs make useful materials for studying grebe food web relationships. I therefore predicted that $\delta^{13}C$ signals of Red-necked Grebe eggs on parkland wetlands would show good agreement with the $\delta^{13}C$ signals of invertebrates such as dytiscid beetles, amphipods and erpobdellid leeches (typical prey; Stout and Nuechterlein 1999), as well as with fishes where they were present. Hobson et al. (2000)

found that pectoral muscle of seabirds arriving on breeding grounds from marine wintering areas was about 2‰ more enriched in ^{13}C than the pectoral muscle of post breeding birds. If Red-necked Grebe were to import nutrients from marine wintering habitats to eggs, then egg $\delta^{13}C$ signatures would be significantly heavier (more positive) than those of invertebrates in the freshwater breeding habitats.

I also used SIA on eggs to document food web associations of the American Coot (*Fulica americana*) on Aspen Parkland wetlands. Like the Red-necked Grebe, this species feeds directly on the water in its nesting wetlands but there is some controversy as to the relative importance of endogenous and exogenous resources for egg production in coots. Alisauskas and Ankney (1985) postulated that egg size in American Coot declines with laying sequence to allow for a 'saving' of nutrient reserves gained prior to migration to the breeding grounds, whilst Arnold (1991) pointed out that since egg yolks overlap in their development, the biggest cost for coots is in the middle of the laying sequence, not at the end. The decline in egg size with laying sequence is also less rapid in re-nesting coots (Arnold 1991), indicating that exogenous resources obtained from the breeding ponds provide the major contribution to egg formation in American Coot. Using SIA of carbon to determine how closely breeding coots are associated with the food webs on nesting wetlands may help to address this controversy. If coot egg carbon signals are similar to the signals from other organisms in the food webs on nesting wetlands, then it is likely that egg resources are primarily obtained from the breeding grounds. More specifically, if egg albumen or lipid-free yolk signals are similar to carbon signals from organisms found on coots' breeding sites, this implies that females coots get their protein from exogenous sources. Thus, I predicted that carbon signals from coot eggs would be similar to the carbon signals of invertebrates, fish and primary producers within the breeding lakes. Coots are generally herbivorous and only eat substantial amounts of invertebrates in the breeding season (Driver 1988, Alisauskas and Arnold 1994). During this time, coots may compete with fish for invertebrate prey. Some studies show that waterbirds switch diets in the presence of fish (e.g., Bendell and McNicol 1995). Thus, coots could change their diets in the presence of fish, possibly eating more primary producer material if invertebrate resources are depleted. Assuming that coot egg constituents are assembled from exogenous materials, I predicted that coot eggs would be less enriched in ^{15}N in Aspen Parkland wetlands with fish than in fishless wetlands. Additionally, since coots tend to be more herbivorous than Red-necked Grebe, coots would be less ^{15}N-enriched than grebes where the two species co-exist.

5.2 Methods

5.2.1 Sample Collection and Preparation

In 2000 and 2001, I collected Red-necked Grebe and American Coot eggs from four wetlands with fish and four wetlands without fish in Elk Island National Park (EINP), Alberta, Canada. EINP is a 195km^2 remnant of Aspen Parkland that is surrounded by agricultural and rural residential land. The eight wetlands from which eggs were collected were a subset of 18 wetlands that were being monitored in a study on grebe foraging activity in the presence/absence of fish. This subset of wetlands represented sites with breeding grebes and/or coots. The fishless wetlands were designated ponds N1, N2, N3 and N4, and the four wetlands with fishes were designated ponds F1, F2, F3 and F4. Table 5.1 shows some of the limnological attributes of these wetlands.

I collected one grebe egg from up to three nests on each site, and two eggs from up to two coot nests on the sites. I collected the cleanest egg on each nest, i.e., the most recently laid egg in the clutch. Eggs were all collected in late May/early June. I used activity traps and benthic grab apparatus to collect invertebrates that were likely to be consumed by Red-necked Grebe and/or American Coot (Driver 1988, Alisauskas and Arnold 1994, Stout and Nuechterlein 1999). These invertebrates were: erpobdellid leeches (*Nephelopsis obscura, Erpobdella punctata* and other Erpobdellidae), dytiscid beetles (*Dytiscus alaskanus* and smaller Dytiscidae were treated separately as *D. alaskanus* is a much larger prey item), and amphipods (primarily *Gammarus lacustris*). Up to three individuals of leeches and beetles were collected from each wetland. To ensure sufficient biomass for SIA, I collected up to 10 amphipods from each wetland. Macrophytes (*Potamogeton, Ceratophyllum*) were collected by hand. I also collected up to 10 sticklebacks and fathead minnows from each of the four wetlands that contained fishes, using activity traps set at 25 m intervals along 100 m transects within 2 m of shore for 24 h periods. I froze all samples before preparation for stable isotope analysis, since this method does not tend to deplete ^{13}C and ^{15}N, as do some other preservation methods, e.g., formalin (Hobson et al. 1997a).

From each grebe egg and each coot egg collected, I used a single sample of freeze-dried albumen, and where possible, I also used egg yolk from each egg. One of the grebe eggs (from N1) was too well developed to obtain albumen or yolk samples, so I dissected the pectoral muscle from the chick in that egg, and freeze-dried it. I extracted the lipids from the freeze-dried yolk samples by soaking them in a 2:1:1 methanol:chloroform:water solution for at least 24h and then freeze-dried them again, as lipids are generally very depleted in ^{13}C and yolk has a high lipid content. The lipid extraction method can also alter ^{15}N ratios in the sample of interest (Bosley and Wainwright 1999, Pinnegar and Polunin 1999) and thus results from lipid-extracted samples should be interpreted with caution. Sotiropoulos et al. (in press) recommend using separate samples of fish muscle for nitrogen and carbon analysis if lipid extraction is performed. Because of this potential problem, and because the main focus of the study was centred around the role of fish in Aspen Parkland food webs, I did not extract lipids from fish, invertebrates, macrophytes or egg albumen (the latter is much lower in lipid than yolk and was the primary bird material used).

Larger invertebrates (leeches, beetles, larger amphipods) were held in water for 24h before preservation to allow them to void their guts. I dissected white muscle from the fathead minnow and brook stickleback collected in each wetland and freeze-dried it before homogenization. Due to logistical constraints, and to reduce individual variation in isotopic signals of each fish for stable isotope analysis, I pooled all the stickleback muscle samples from each wetland and took two subsamples of the resulting homogenate, and did the same for fathead minnows where they were collected. Inorganic carbonates were removed from invertebrates using 1N hydrochloric acid (Beaudouin et al. 1999); then these samples were rinsed, freeze-dried and homogenized. Similarly to the fish, I pooled invertebrates of the same taxa from the same wetlands. For example, all small dytiscid beetles from the same wetland would be homogenized together. From the homogenized invertebrate matter, I typically took two subsamples for stable isotope analysis. Finally, macrophytes from each wetland were rinsed to ensure that they were free of attached algae, freeze-dried and homogenized before being sub sampled once.

From the homogenized materials, I prepared the subsamples of each taxon as follows: I weighed 1mg of material into 4 x 6mm tin capsules which were folded and crushed closed prior to sending them for analysis on an ANCA g/s/l Sample Preparation Module coupled to a Europa Scientific Tracer/ 20 continuous flow isotope ratio mass spectrometer (CF-IRMS), at the Department of Soil Science Stable Isotope Facilities, University of Saskatchewan (Saskatoon, SK, Canada). The prepared samples were combusted at 1000°C in an oxygen atmosphere, and then passed through a bed of chromium trioxide via helium carrier gas to ensure complete oxidation. The excess oxygen was then removed and nitrogen oxides were reduced to elemental nitrogen at 550°C. Water was removed with magnesium perchlorate and the carbon and nitrogen components of interest separated chromatographically, then bled into the mass-spectrometer where the isotopes were ionized and separated in a magnetic field. Isotopic species were detected separately and the level of ^{15}N and ^{13}C calculated from their ratios. The system was calibrated using known standard samples (chicken egg albumen for animal samples and ground pea for macrophytes) after every five samples. Measurements were accurate to 0.3‰.

There is often a lot of variation in primary producer $\delta^{15}N$ signals, and some workers in aquatic systems address this by using the $\delta^{15}N$ of a large, long-lived and widespread primary consumer, such as a mussel (Vander Zanden et al. 1997), as the baseline from which to determine the trophic positions of other organisms in the system of interest. In this study, large, long-lived primary consumers were not always available; large gastropods were only present in one or two sites with any regularity. Thus, I chose to use amphipod $\delta^{15}N$ signals as baselines, since they were generally least enriched in ^{15}N of the taxa examined, showed good agreement in signals both within and between ponds, and were available in most of the ponds studied. Amphipods will also consume a range of algae, epiphytes, and POM and thus would make reasonable integrators of primary production inputs. Trophic position of other organisms in the food web were determined using the equation of Vander Zanden et al. (1997)

$$\text{Trophic position} = [(\text{consumer of interest } \delta^{15}N - \text{baseline } \delta^{15}N)/3.4] + 2$$

where 3.4 is the average enrichment in ^{15}N that is seen between trophic levels, 2 being the estimated trophic position of the baseline/primary consumer. In this study, the least ^{15}N-enriched amphipod sample in each study pond was the baseline. I also calculated trophic positions using nitrogen fractionation factors based on patterns seen for eggs in Mallard (*Anas platyrhynchos*) by Hobson (1995), which showed only 3.2‰ fractionation of nitrogen for yolk and 3.0‰ fractionation for albumen. The Mallard in Hobson's study were fed wheat/pellet mix, but showed ^{15}N fractionation comparabe to carnivores, such as Peregrine Falcon, for most egg components).

5.2.2 Data analysis

I used a one-way ANOVA to determine whether there was any significant difference in grebe trophic position, which was based on $\delta^{15}N$ signals, between ponds with and without fishes. I used Wilcoxon signed rank tests to determine if there were any differences between grebe egg carbon ratios and invertebrate carbon ratios within each pond, using all samples of small dytiscids, *D. alaskanus* and amphipods (since grebes will eat all of these and sample size was too small to do a valid taxon-by-taxon analysis). For coot egg materials, I could not compare trophic position due to the lack of usable amphipod samples for which to calculate baseline $\delta^{15}N$ in the two ponds on which coot eggs were sampled. Thus, I used a t-test to determine if there were any differences in mean $\delta^{15}N$ ratios of coot egg between the ponds with and without fishes, rather than to determine any difference in coot trophic position. I used a t-test to determine if there were any differences in mean coot $\delta^{13}C$ between ponds with and without fishes, and Wilcoxon signed rank tests to establish any difference in coot and invertebrate carbon isotope ratios within each pond.

5.3 Results

Of all the tissues examined, Red-necked Grebe eggs were the most enriched in ^{15}N in any of the ponds in which they were present, regardless of fish presence/absence (Figures 5.1a-c and 5.2a-d). Fish were more enriched in ^{15}N than any other organisms sampled except for grebes in all of the wetlands with fish (Figure 5.2a-d). Among the invertebrates, erpobdellids were generally the most ^{15}N-enriched where present, followed by beetles (small dytiscids and *D. alaskanus*), daphnids and amphipods. Coot eggs were less enriched in ^{15}N than fish and more enriched than small dytiscids on the two wetlands where they were sampled (Figures 5.1d and 5.2c). Coot eggs were less enriched in ^{15}N than *D. alaskanus* in the presence of fish and more enriched than *D. alaskanus* in the absence of fish.

Grebe egg $\delta^{13}C$ values were intermediate between those of fishes and invertebrates, with fish generally being the least ^{13}C-depleted organisms in ponds where they were sampled. In contrast, small dytiscids were almost always the most ^{13}C-depleted organisms in any of the wetlands. American Coot carbon values were similar to those of all other organisms sampled on N4 and F3 regardless of fish presence/absence, except for the macrophytes sampled on fishless pond N4 (Figure 5.1d). Grebe, coot and invertebrate $\delta^{13}C$ signals showed good agreement with macrophyte $\delta^{13}C$ signals in ponds N2, N3, F2 and F3 (Figure 5.1b and c, Figure 5.2b and c). $\delta^{15}N$ signals and $\delta^{13}C$ signals from grebe and coot eggs also showed good agreement between nests on the same wetland (Figures 5.1 and 5.2).

5.3.1 Red-necked Grebe Isotopic Signals

Within each pond, regardless of fish status, the $\delta^{15}N$ ratios from Red-necked Grebe eggs never spanned more than 1‰ (Figures 5.1a-c and 5.2a-d). Grebe materials showed greater mean ^{15}N-enrichment over some of their typical invertebrate prey, such as small dytiscids, on wetlands with fish than they did on fishless wetlands (Table 5.2, Figures 5.1a-c and 5.2a-d).

Using the formula of Vander Zanden et al. (1997) with the least ^{15}N-enriched amphipods as the baseline δ^{15}N, the results from ponds N1, N2, N3, F1, F2 and F4 show that Red-necked Grebes in ponds with fish were about 0.52 trophic positions higher than grebes in fishless ponds (Table 5.3), and this difference was significant (one-way ANOVA, $F_{1,8}$ = 6.563, p = 0.034). These calculations of trophic position did not include ponds F3 and N4 because no usable amphipod samples were available from these ponds. Using the fractionation factors for yolk and albumen of Hobson (1995), mean trophic positions of Red-necked Grebe were 4.15± 0.13 in the absence of fish and 4.72 ± 0.46 in the presence of fish (one-way ANOVA, $F_{1,8}$ = 6.98, p = 0.03), i.e., grebes were 0.57 trophic positions higher when fish were present in ponds.

The δ^{13}C values of Red-necked Grebe albumen and yolk were on average 0.96‰ $\pm$ 2.05‰ more depleted than fish, except in pond F3 where they were slightly less depleted relative to fish (Figure 5.2c). Grebe egg materials tended to be more enriched for δ^{13}C than any of the invertebrate samples, by about 2-6‰ in each pond, but these differences were not significant within ponds (Wilcoxon signed rank tests, Table 5.4).

5.3.2 American Coot Isotopic Signals

Coot egg albumen and yolk δ^{15}N values never spanned more than 1.06‰ within either the fishless pond N4 or the pond with fish, F3. Coot egg tissues were significantly less enriched in ^{15}N in the presence of fish than in their absence (t_9= 8.502, p= 0.000, mean δ^{15}N =7.09‰ $\pm$ 0.33‰ in fishless pond N4 vs. 5.19‰ $\pm$ 0.41‰ in fish pond F3). Relative to invertebrate prey (small dytiscids), coots were significantly less enriched in ^{15}N in the presence of fish than in their absence (t_{20} = 4.154, p=0.000, mean fractionation of δ^{15}N of coot eggs over dytiscids in fishless pond = 2.83‰ $\pm$ 0.39‰, mean fractionation in F3 = 2.10‰ $\pm$ 0.42‰). Coot egg δ^{15}N values were also lower than those of grebe eggs in the pond where both species co-existed, F3.

Coot egg δ^{13}C values were similar to δ^{13}C values of fish in pond F3 (Wilcoxon Z = 0.447, p= 0.655), and to δ^{13}C values of all invertebrate taxa in ponds F3 and N4. (Z = 1.826, p = 0.068 in both ponds).

5.4 Discussion

Red-necked Grebe in North America breed and feed on wetlands with and without fishes (Stout and Nuechterlein 1999), in contrast to Red-necked Grebe in Europe, which have been shown to avoid wetlands with fish (Wagner and Hansson 1998). American Coot and other waterbirds that are seasonally invertivorous may have to switch diets in the presence of competing fishes (e.g., DesGranges and Rodrigue 1986). Based on stable isotope analyses, this study suggested that small-bodied fishes in Aspen Parkland could influence the trophic positions of Red-necked Grebe and American Coot that breed and feed in North America's Aspen Parkland wetlands.

Stable isotope analysis of nitrogen suggested that Red-necked Grebe were the top predators in all the Aspen Parkland food webs studied, followed by fish (where present), erpobdellid leeches, dytiscid beetles, and then the omnivorous amphipods. American Coot appeared to forage at a lower trophic level in the presence of fishes than in their absence, and were also at a lower trophic level than grebes where the two species co-existed. The fish and invertebrate relationships revealed by SIA were also consistent with food webs of small-bodied fishes and invertebrates in the western Boreal Plains (Beaudouin et al. 2001). Since the Aspen Parkland is a transitional zone between prairies and boreal forest (Nicholson and Vitt 1994), it is not surprising that many of the food web relationships are similar between parkland and western boreal aquatic ecosystems. Although the food webs constructed in this study are far from complete, the carbon isotope data suggested that Red-necked Grebe and American Coot both obtain protein resources for eggs from breeding wetlands, rather than from endogenous stores. This is consistent with Paszkowski et al. (in review) and Arnold (1991) and makes sense for species that are highly territorial when breeding and do not move around between wetlands to obtain resources (Stout and Nuechterlein 1999, Rohwer et al. 2002). Had the grebes been importing nutrients for eggs from marine wintering habitats, both their $\delta^{13}C$ and $\delta^{15}N$ values would have been much more enriched relative to fish and invertebrates in their breeding ponds, rather than showing good agreement with isotopic ratios of invertebrates and fish sampled on breeding ponds. For example, pectoral muscle of six species of colonial waterbirds arriving at a boreal freshwater breeding lake was more enriched in ^{13}C and ^{15}N than pectoral muscle of post breeding birds on the same lake (Hobson et al. 2000). Thus, arriving birds more closely reflected the isotopic environment of their marine breeding grounds than that of their freshwater breeding grounds.

5.4.1 Red-necked Grebe Isotopic Signals

I predicted that Red-necked Grebe would occupy a higher trophic level in the presence of small-bodied Aspen Parkland fishes than in their absence, and the $\delta^{15}N$ enrichment of Red-necked Grebe egg tissues over invertebrates on 3 of the ponds with fish compared to 3 of the fishless ponds supports this prediction. Using a modification of the formula of Vander Zanden et al. (1997) for calculating trophic position from $\delta^{15}N$ signals, I found that Red-necked Grebe were at a significantly higher trophic position on ponds with fishes than on fishless ponds (Table 5.3). This is also consistent with studies of Red-necked Grebes in the boreal forest of Alberta (Paszkowski et al. in review), where isotopic data showed that breeding Red-necked Grebe were feeding at higher trophic levels in the presence of fish than in their absence. Thus, the small-bodied fish in Aspen Parkland food webs may add to the length of food chains in which Red-necked Grebe are the top predators.

At first glance, the $\delta^{13}C$ signals of this study show considerable trophic fractionation of carbon for food webs associated with Red-necked Grebe, with grebes being more enriched in ^{13}C by 2-6‰ than smaller dytiscids, *Dytiscus alaskanus*, erpobdellids and amphipods. Typical $\delta^{13}C$ fractionation between trophic levels for birds and other organisms such as fish is about 1-3‰ (e.g., Hobson and Clark 1992a, 1992b, Vander Zanden and Rasmussen 2001, Paszkowski et al. in review). Egg albumen is generally about 1.4‰ enriched over whole diet for breeding Mallard (*Anas platyrhynchos*), whilst lipid-free yolk matches dietary signals (Hobson 1995). In carnivorous birds albumen is thought to be about 0.9‰ enriched in ^{13}C over dietary protein (Hobson 1995), which is an important component of invertebrate prey used by breeding waterbirds (e.g., Krapu and Reinecke 1992) like Red-necked Grebe. However, within the individual ponds in Aspen Parkland the differences in $\delta^{13}C$ signals between grebe egg materials and those of the invertebrates examined were not significant (Table 5.4). Thus, my prediction that carbon signals from grebe eggs would show good agreement with $\delta^{13}C$ of invertebrates and fish in Aspen Parkland wetlands was broadly supported.

Grebe carbon signals were also intermediate between $\delta^{13}C$ signals of fish and invertebrates on the wetlands with fish, and there was no significant difference in mean $\delta^{13}C$ of fish or invertebrates compared to grebes (Wilcoxon tests), whilst fish were generally 2-15‰ less ^{13}C-depleted than invertebrates of any taxon (Figure 5.2). This suggested that Red-necked Grebe ate a mixed diet of invertebrates and fish in those ponds, which is consistent with Paszkowski et al. (in review), where gut content data suggested this mixed diet for Red-necked Grebe. Grebe $\delta^{13}C$ also did not differ significantly between wetlands with and without fishes (t-tests). Thus, although fish appeared to alter the length of food chains in which Red-necked Grebes were top predators, they did not appear to link grebes to different primary producers than those available in fishless wetlands, as has been seen in studies involving fish and invertebrates (e.g., Vander Zanden and Vadeboncoeur 2002). This is most likely because the shallow wetlands of the Aspen Parkland are much more uniform than larger, deeper lakes that have fairly well differentiated littoral and pelagic zones (e.g. Vander Zanden and Vadeboncoeur 2002), as the low standard deviation in the Aspen Parkland depth data (Table 5.1) suggests. Thus, fish in Aspen Parkland wetlands do not integrate carbon from multiple food webs as they do in more complex lakes, and their effects on Red-necked Grebe isotopic signals appeared to be limited to their effects on nitrogen signals.

Grebes also did not show good agreement with macrophyte carbon ratios in all lakes, and their signals were often more depleted than –20‰. Algal carbon $\delta^{13}C$ values usually range between –20‰ and –40‰ (France 1995, Keough et al. 1998), and Finlay (2001) reviewed detritus $\delta^{13}C$ values of between –25‰ and –30‰, which are similar to the values for Red-necked Grebes in this study. Thus, grebes on Aspen Parkland wetlands that did not show good agreement with macrophyte $\delta^{13}C$ ratios were most likely part of food webs based on algae or detritus. France (1995) postulated that herbivores can be somewhat flexible in their diets, typically using algal or detrital carbon sources or, if they are very dominant, macrophyte carbon sources. Thus, in Aspen Parkland ponds, it may be possible for food webs to be based on either macrophytes or algae/detritus, depending on whether or not there are very dominant stands of macrophytes available.

5.4.2 American Coot Isotopic Signals

In contrast to my prediction for Red-necked Grebe, I predicted that American Coot would be less enriched in ^{15}N in the presence of fish than in their absence, since they would obtain resources for eggs from primary producers where fish had reduced the availability of invertebrates. Similarly to Red-necked Grebes, inherent in this prediction was the assumption that coots obtain protein resources for egg production exogenously, i.e., from breeding ponds, as indicated by Arnold (1991). The $\delta^{15}N$ signals of coot eggs showed that they were indeed less enriched in ^{15}N in the presence of fish than in their absence, although trophic position could not be calculated using amphipod $\delta^{15}N$ as a baseline. It is not known whether eating at a lower trophic level in the presence of fish makes a difference to coot reproductive success. Coot chicks rely heavily on some of the invertebrates sampled in this study, such as dytiscids and erpobdellids (Driver 1988). Thus, it may be detrimental to coot chicks to be hatched on wetlands with fish, regardless of the effects of fish presence on egg composition.

In ponds F3 and N4, the lack of significant difference in $\delta^{13}C$ signals between coot egg material and the invertebrates sampled suggests that coots produce eggs using the same carbon sources as invertebrates in both ponds. Thus, this study, although it focused only on two ponds of the Aspen Parkland in which American Coot bred, supports the postulation of Arnold (1991) that this species obtains resources for egg formation exogenously, rather than endogenously as postulated by Alisauskas and Ankney (1985).

5.4.3 Conclusions

Stable isotope analysis is an increasingly popular technique in trophic ecology, and in this study it illustrated three main aspects of Aspen Parkland waterbird diets in relation to fish presence/absence. Firstly, small-bodied fishes altered the trophic position of two species of birds with fairly different diets. Secondly, isotopic patterns support the proposition that both species obtain resources for eggs from breeding wetlands, which for the coot at least has been a source of some controversy (Alisauskas and Ankney 1985, Arnold 1991). Thirdly, Red-necked Grebe and American Coot were flexible in their diets. Grebe ate a mixture of fishes and invertebrates where available, or just invertebrates when breeding on fishless wetlands. Coots appeared to eat more primary producer material in the presence of fishes than in their absence. Such flexibility in diet may be adaptive in this highly variable ecosystem (Nicholson and Vitt 1994), where fish colonize wetlands in wet years and are extirpated in dry years. Additionally, not all food webs sampled appeared to be based on macrophytes, which suggested that invertebrates, and fishes in these productive wetlands were also flexible in their diets as France (1995) speculated. These dietary relationships might be more fully assessed using mixing models to trace different dietary inputs to eggs (e.g., Phillips 2001), but Ben-David and Schell (2001) note that such mixing models can at times under- or over-estimate the actual proportions of different food items in the diet by over 40%, and encourage workers to analyze diets based on raw isotopic data rather than the results of mixing models. Thus, such models, although a useful attempt at quantitatively assessing the relative contributions of multiple inputs to diet and tissues, including eggs, provide only an index of dietary composition (Ben-David and Schell 2001). Further studies of grebe and coot diets could use SIA to address (1) whether Red-necked Grebe in Europe are really not as flexible in diets as North American populations appear to be (Stout and Nuechterlein 1999), despite wide fluctuations in some European aquatic ecosystems (Blindow et al. 1993); and (2) whether coot chicks forage at a lower trophic level in the presence of fish and if this subsequently affects coot fledging success.

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Table 5.1: Limnological attributes of the 8 Aspen Parkland wetlands in which food webs were documented using stable isotope analysis (SIA) of carbon and nitrogen. Phosphorus, depth and chlorophyll data are based on samples collected in June, when the materials for SIA were collected. Area data are taken from GIS databases in Elk Island National Park. RNGR = Red-necked Grebe, AMCO = American Coot.

Pond	**Lat/Lng**	**Area (ha)**	**Mean Depth/m (± s.d.)**	**Chlorophyll a (μg/L)**	**Total Phosphorus (μg/L)**	**Birds Examined**
N1	53°43'N 112°50'W	13.51	1.49 ± 0.18	30.58	76.55	RNGR
N2	53°40'N 112°50'W	14.78	0.40 ± 0.05	1.30	46.05	RNGR
N3	53°40'N 112°47'W	12.03	1.27 ± 0.22	1.98	91.85	RNGR
N4	53°34'N 112°49'W	0.74	0.59 ± 0.11	3.90	240.10	AMCO
F1	53°33'N 112°58'W	24.85	1.03 ± 0.47	17.38	62.70	RNGR
F2	53°36'N 112°55W	89.57	1.31 ± 0.62	40.89	113.40	RNGR
F3	53°40'N 112°52'W	12.77	1.19 ± 0.07	4.67	113.80	RNGR
F4	53°35'N 112°47'W	13.20	1.40 ± 0.19	13.95	120.10	RNGR/AMCO

Table 5.2: Mean ^{15}N-enrichment of Red-necked Grebe tissues over some of their typical invertebrate and fish prey in Aspen Parkland wetlands with and without fish. BRST = brook stickleback, FTHD = fathead minnow.

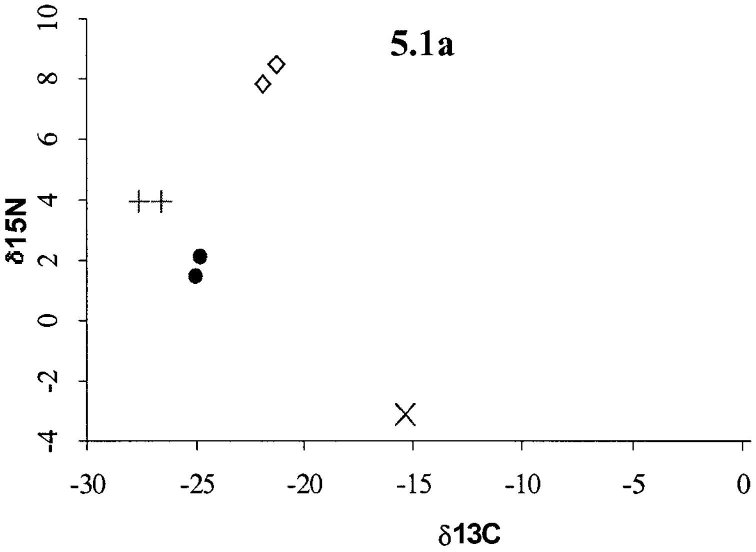
Pond	**Sample Type**	**Mean ± s.d. ^{15}N Enrichment of Grebe Tissue over Sample**
N1	Dytiscidae	4.18 ± 0.38‰
N2	Dytiscidae	3.70 ± 0.71‰
	D. alaskanus	4.29 ± 0.16‰
N3	Dytiscidae	0.92 ± 0.56‰
	D. alaskanus	4.30 ± 0.64‰
	Erpobdellidae	2.96 ± 0.54‰
F1	BRST	2.74 ± 0.35‰
	Dytiscidae	5.98 ± 0.42‰
	D. alaskanus	5.64 ± 0.36‰
F2	BRST/FTHD	2.71 ± 0.41‰
	Dytiscidae	7.34 (one sample)
	D. alaskanus	6.74 ± 0.04‰
	Erpobdellidae	4.23 ± 0.43‰
F3	BRST	0.74 ± 0.10‰
	Dytiscidae	4.84 ± 0.42‰
	D. alaskanus	1.97 ± 0.53‰
F4	BRST/FTHD	0.21 ± 0.54‰
	Dytiscidae	3.66 ± 0.36‰
	D. alaskanus	3.41 ± 0.43‰
	Erpobdellidae	1.62 ±0.76‰

Table 5.3: Estimated trophic positions of Red-necked Grebes on Aspen Parkland ponds with and without fish. Trophic position is calculated using $\delta^{15}N$ signals of amphipods as the baseline $\delta^{15}N$ for each pond, after **(a)** Vander Zanden et al. (1997), and **(b)** substituting fractionation factors from Hobson (1995) for Mallard eggs. Samples for Ponds F3 and N4 were not included in this analysis as no suitable amphipods were collected from those ponds. Where more than one sample of a given type of grebe egg material (albumen, yolk, chick pectoral muscle) was obtained, the average $\delta^{15}N$ signals for that material was used in the calculation of trophic position. Mean trophic position for grebes (all materials) on fishless ponds based on **(a)** was 3.94 ± 0.13; mean trophic position on fish ponds was 4.46 ± 0.43. Mean trophic positions based on **(b)** were 4.15 ± 0.13 on fishless ponds and 4.72 ± 0.46 on ponds with fish.

Pond	**Fish Status**	**Sample Type**	**Estimated Trophic Position**	
			(a)	**(b)**
N1	None	RNGR (pectoral)	3.95	4.21
N2	None	RNGR (albumen)	4.03	4.30
		RNGR (yolk)	4.04	4.17
N3	None	RNGR (albumen)	3.71	3.94
		RNGR (yolk)	3.98	4.15
F1	BRST	RNGR (albumen)	4.82	5.20
		RNGR (yolk)	5.02	5.22
F2	FTHD/BRST	RNGR (albumen)	4.27	4.57
F4	FTHD/BRST	RNGR (albumen)	4.02	4.30
		RNGR (yolk)	4.18	4.31

Table 5.4: Wilcoxon signed rank test results for comparison of Red-necked Grebe $\delta^{13}C$ signals with all invertebrate $\delta^{13}C$ signals (small dytiscids, *D. alaskanus*, amphipods and erpobdellids) and with fish $\delta^{13}C$ signals within each of the ponds where grebes were sampled. Tests could not be completed for ponds F2 and F3 because there was only one grebe egg sample available from each of these ponds.

Pond	**Comparison**	**Wilcoxon Test Statistic (Z)**	**P-value**
N1	Grebes with invertebrates	1.342	0.180
N2	Grebes with invertebrates	1.604	0.109
N3	Grebes with invertebrates	1.342	0.180
F1	Grebes with invertebrates	1.826	0.068
	Grebes with fish	1.342	0.180
F4	Grebes with invertebrates	1.604	0.109
	Grebes with fish	0.535	0.593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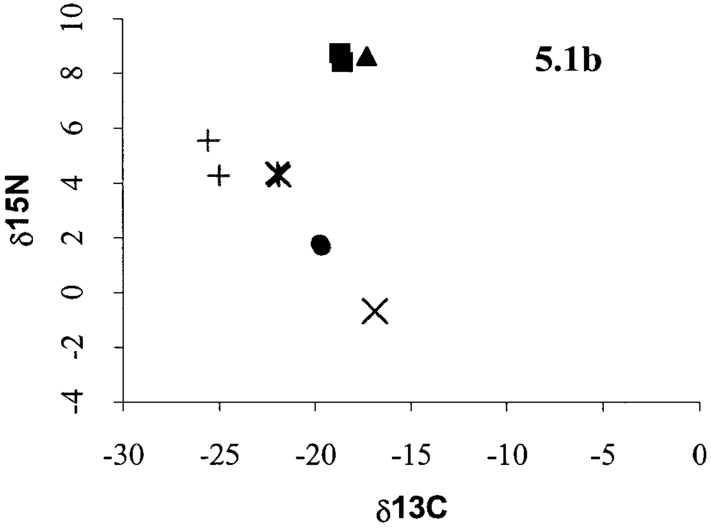
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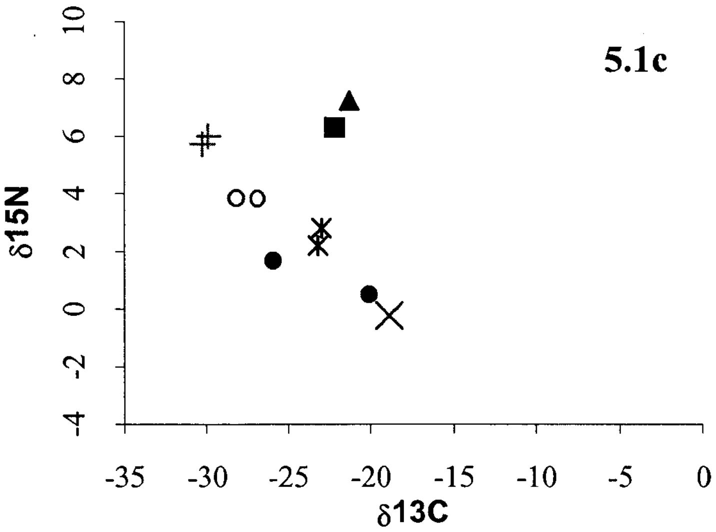
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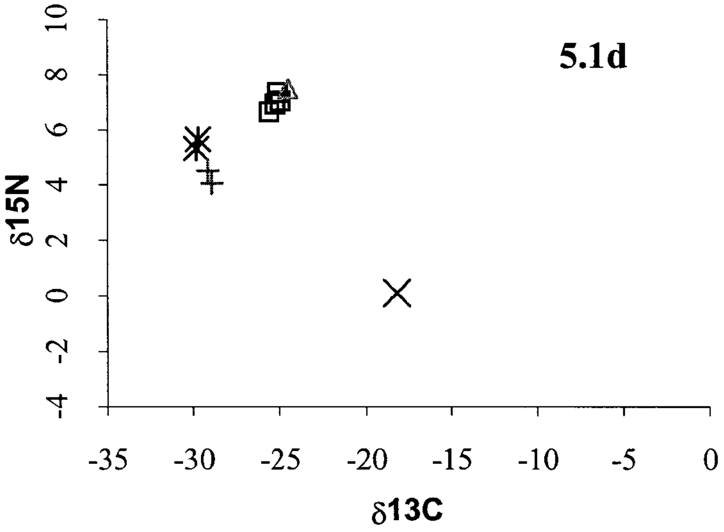
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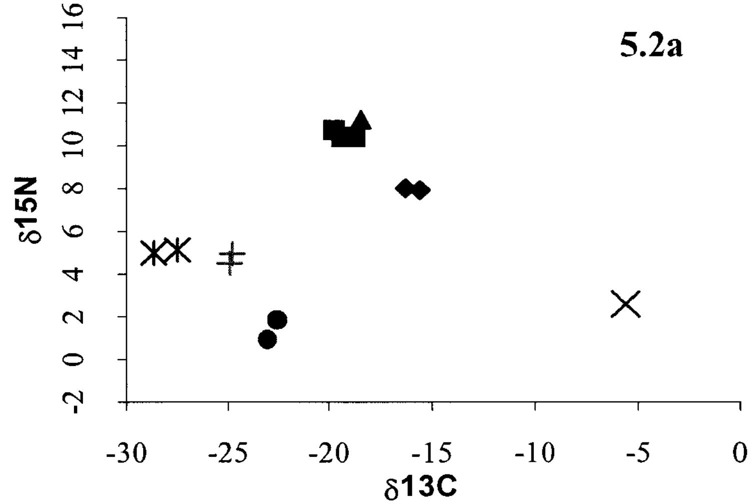
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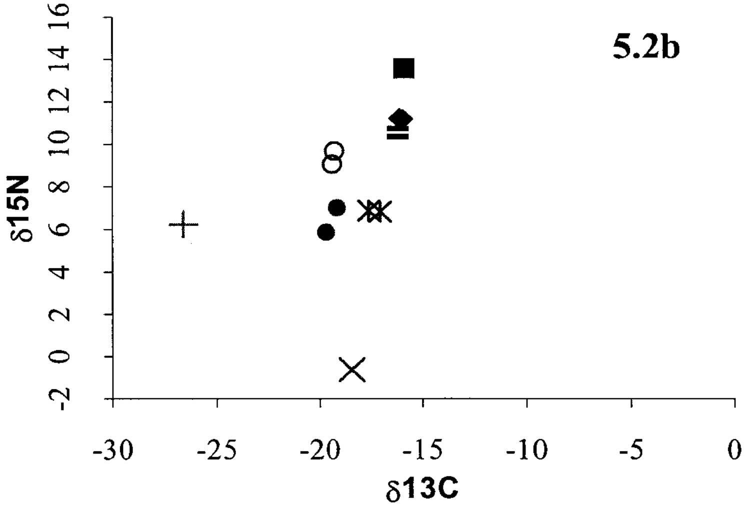
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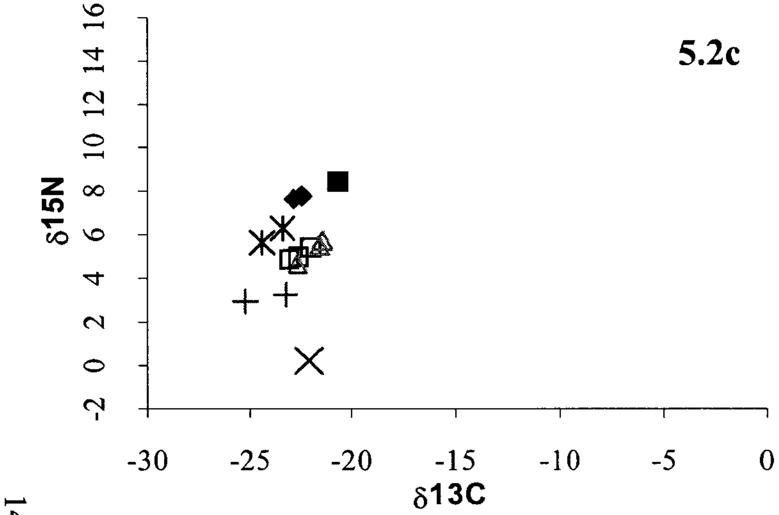
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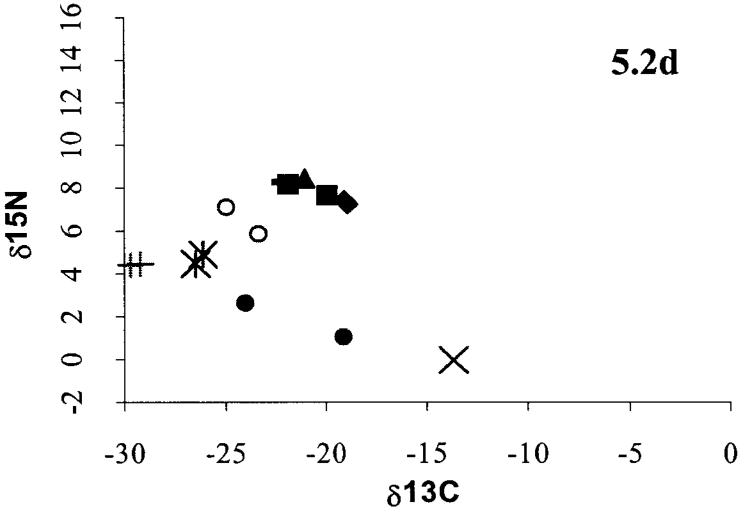
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Figure 5.1: Scatter plots of δ^{15}N and δ^{13}C values (in ‰) of grebe and coot egg material, invertebrates and macrophytes collected in fishless ponds N1 (a), N2 (b), N3 (c) and N4 (d). Each egg sample represents material from a single egg. Amphipod samples represent up to ten individuals taken from each pond, dytiscid samples, erpobdellids and *D. alaskanus* are composed of up to three individuals from each pond.

Figure 5.2: Scatter plots of δ^{15}N and δ^{13}C values (in ‰) of grebe and coot egg material, invertebrates and macrophytes collected in fishless ponds F1 (a), F2 (b), F3 (c) and F4 (d). Each egg sample represents material from a single egg. Amphipod samples represent up to ten individuals taken from each pond, dytiscid samples, erpobdellids and *D. alaskanus* are composed of up to three individuals from each pond.

◇ = Red-necked Grebe chick pectoral, ■ = Red-necked Grebe egg albumen, ▲ = Red-necked Grebe egg yolk, □ = American Coot egg albumen, △= American Coot egg yolk, _= fathead minnow white muscle, ◆= brook stickleback white muscle, + = small dytiscid beetles, ✳ = Dytiscus alaskanus, ○= erpobdellid leeches, ● = amphipods, ×= macrophytes.

Chapter 6: Conclusions

6.1 Summary of main research results

My research focused on waterbird-fish interactions in highly productive wetlands of Alberta's Aspen Parkland that are prone to natural disturbance such as drought and winter hypoxia. Waterbird-fish interactions have never been previously studied in any of North America's Aspen Parkland wetlands. Initial community analyses (Chapter 2) showed that the most important factors driving bird and invertebrate assemblage compositions were chlorophyll a and TDN, and that invertebrate assemblage differed in composition between waterbodies with and without small-bodied fishes. Although no clear link could be established between fish presence/absence and waterbird assemblage composition, there was a strong correlation between the compositions of bird and invertebrate assemblages and the composition of invertebrate assemblages differed markedly between waterbodies with and without fish. These patterns suggest that fish may have had an indirect effect of the composition of waterbird assemblages through their direct effect on invertebrate assemblages. This baseline information established that invertebrate prey available to birds were different in wetlands with and without fish and thus was somewhat consistent with Mallory et al. (1994).

The observational and experimental studies of Red-necked Grebe and Blue-winged Teal foraging activity in the presence/absence of fish (Chapters 3 and 4) established that fish do not universally reduce the biomass of invertebrate prey for breeding waterbirds as other studies of small-bodied fish in productive, disturbed systems have indicated (Cox et al. 1998, Zimmer et al. 2001). Further, foraging activities of both bird species was positively associated with the biomass of invertebrate prey. Chapter 3 suggests that, for small-bodied fish to have any impact on bird foraging activities, they must be able to have an impact on invertebrate biomass.

The abundance of Blue-winged Teal was negatively associated with the presence of fathead minnow and brook stickleback (Chapter 3), as was the abundance (CPUE) of some of their omnivorous invertebrate prey (chironomids and amphipods). Since teals do not use invertebrate prey much larger than 12.5mm (Nudds and Bowlby 1984), the reduced abundance of these invertebrates, coupled with unchanged biomass in the presence of fish, suggests that teals foraging on Aspen Parkland wetlands with fishes had access to fewer, larger individual prey, at least for some guilds. The lack of difference in teal foraging activity in wetlands with and without fish in Chapter 3, coupled with the difference in their abundance, suggests that teals distribute themselves in such a way as to spend similar amounts of time foraging in both types of wetland, with more teals using the fishless wetlands than the wetlands with fish. For Red-necked Grebe, there were similarly fewer, larger individuals of prey such as the large predatory beetles and leeches on wetlands with fish than on fishless wetlands, but this was not reflected in any difference in grebe abundances or foraging activities. Red-necked Grebe eat fathead minnow and brook stickleback (Stout and Nuechterlein 1999, Paszkowski et al. in review), so any changes in the population structure of their invertebrate prey is most likely offset by the availability of these fish. Energetically, these large invertebrates and fish are similar, and thus it is possible that the grebes treat them as equivalent prey (Driver 1981, Gingras 1997).

The experimental addition of fish documented in Chapter 4 showed a convergence in the biomasses of herbivores and small predatory invertebrates between an experimental wetland and a reference wetland with fish, contrary to the total lack of differences in biomass in the observational study of Chapter 3. The Chapter 4 results were, however, consistent with Zimmer et al. (2001) for herbivorous invertebrates. Fish addition was also associated with increased foraging activity in Blue-winged Teal relative to reference wetlands with and without fish, which was not reversed when the fish underwent winterkill. Assuming that all other potential drivers of teal behaviour (e.g., intraspecific competition) were equivalent, this suggests that the experimental addition of small-bodied fish did not reflect the natural effects (or rather, lack of effects) of fish presence in Aspen Parkland wetlands. However, colonization of fish into previously fishless wetlands may have more of an effect on invertebrates than the presence of pre-existing fish populations, particularly where those pre-existing populations are at relatively low densities as they were in the study described in Chapter 3. Long-term studies that monitored invertebrate responses to small-bodied fish for a number of years after fish colonization would help to elucidate the point at which invertebrate populations begin to recover from the initial colonization. In my study, the added fish did not survive their first winter, and so it was not possible to study the longer-term effects of fish colonization on invertebrate biomasses or bird foraging activities. In the only comparable study that I am aware of, Zimmer et al. (2001) removed fathead minnows after they colonized a prairie pothole, and thus did not gain any insights into longer-term effects of fish colonization on invertebrates. Little is known about invertebrate life cycles in prairie and parkland wetlands (Krapu and Reinecke 1992), and there may be time lags in invertebrate responses to fish colonization that neither my work nor that of Zimmer et al. (2001) can account for.

Other studies of waterbird-fish competition for invertebrates have primarily involved either large-bodied fishes (e.g., DesGranges and Rodrigue 1986, Giles et al. 1990) or high densities of small-bodied fishes (Zimmer et al. 2001). My research dealt with small-bodied fishes at low densities. The lack of response to fish presence/absence in the Aspen Parkland suggests that fish presence/absence *per se* is not the most reliable cue to invertebrate numbers (and hence bird use of wetlands) as Mallory et al. (1994) suggest. Rather, the profound reductions in invertebrate biomasses and the changes in bird foraging activities seen in some of the studies cited above are due to the fact that the fish involved were so abundant in the study systems. There were weak relationships between fish CPUE and CPUE of medium-sized predatory invertebrates (hemipterans and small dytiscid beetles) and gastropods (see 3.3.3), but there was not a very steep gradient of fish CPUE values in the wetlands I studied. The main consistency between my research findings and those of others is the reduction in abundance of Blue-winged Teal in the presence of fish: many classic studies that involved large-bodied fish in oligotrophic and eutrophic systems have shown a greater use of lakes by waterbirds in the absence of fish than in their presence (e.g., Eriksson 1983, Hanson and Butler 1994, Andersson and Nilsson 1999).

Finally, Chapter 5 detailed the effects of fathead minnow and brook stickleback on trophic relations of Aspen Parkland waterbirds, as determined by stable isotope analysis (SIA) of Red-necked Grebe and American Coot eggs. In this case, fish presence was associated with an increase in the trophic position of Red-necked Grebe and a decrease in the trophic position (as indicated by $\delta^{15}N$ signals) of American Coot. Thus, even in a system where fish have limited or no effects on bird foraging activities or the biomass of their invertebrate prey, the presence of fish can still have an impact on food web relationships for waterbirds. It is not known whether being at a higher or lower trophic level in the presence of fish has any effect on the reproductive success of either grebes or coots.

6.2 Other factors that influence invertebrates and waterbirds

Aspen Parkland is naturally frequently disturbed, and its wetlands are strongly influenced by a 5-20 year wet-dry cycle of precipitation that results in extreme fluctuations in water depth (Nicholson and Vitt 1994, Mitsch and Gosselink 2000). In this regard Aspen Parkland is very similar to the Prairie Pothole Region and in fact some regard Aspen Parkland to be a part of the PPR (e.g., Tangen et al. 2003). During the course of these studies, the parkland and prairies were undergoing a severe drought that would have resulted in the loss of fish due to increased winter hypoxia (Robinson and Tonn 1995, Danylchuk and Tonn 2003). Thus, it is likely that any fish effects on invertebrate prey of waterbirds in such a disturbed system as Aspen Parkland would be strongly mediated by the effects of drought. At the community level, Bethke and Nudds (1993) have found that changes in duck community richness in the prairies are more tied to the occurrence of drought than to competition. The findings of Bethke and Nudds (1993), and my own findings at the species level in a naturally highly disturbed aquatic ecosystem, highlight the importance of being aware that environments can be highly variable when studying competition in the real world (Wiens 1977). Often, severe environmental fluctuations can mask the influence of competition on the distributions of species. In my research, drought conditions may have eliminated waterbirds' competition with fish in wetlands where fish were extirpated. Chapter 2 also highlighted the importance of abiotic factors such as nutrient status and waterbody size in determining community composition in Aspen Parkland.

Additionally, use of Randomized Intervention Analysis to document responses of birds and invertebrates to fish extirpation and recovery, and to fish colonization (Chapters 3 and 4), suggests that small-bodied fish may be just one of many factors that can influence invertebrate availability for waterbirds, and hence waterbird foraging behaviour. For example, the biomasses of some invertebrate guilds increased over a period of 3 years in a consistently fishless reference wetland studied in Chapter 3. Clearly, these changes were not due to the presence of fish. Some invertebrate prey of waterbirds, such as amphipods, have no terrestrial component to their life cycles (Clifford 1991) and so are often extirpated by drought conditions. In wet years, if fish were at high densities as found in some PPR studies (Zimmer et al. 2001), the effects of water levels on birds and invertebrates might be manifested as a fish effect, but this would be less obvious in drought periods when fish, if present at all, would be at low densities due to increased incidence of winter hypoxia (Danylchuk and Tonn 2003). The relatively short time frame of my research only viewed fish, invertebrates and waterbirds in a drought period: longer term studies that also deal with the relative importance of abiotic factors and competition with fish in determining bird habitat uses and foraging activities in wet years would be very useful.

Finally, there is some evidence that tiger salamanders (*Ambystoma tigrinum*) can also compete with waterbirds for invertebrate prey in fishless prairie wetlands, apparently functioning in much the same way as fish when at high densities (Benoy et al. 2002). In Aspen Parkland, I encountered these amphibians only occasionally, in contrast to Benoy et al. (2002) who had densities of tiger salamanders ranging from 6-306 individuals/ha/survey. Tiger salamander surveys of Aspen Parkland wetlands in my study area in 2001 (S. Eaves, unpubl. data) showed a total of 21 adult and larval salamanders in a total of 5893 traps nights over the period 1 June-28 August (pitfall traps and minnow traps set along wetland edges combined). Thus, in Aspen Parkland, there appears to be a much lower abundance of tiger salamanders than in prairie potholes.

6.3 Future directions for studies of waterfowl-fish competition

If the density of fish must be high before they can affect the biomasses of invertebrates and hence the foraging activities of birds as they do in the PPR (Cox et al. 1998, Zimmer et al. 2001) and other aquatic ecosystems (e.g., acidified lakes or gravel pit lakes; DesGranges and Rodrigue 1986, Giles 1994), it would be useful to document invertebrate biomasses, bird abundance and bird foraging activity in wetlands along a sufficiently long gradient of fish density. A gradient that included densities such as those in New York marshes studied by Batzer (1998; about 1.25 fish/trap/hour) as well as the fish densities of less than 0.1 fish/trap/hour found in Aspen Parkland would be a good starting criterion for choosing study wetlands or setting up mesocosms in such studies. A similar approach could be used to study the relative importance of competition with tiger salamanders (Benoy et al. 2002) at different densities.

Stable isotope analysis (SIA) is clearly a useful technique for documenting the role of fish in waterbird trophic relations. Additionally, SIA is useful for determining whether conservation efforts should be focused on a species' wintering grounds or its breeding grounds. The technique has previously been used successfully to track migration patterns of wildlife that are often hard to monitor directly due to the large areas that they cover (Hobson 1999). If SIA showed that other waterbirds of greater conservation concern than Red-necked Grebe or American Coot, such as Lesser Scaup (Anteau 2002), also obtain resources for eggs directly from breeding wetlands rather than importing those resources from wintering areas, then management resources for such species should be focused on breeding grounds more than on wintering areas. In Aspen Parkland, fish had quite clear effects on the trophic position of two species of waterbird, despite weak or non-existent interactions with invertebrates and poor correlation with foraging activities of adult birds. But the generality of the patterns observed in Aspen Parkland (i.e. that fish are associated with a change in the trophic position of waterbirds) has not been tested, nor have the implications of foraging at a lower or higher trophic level in the presence of fish. Whilst the behavioural and abundance data from Chapter 3 and 4 show that Red-necked Grebes appear to treat fish and invertebrates as equivalent prey, there is always a lot of energy lost in transfer up trophic levels (Begon et al. 1990). Thus, although fish and invertebrates appear equivalent for grebes (Driver 1981, Gingras 1997), the grebes may be gaining less energy by being at the top of a longer food chain in the presence of fish than in their absence. One way to test this hypothesis would be to measure survival of Red-necked Grebe chicks on wetlands with and without fish (assuming that factors such as digestibility of fish and invertebrates were equal). One could use a similar approach for coots, which were at a lower trophic level in the presence of fish than in their absence.

In systems like Aspen Parkland where the high amount of natural disturbance results in strong fluctuations in many features of the abiotic environment (e.g., depth, winter oxygen levels) as well as in the distributions of fish, it would be useful for managers to know under what circumstances competition with fish becomes an important determinant of bird habitat use. Many management strategies for wetlands have involved removals of fish to improve water quality (biomanipulations; see Bergman et al. 1999 for a review). Fish removals are time consuming and costly (Bergman et al. 1999), and in situations where competition with fish for invertebrates is less important to waterbirds than, for instance, the depth of the wetlands on which they feed and breed (Kaminski and Prince 1981), it would be unnecessary and inappropriate to manage the birds' habitat by performing fish removals. In addition, some land use practices could potentially reduce the heterogeneity of fish distributions in dynamic ecosystems like Aspen Parkland wetlands or prairie potholes. For example, wetland consolidation could encourage fish like fathead minnow and brook stickleback to survive through drought periods by providing them with larger, deeper, more permanent wetlands rather than the more typical mosaic of small, shallow wetlands in the system. Besides loss of small wetland habitats that include an appropriate mix of open water and vegetative cover for breeding waterbirds (hemi-marsh *sensu* Kaminski and Prince 1981), this enhancement of fish survival and any associated reduction in invertebrate prey availability could be detrimental to breeding waterbirds in Aspen Parkland and similar regions such as the PPR. Thus, managers might be best advised to discourage these land use practices, rather than to manipulate fish status in an ecosystem where fish status of any given wetland is highly variable.

Thus, there are two possible avenues of research that could allow us to determine the point at which small-bodied fish become an important factor in determining the distributions and habitat uses (including foraging activities) of waterbirds in Aspen Parkland. Firstly, one could monitor bird abundance and foraging activity, along with invertebrate biomasses, in wetlands along a sufficiently long gradient of fish density. Previous studies of small-bodied fish/invertebrate/waterbird interactions (Zimmer et al. 2001), including the studies presented in this thesis, and studies that have involved larger fish (Eriksson 1978, 1979), have focused on fish presence/absence rather than fish abundance. The weak responses of invertebrates and birds to fish in Aspen Parkland during a period when fish were scarce suggests that there may be some critical density below which small-bodied fish are less important than abiotic factors such as TDN, TP or chlorophyll a (Chapter 2) or drought (Bethke and Nudds 1993).

Secondly, one could monitor birds and invertebrates immediately after fish colonization and for a number of years thereafter, rather than monitoring the immediate effects of that colonization and a subsequent extirpation of the colonizing fish. In this thesis, the extirpation was due to a natural event, winter hypoxia, which could not be controlled. However, my study could be repeated during the wet part of the wet-dry precipitation cycle that dominates the hydrology of Aspen Parkland wetlands and similar areas such as the PPR (Mitsch and Gosselink 2000). Longer term monitoring, if it incorporated periods where winter hypoxia was less frequent, could follow a colonization experiment to document the long-term effects of fish colonization and perhaps reconcile the lack of invertebrate response to fish presence (Chapter 3) with the partial response of invertebrates to fish addition (Chapter 4). From the viewpoint of applying competition theory to the real world, it would also be in line with the recommendations of Wiens (1977) for using long-term monitoring of populations rather than conducting short-term studies of competition in variable environments. My research provides data on fish-waterbird interactions and the roles of other biotic and abiotic factors in determining waterbird assemblage compositions during the drought part of the cycle, and thus has already taken the first steps towards such long-term monitoring.

Some 70% of North America's wetlands have been lost due to agriculture and urbanization, with further losses expected due to anticipated drying out of western Canada via anthropogenically induced climate change (Danylchuk and Tonn 2003). Given these factors, and given the infeasibility of traditional management methods such as biomanipulations of fish in highly disturbed aquatic systems like Aspen Parkland wetlands, long term monitoring is crucial to developing and implementing management strategies that are adapted to the high degree of natural disturbances in these important bird habitats. Prairie and Aspen Parkland potholes provide prime breeding habitat for many of North America's waterbirds (Krapu and Reinecke 1992). A greater understanding of the long-term relative importance of fish competition and abiotic factors such as drought and nutrient status is crucial for development of management strategies that discourage unnatural changes to the physical and biotic features of these important waterbird habitats.

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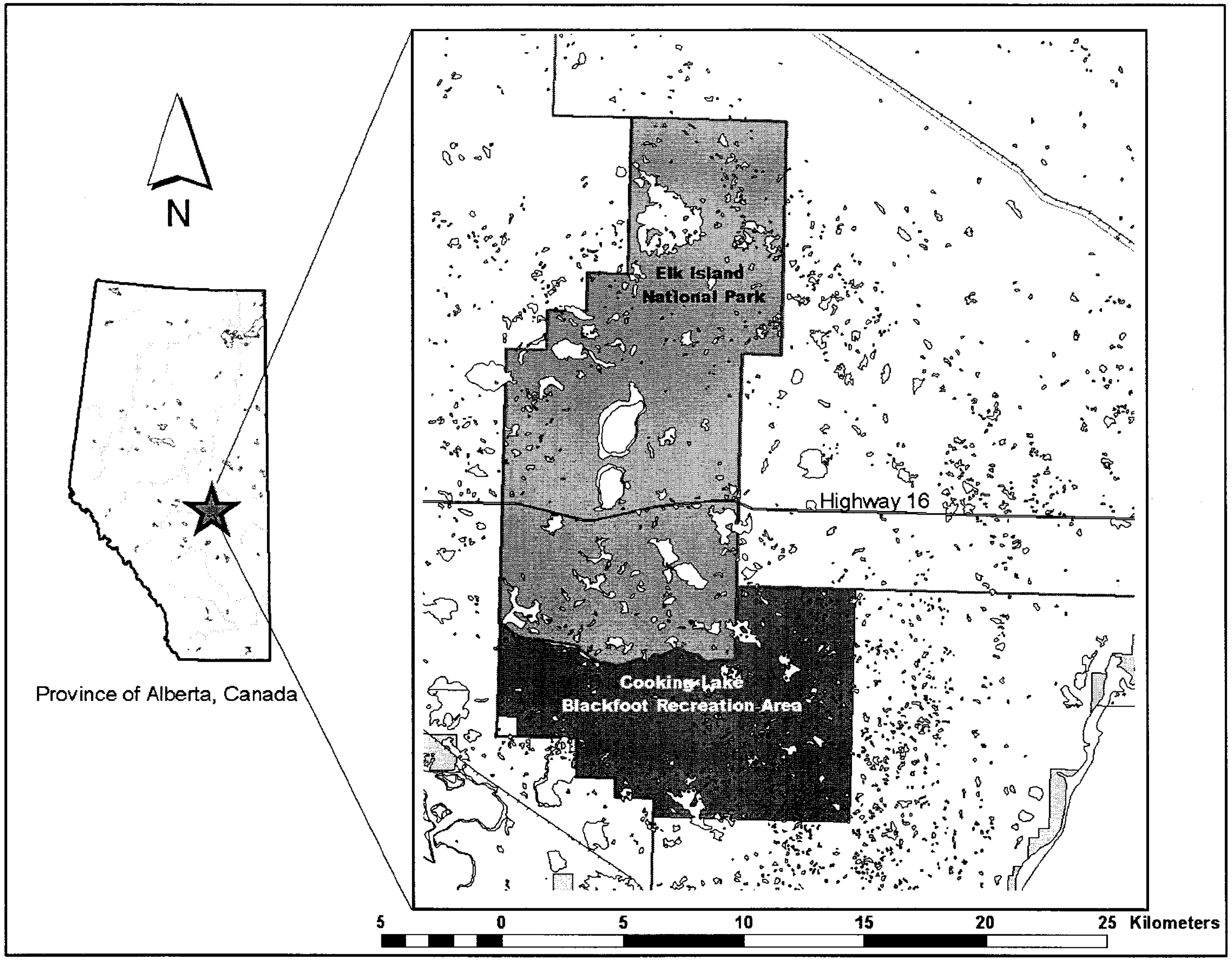


Appendix 1: Map of the study area showing the range of wetlands studied in 1999-2002.

Appendix 2.1: limnological and morphometric features of the 25 waterbodies in the Aspen Parkland assemblages study (Chapter 2). P90491 was not used in ordinations as no invertebrates were collected there. FM= fathead minnow,

site	symbol	Lat/Lng	area (ha)	Mean depth (m)	pH	conductivity (µS/cm)	TP (µg/L)	TDN (µg/L)	chlorophyll a	Mean Secchi (cm)	invertebrate richness	fish	species number
Moss Lake	MS	53°40' N 112°50'W	14.78	3.20	9.43	354	53.6	2076.6	8.3	53.5	4	none	4
NE1	N1	53°44'N 112°47'W	0.50	0.15 ± 0.01	8.09	299	83.9	1110.8	6.7	14.6	3	none	5
NE2	N2	53°43'N 112o47'W	0.50	0.34 ± 0.10	8.45	488	30.2	1178	1.9	33.6	6	none	4
P3033	P33	53°34'N 112°49'W	0.74	0.59 ± 0.04	7.47	907	240.1	2737.9	3.9	49.4	7	BS	8
P3043	P43	53°34'N 112°48'W	1.46	2.24 ± 0.73	8.1	259	38.3	937	4.3	158.8	1	FM	2
P1814	P14	53°35'N 112°48'W	1.50	0.51 ± 0.06	7.72	680	180	2453.3	0.8	51	4	none	8
P1813	P13	53°35'N 112°49'W	1.00	0.51 ± 0.18	7.42	835	441.5	1558.9	0.9	51	9	none	11

Appendix 2.1 continued

site	Lat/Lng	symbol	area (ha)	Mean depth (m)	pH	conductivity (μS/cm)	TP (μg/L)	TDN (μg/L)	chlorophyll a	Mean Secchi (cm)	invertebrate richness	fish	species number
Goose Lake	53°33' N 112°48'W	GS	50.14	0.70 ± 0.10	8.55	503	123.7	2382.1	1.8	70	6	FM/BS	20
Blackfoot Lake	53°31'N 112°48'W	BF	64.24	0.78 ± 0.18	7.17	706	194.6	2156	44	19.5	8	FM/BS	6
P1	53°43'N 112°52'W	P1	0.50	0.33 ± 0.08	8.1	437	105.1	1656.7	4.1	33	6	none	9
P86	53°43'N 112°50'W	P86	0.50	1.17 ± 0.11	8.69	366	107.9	1651.3	26.1	57.3	5	none	5
P321	53°42'N 112°47'W	P321	4.01	1.74 ± 0.45	7.65	356	34.5	1037.2	4.8	122.8	7	none	6
Astotin Lake	53°41'N 112°51'W	AS	559.50	1.64 ± 0.32	9.04	399	45.6	1391.7	39.1	61.6	8	FM/BS	26
Oster Lake	53°36'N 112°55'W	OS	120.05	2.21 ± 0.62	8.80	283.0	73.0	1837.8	11.0	59.0	6	FM/BS	13

Appendix 2.1 continued

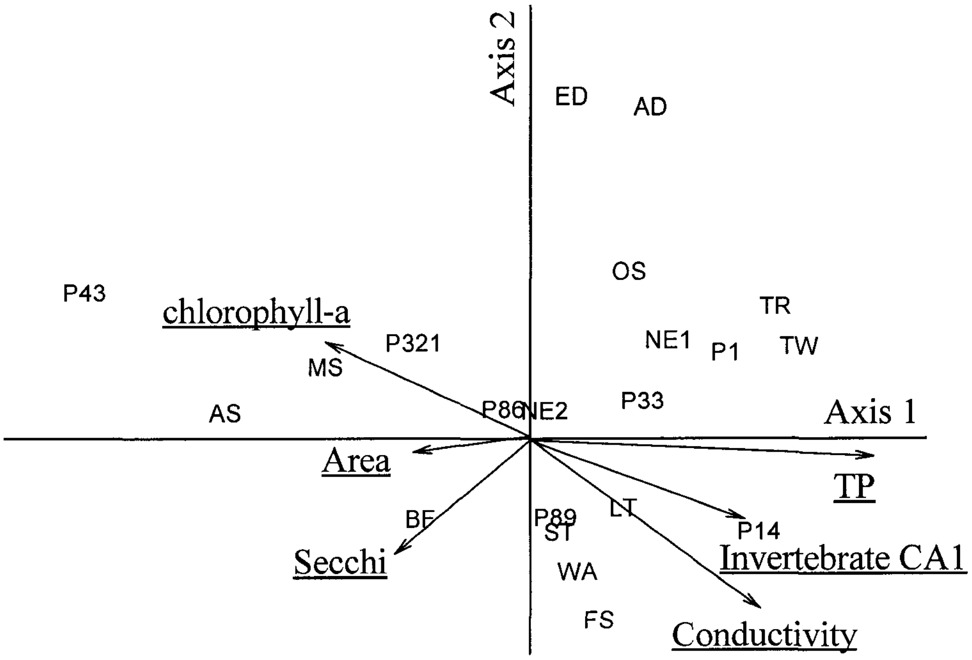
site	Lat/Lng	symbol	area (ha)	Mean depth (m)	pH	conductivity (µS/cm)	TP (µg/L)	TDN (µg/L)	chlorophyll a	Mean Secchi (cm)	invertebrate richness	fish	species number
Eddy Lake	53°36' N 112°54'W	ED	35.13	1.47 ± 0.28	8.65	310.0	69.8	1799.1	9.5	74.5	5	FM/BS	12
Trappers' Lake	53°34'N 112°58'W	TR	161.02	1.32 ± 0.30	8.95	305.0	101.8	1947.4	20.7	98.6	8	none	12
Shirley Lake	53°38'N 112°55'W	SL	33.38	1.03 ± 0.32	9.05	264.0	153.4	1650.3	22.1	30.0	5	none	13
Adamson Lake	53°36'N 112°55'W	AD	89.57	1.47 ± 0.29	8.80	283.0	95.5	1660.3	11.9	44.2	8	none	12
Tawayik Lake	53°35'N 112°47'W	TW	391.89	0.86 ± 0.45	8.88	766.0	136.1	3132.7	25.7	37.8	9	FM	20
P90491	53°40'N 112°49'W	P91	1.63	1.12 ± 0.16	8.24	294.0	34.3	1462.8	7.0	76.0	0	none	7
P90489	53°40'N 112°48'W	P89	1.00	1.42 ± 0.50	7.55	275.0	36.5	854.3	7.3	87.3	5	none	3

Appendix 2.1 continued

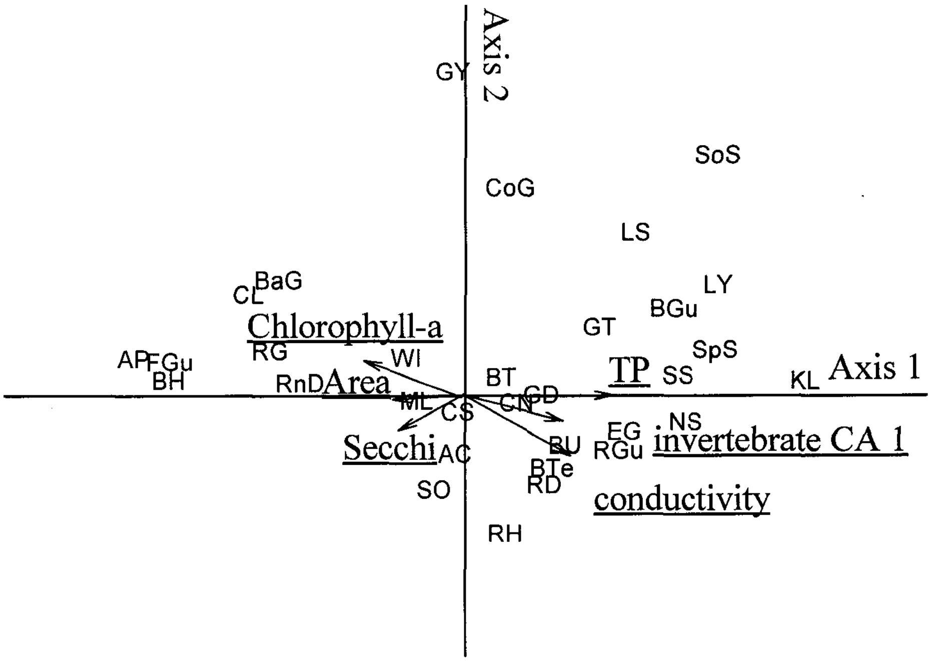
site	Lat/Lng	symbol	area (ha)	Mean depth (m)	pH	conductivity (μS/cm)	TP (μg/L)	TDN (μg/L)	chlorophyll a	Mean Secchi (cm)	invertebrate richness	fish	species number
Star Lake	53°34' N 112°54'W	ST	15.01	0.62 ± 0.03	7.04	834.0	61.0	1572.2	4.2	62.0	6	BS	10
Little Tawayik	53°33'N 112°47'W	LT	179.27	1.16 ± 0.17	9.06	714.0	128.9	3012.2	23.9	52.3	11	FM	23
Walter Lake	53°31'N 112°55'W	WA	122.82	1.10 ± 0.09	8.26	632.5	123.2	1686.5	12.6	110.0	9	FM/BS	12
Flyingshot Lake	53°32'N 112°50'W	FS	251.72	0.89 ± 0.25	8.21	706.5	85.1	2871.9	9.3	63.0	11	FM	22

Appendix 2.2: Alphabetical list of invertebrate taxa encountered in the study. Taxa were identified as far as possible, with common taxa being identified more finely than scarce taxa.

Taxa	Abbreviation
Amphipoda	amph
Cladocera	clad
Coleoptera: Curciulionidae	curc
Coleoptera: Dytiscidae	dyti
Coleoptera: Haliplidae	hali
Coleoptera: other families	cole
Conchostraca	conc
Diptera	dipt
Ephemeroptera	ephe
Gastropoda: Lymnaeidae	lymn
Gastropoda: Physidae	phys
Gastropoda: Planorbidae	plan
Hemiptera	hemi
Hirudinea: Erpobdellidae	erpo
Hirudinea: Glossiphoniidae	glos
Hirudinea: Hirudinidae	hiru
Hydrachnidia	hydr
Odonata	odon
Ostracoda	ostr
Trichoptera	tric



Appendix 2.3a: CCA ordination biplot of environmental variables showing waterbodies in EINP at which bird assemblages were surveyed in May 1999. The arrows shown for environmental variables are vectors that indicate the size of their influence on the bird census data. Longer arrows indicate a stronger influence in that direction. TP = total phosphorus. Abbreviations for site names are explained in Appendix 2.1.



Appendix 2.3b: CCA ordination biplot of environmental variables showing the species that occurred at the waterbodies surveyed in May 1999. Overlaying the species on the biplot in Appendix 2.3a indicates which species characterized which waterbodies. The arrows shown for environmental variables are vectors that indicate the size of their influence on the bird census data. Longer arrows indicate a stronger influence in that direction. TP = total phosphorus. Abbreviations for species are explained in Table 2.1.