

## Effects of small-bodied fish on invertebrate prey and foraging patterns of waterbirds in Aspen Parkland wetlands

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### Abstract

Competition between large-bodied fish and waterbirds for aquatic invertebrates is well documented in oligotrophic lakes. Recent evidence suggests that small-bodied fish that colonize eutrophic, hypoxia-prone wetlands such as prairie potholes can also reduce aquatic invertebrates, but the effects of these reductions on breeding waterbirds have so far not been directly documented. We added brook stickleback (*Culaea inconstans*) and fathead minnow (*Pimephales promelas*) to a fishless wetland in Aspen Parkland potholes in central Alberta, Canada. We monitored invertebrate biomasses and the foraging effort of blue-winged teal (*Anas discors*) and red-necked grebe (*Podiceps grisegena*) before and after the addition, relative to reference wetlands with and without fish. Fish reduced the biomass of gastropod prey of blue-winged teal, and teals increased foraging effort when fish were added. When the fish failed to overwinter due to hypoxic conditions, gastropod biomass increased, but teal foraging effort did not return to pre-treatment levels. Amphipods and chironomids increased following fish addition, possibly due to indirect positive effects of fish. Red-necked grebes did not exhibit any changes in foraging effort as a result of the fish addition or the subsequent fish extirpation. Grebes in Aspen Parkland appear to treat fish and invertebrates as equivalent prey. This study suggests that small-bodied fish in eutrophic systems can reduce some important invertebrate prey and change foraging behaviour of blue-winged teal and other waterbirds that rely on those invertebrates. Land-use practices that encourage survival of colonizing fish through drought years in Aspen Parkland wetlands, such as wetland consolidation, should not be encouraged.

### Introduction

Competition between large-bodied fish and waterbirds for invertebrate prey is well documented in North American and European oligotrophic lake systems. Perch, *Perca fluviatilis* (L.), yellow perch, *Perca flavescens* (Mitchill), and roach, *Rutilus rutilus* (L.), show substantial diet overlap with common goldeneye, *Bucephala clangula* (L.), American black duck, *Anas rubripes* (Brewster), mallard, *Anas platyrhynchos* (L.), and teal, *Anas crecca* (L.), (Eriksson, 1978; Eadie & Keast, 1982; DesGranges & Rodrigue, 1986; Giles et al., 1990).

However, waterbird-fish competition is poorly understood in shallow eutrophic systems (but see Giles et al., 1990), such as prairie potholes or Aspen Parkland potholes. These systems often experience winter hypoxia that leads to mortality ('winterkill') of intolerant, often large-bodied fish species (Robinson & Tonn, 1989; Tonn et al., 1995).

Fishes reduce invertebrates even in eutrophic, hypoxia-prone systems like prairie potholes that only support small-bodied fishes (Hanson & Riggs, 1995; Zimmer et al., 2000; Zimmer et al., 2001). Waterbirds' use of eutrophic wetlands can also increase when fishes are removed in

biomanipulations (Hanson & Butler, 1994; Andersson & Nilsson, 1999). It may therefore benefit breeding waterbirds that rely on invertebrates if small fishes are removed or excluded from such systems (e.g., Bouffard & Hanson, 1997). 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 & Schindler, 1994). Predatory invertebrates such as *Chaoborus obscuripes* (van der Wulp) 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 (Peterka, 1989). 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 & 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. Therefore, 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* (Rafinesque). It is not clear whether these reductions are limited to highly omnivorous fish species such as fathead minnow (Keast, 1985), or can be exerted by species of a more restricted diet, such as brook stickleback, *Culaea inconstans* (Kirtland). 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.

We added fathead minnows and brook sticklebacks to a fishless Aspen Parkland wetland, monitoring invertebrates and foraging activities of blue-winged teal, *Anas discors* (L.), and red-necked grebe, *Podiceps grisegena* (Boddaert), 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. Based on previous studies of bird foraging in the presence/absence of fishes (DesGranges & Rodrigue, 1986; Giles, 1990), we 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 & 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 particularly likely to hold true if the added fish reduce some of the invertebrate prey available to grebes, effectively replacing invertebrate food sources for grebes (see below). Since fathead minnows reduce the biomass of planorbid snails, amphipods and chironomids (Cox et al., 1998; Zimmer et al., 2001), we 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, we predicted that if the introduced fishes failed to overwinter due to hypoxic conditions, their effects on invertebrates and birds would be reversed.

### Study area

North America's Aspen Parkland, a transitional zone between prairies and boreal forest (Nicholson

& Vitt, 1994), contains many shallow meso- to hypertrophic freshwater potholes ( $\sim 30 \mu\text{g/l}$  to  $>400 \mu\text{g/l}$  total phosphorus; Nicholson, 1995; C. McParland, unpubl. data) that support many species of waterbird (Savard et al., 1994). Most parkland wetlands are rarely deeper than 1.5 m (Savard et al., 1994; C. McParland, unpubl. data). The fish fauna often consists only of fathead minnow and brook stickleback, which are very tolerant to low oxygen levels (Nelson & Paetz, 1992). We focused on Elk Island National Park (EINP) and Blackfoot Provincial Recreation Area (BPRA), two adjacent reserves that comprise a  $292 \text{ km}^2$  remnant of the Aspen Parkland in central Alberta, Canada (Lat  $53^\circ\text{N}$ , Long  $112^\circ\text{W}$ ).

### Materials and methods

In June–August 2000, we monitored invertebrates and foraging activity of red-necked grebes and blue-winged teals on one wetland with fishes and two fishless wetlands in the Aspen Parkland. We measured average depth (using a marked rope), total phosphorus and chlorophyll-*a* (Table 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 (C. McParland, unpubl. data; Savard et al., 1994).

In early June, late June, mid July and early August 2000, we sampled nektonic invertebrates using bottle activity traps placed for 24 h at 25 m intervals along 100 m transects within 2 m of

shore. Each wetland had 2–3 transects (10–15 traps). In deeper lakes, this technique would only be appropriate for sampling the littoral invertebrate community. In shallow parkland systems, however, the entire wetland shows little differentiation in depth, chlorophyll-*a* concentrations or invertebrate communities between the edges and centres of open water areas (C. McParland, pers. obs.). Using activity traps in such shallow wetlands provides a quick and readily employed index of invertebrate abundance. Benthos was sampled using a combination of Ekman grabs and kick-sampling along shore with a D-net.

Since birds do not select invertebrate prey based on taxonomic identity, we chose to sort invertebrates into guilds rather than employing fine taxonomic resolution. Invertebrates smaller than  $250 \mu\text{m}$  were excluded from our analyses, since it was unlikely that the birds would consume them (Nudds & Bowlby, 1984; Stout & Nuechterlein, 1999). We sorted invertebrates as follows: omnivores (Chironomidae, Amphipoda), herbivores (Gastropoda), small predators (Glossiphoniidae), medium predators (Corixidae, Notonectidae, Dytiscidae except *Dytiscus alaskanus* (Balfour-Browne)), and large predators (*Dytiscus alaskanus*, Erpobdellidae and Hirudiniidae). Zooplankton was 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

Table 1. Some limnological features of the experimental wetland and references, as sampled each of the 3 years of the experiment. EW, Experimental Wetland; FW, Fish Reference; NW, Fishless Reference

	Year	Avg depth (m)	Chlorophyll- <i>a</i> ( $\mu\text{g/l}$ )	Total phosphorus ( $\mu\text{g/l}$ )
EW	2000	$1.0 \pm 0.07$	22.0	104
EW	2001	$0.59 \pm 0.11$	71.6	147.1
EW	2002	$0.63 \pm 0.09$	2.3	95.2
FW	2000	$1.22 \pm 0.12$	18.3	133
FW	2001	$0.81 \pm 0.23$	3.0	100.8
FW	2002	$0.87 \pm 0.17$	2.8	84.1
NW	2000	$1.53 \pm 0.05$	10.2	37
NW	2001	$1.06 \pm 0.2$	2.4	34.0
NW	2002	$0.94 \pm 0.25$	1.6	38.0

glossiphoniid leeches per wetland, up to 10 chironomids and up to 10 amphipods per wetland. We 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) to account for the different types of collection methods. We summed the CPUE values obtained from each collection method to get a single CPUE value for each guild. In calculating CPUE as numbers/l/h, the time for grab and net samples was taken as time to process grab or net contents. Time for activity trap samples was taken as the duration the traps were set (24 h). We 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.

During the same four periods described above, we collected activity data on teal and grebe from all wetlands. We focused on up to three individuals of each species on each wetland per sampling session. As far as possible, we focused on females since they generally require more invertebrates than males during breeding, and hence are more likely to compete with fish (Krapu & Reinecke, 1992). Each activity budget lasted for 20–25 min and was conducted between 0500 and 1000. Activities for each individual were recorded every 30 s, to allow calculation of the proportion of total observed time spent in each activity. We then calculated the average proportion of observed time spent foraging (dabbling for teals, diving for grebes) by all grebes and teals on each wetland from these data. In the wetland with fishes, we used standard wire mesh traps (6 mm mesh) to collect fathead minnows and brook sticklebacks. Since the study area entered a severe drought period in 2000, we wished to be certain that fish had not disappeared from this wetland early in the study. These traps were set at 25 m intervals along the same 100 m 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.

In late May 2001, we collected 8000 brook stickleback and fathead minnow (4000 of each species) from a lake in the same watershed as the study wetlands. We added 2000 individuals of

each species to one of the wetlands that had been fishless in 2000. This wetland, about 10 ha in area, was designated Experimental Wetland (EW). The other two wetlands from 2000 were used as references: a fishless reference (NW) and a fish reference (FW). In 2001, we sampled bird activity, fishes and invertebrates in the three wetlands as described for 2000, and repeated the sampling in 2002. We did not find fish in EW in 2002. Thus, we 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.

#### *Data analysis*

We 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. We followed the graphical approach of Carpenter et al. (1989), where plots of RIA show changes in the difference between systems, rather than the changes in the raw data of interest (Carpenter et al., 1989). Wallace et al. (1999) show plots of changes in the raw data of interest rather than changes in intersystem difference. This approach does not always clearly depict changes within the experimental system relative to its reference (which RIA directly tests), due to the large within-system variation that is a common feature of single-system studies.

## Results

### *Invertebrate responses to fish addition within the experimental wetland*

Within EW, wet biomasses of small predators (glossiphoniids) and herbivores (gastropods) decreased following addition of fish (Table 2a). After the 2002 winterkill, herbivore biomass increased, 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 2a). Biomasses of large predators (*D. alaskanus*, large leeches) and omnivores (amphipods/chironomids) increased in 2001 and remained elevated in 2002. Catch per unit effort of all guilds except large predators increased in EW across the period 2000–2002 (Table 2b).

### *Invertebrate wet biomasses in experimental wetland compared to fish reference*

Randomized Intervention Analysis (RIA) assessed changes in intersystem differences in invertebrate wet biomasses between EW and FW pre- and post-manipulation. The absolute values of those changes in intersystem differences,  $|\bar{D}_{pre} - \bar{D}_{post}|$ , and their associated  $p$ -values, are shown in Table 3. Wet biomass of all invertebrate guilds was similar between EW and FW in 2000, the year before fish addition, and remained similar between these two ponds following the 2001 manipulation, despite changes in biomass within each pond (Table 2a, Fig. 1a–e). RIA reflected this lack of change, revealing no significant changes in intersystem differences for invertebrate biomasses between EW and FW for the period 2000–2001 (Table 3).

Table 2. (a) Biomass (mg/l/h), (b) CPUE (#/l/h) of invertebrate omnivores, larger herbivores, and predators in Experimental Wetland, Fish Reference, and Fishless Reference before (2000), after (2001) and one year after (2002) the fish addition. Values are averages ( $\pm$ SD) based on sampling in early June, late June, mid-July and early August of each year

	Experimental wetland (EW)				Fish reference (FW)				Fishless reference (NW)		
	2000	2001	2002		2000	2001	2002		2000	2001	2002
<b>(a) Biomass (mg/l/h)</b>											
Herbivores	1.4 (1.5)	0.7 (1.0)	1.1 (1.7)	Herbivores	4.4 (4.9)	1.3 (0.5)	7.0 (6.6)	Herbivores	1.1 (1.1)	5.5 (10.7)	14.0 (9.8)
Small predators	1.3 (1.6)	0.6 (1.0)	0.10 (0.03)	Small predators	1.0 (1.1)	0.2 (0.3)	2.8 (3.5)	Small predators	0.0 (0.0)	4.8 (9.7)	5.5 (5.9)
Medium predators	1.2 (1.7)	1.2 (1.2)	5.6 (0.4)	Medium predators	0.2 (0.3)	3.5 (1.7)	14.4 (19.8)	Medium predators	29.8 (57.4)	0.9 (1.3)	2.2 (3.0)
Large predators	1.3 (1.0)	14.1 (16.8)	23.6 (37.7)	Large predators	0.1 (0.2)	15.2 (12.8)	84.2 (54.0)	Large predators	4.3 (5.3)	14.0 (27.2)	6.6 (5.2)
Omnivores	0.1 (0.1)	0.6 (1.1)	0.6 (0.6)	Omnivores	0.8 (0.8)	0.2 (0.1)	4.8 (2.0)	Omnivores	0.2 (0.2)	0.15 (0.3)	1.8 (2.7)
<b>(b) CPUE (#/l/h)</b>											
Herbivores	3.4 (2.8)	14.2 (24.1)	392 (279)	Herbivores	1.8 (1.8)	70.4 (75.4)	4524.7 (1001.7)	Herbivores	1.1 (0.7)	9.3 (16.9)	7896.3 (9053.9)
Small predators	4.8 (4.8)	21.3 (42.5)	69.5 (127)	Small predators	0.2 (0.4)	15.8 (27.3)	174.3 (140.4)	Small predators	0.3 (0.4)	270.6 (522.0)	177.2 (202.1)
Medium predators	9.0 (4.2)	10.6 (18.6)	98.9 (64.5)	Medium predators	5.0 (6.8)	5.9 (4.5)	138.8 (165.9)	Medium predators	19.9 (17.6)	20.8 (33.7)	383.6 (587.2)
Large predators	23.5 (30.0)	5.7 (7.6)	259 (200.8)	Large predators	6.2 (7.3)	55.9 (80.3)	174.0 (193.6)	Large predators	3.9 (5.9)	2.5 (5.0)	17.4 (21.9)
Omnivores	9.1 (13.8)	21.4 (24.1)	561.7 (466)	Omnivores	31.3 (24.5)	173.3 (56.7)	5989.6 (7107.3)	Omnivores	42.7 (47.2)	23.1 (26.8)	2032.6 (1453.1)

Table 3. The absolute values of the changes in average intersystem differences,  $|\overline{D}_{pre} - \overline{D}_{post}|$ , between Experimental Wetland (EW) and references for RIA on wet biomass (mg/l) of five invertebrate guilds

Comparison	EW/FW			EW/NW		
	2000/2001	2001/2002	2000/2002	2000/2001	2001/2002	2000/2002
Herbivores	2.4 (0.648)	<b>5.3</b> <b>(0.044)</b>	2.9 (0.462)	0.04 (0.971)	13.5 (0.561)	13.5 (0.619)
Small predators	0.03 (0.790)	<b>3.1</b> <b>(0.000)</b>	3.0 (0.120)	0.7 (0.384)	<b>1.7</b> <b>(0.000)</b>	<b>2.4</b> <b>(0.000)</b>
Medium predators	3.3 (0.100)	6.5 (0.137)	<b>9.7</b> <b>(0.000)</b>	<b>1.1</b> <b>(0.000)</b>	3.7 (0.158)	4.8 (0.113)
Large predators	2.3 (0.975)	59.5 (0.147)	<b>61.8</b> <b>(0.000)</b>	16.7 (0.193)	45.5 (0.150)	28.8 (0.382)
Omnivores	1.0 (0.224)	<b>4.5</b> <b>(0.000)</b>	<b>3.5</b> <b>(0.000)</b>	0.1 (0.969)	0.4 (0.680)	0.3 (0.673)

Comparisons with Fish Reference (FW) and Fishless Reference (NW) 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.

Between 2001 and 2002, average intersystem differences between EW and FW in wet biomass of herbivores, small predators and omnivores changed significantly, following winterkill events in both wetlands (Table 3, Fig. 1a, b and e). For herbivores and small predators, intersystem differences between EW and FW in 2002 converged upon the original differences in 2000. Medium and large predator biomasses became less similar between EW and FW over the period 2001/2002, and the intersystem differences in biomass of these guilds diverged significantly from 2000 values (Fig. 1c and d). 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 FW during 2002 (from 3.5 mg/l in 2001 to 14.4 mg/l; Table 2a, Fig. 1c). Intersystem differences in omnivore biomass (Fig. 1e) in 2002 diverged from both 2000 and 2001.

#### *Invertebrate wet biomasses in experimental wetland compared to fishless reference*

Wet biomass of all five guilds was similar between EW and NW in the pre-treatment year, 2000. None of the changes in intersystem difference between EW and NW 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 EW and NW

was significant for 2001 vs. 2002, when the added fish were lost from EW, and for 2000 vs. 2002 (Fig. 1b). This change was due to an increase in biomass of small predators in NW and a decrease in biomass in EW during 2002, i.e., changes in intersystem differences of small predators for EW vs. NW were driven by events in 2002. Wet biomass of medium predators between EW and NW 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 NW during 2001 and 2002 (Fig. 1c).

#### *Bird responses to fish addition*

Within EW, the proportion of observed time spent foraging by blue-winged teals and red-necked grebes increased after addition of fish in 2001, and did not return to pre-treatment levels in 2002. The values in Table 4 are the averages of the four measures of foraging activity calculated in early June, late June, mid July and early August for EW and the references in each year. Foraging activity by both species also increased within each of the two references in 2001.

The intersystem difference in teal foraging effort between EW and FW increased between 2000 and 2001 ( $|\overline{D}_{pre} - \overline{D}_{post}| = 28\%$ ,  $p = 0.105$ ), decreased by nearly 14% between 2001 and 2002 ( $p = 0.684$ ), and decreased by approximately 15% when comparing 2000–2002 ( $p = 0.662$ ). Thus, teal

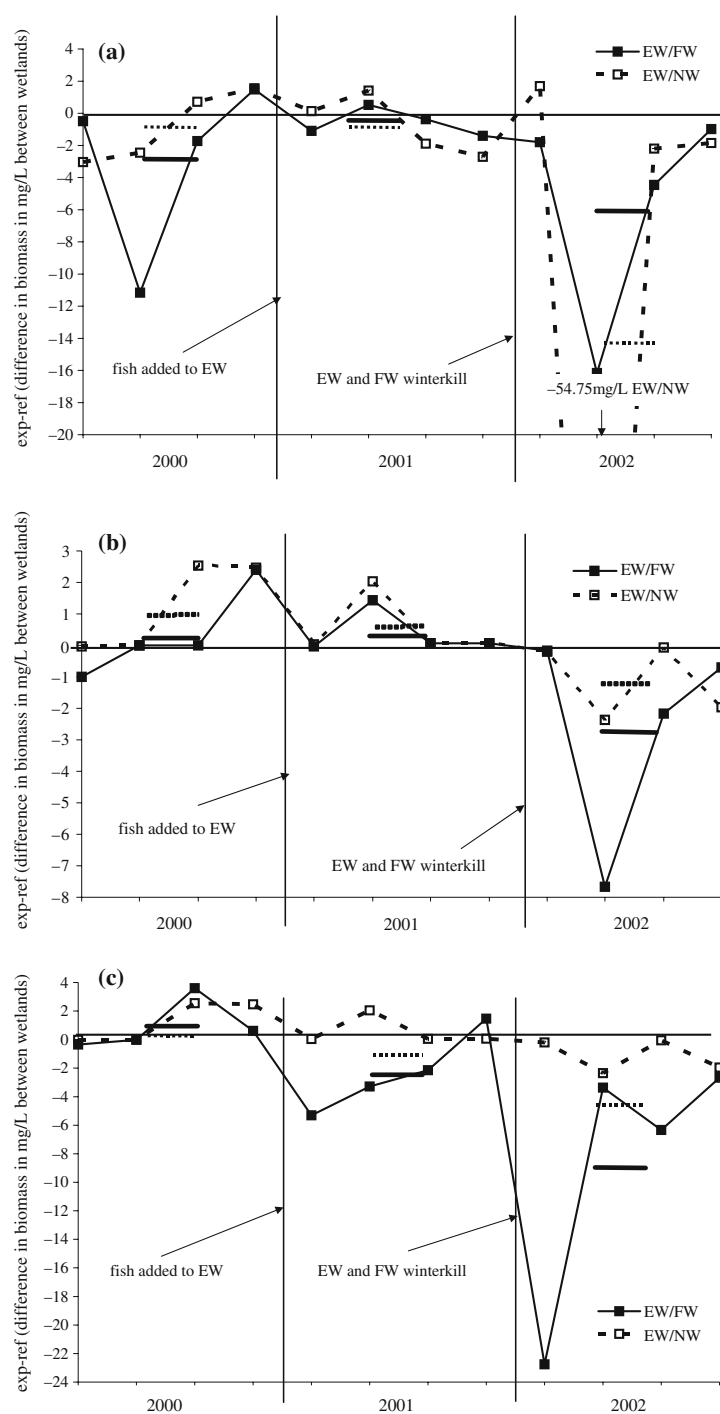


Figure 1. Intersystem differences in invertebrate biomass between experimental wetland (EW) vs. fish (FW) and fishless (NW) references. Solid horizontal bars = mean difference in biomass (mg/l/h) between EW and FW; dashed horizontal bars = mean difference between EW and NW, as calculated from the series of intersystem differences (exp-ref) in each year. RIA tests changes in these average intersystem differences ( $|\bar{D}_{pre} - \bar{D}_{post}|$ ) between years. Invertebrate guilds: (a) herbivores (gastropods), (b) small predators (glossiphoniid leeches), (c) medium predators (hemipterans, beetles except *D. alaskanus*), (d) large predators (large leeches, *D. alaskanus*), and (e) omnivores (amphipods, chironomids).

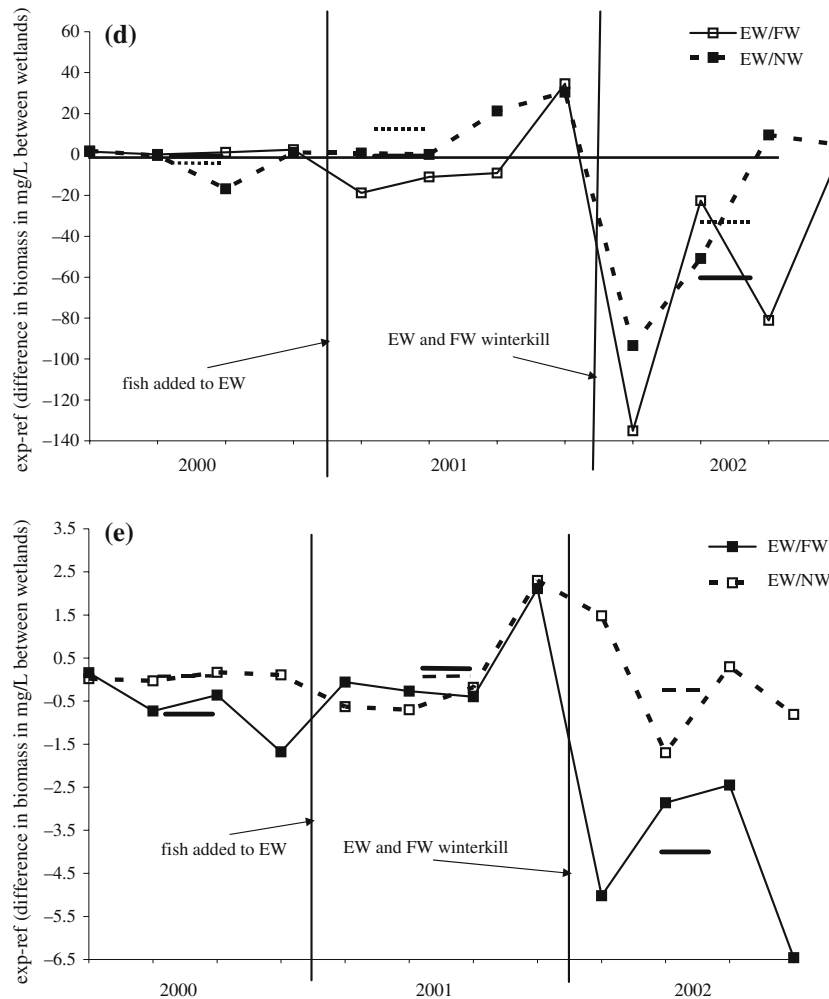


Figure 1. (Continued)

foraging effort tended to be less similar between EW and FW after fish addition than it was before fish addition or after fish extirpation (Fig. 2). The largest change in the intersystem difference in red-necked grebes foraging effort between EW and FW (Fig. 2) occurred when comparing 2000–2002 ( $|\bar{D}_{pre} - \bar{D}_{post}| = 25\%$ ,  $p = 0.184$ ), 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 EW ( $p = 0.678$ ).

Average intersystem difference in teal foraging effort between EW and fishless reference NW increased significantly between 2000 and 2001 (the change in difference,  $|\bar{D}_{pre} - \bar{D}_{post}|$ , was 27%;  $p = 0.000$ ), so that blue-winged teals spent a greater

Table 4. Average foraging effort ( $\pm$ SD) of red-necked grebes (RNGR) and blue-winged teals (BWTE) within the experimental and reference wetlands EW, FW and NW. Values are average % of time spent foraging during 4 observation sessions over the period early June–early August each year

BWTE	2000	2001	2002
EW	3.8 $\pm$ 4.4	51.4 $\pm$ 8.2	53.3 $\pm$ 29.9
FW	11.3 $\pm$ 14.9	34.5 $\pm$ 29.2	50.1 $\pm$ 28.1
NW	0.3 $\pm$ 0.6	20.7 $\pm$ 17.9	29.8 $\pm$ 14.5
RNGR	2000	2001	2002
EW	14.0 $\pm$ 6.1	21.1 $\pm$ 14.9	28.7 $\pm$ 42.2
FW	6.8 $\pm$ 8.1	19.3 $\pm$ 18.2	46.9 $\pm$ 24.0
NW	15.9 $\pm$ 6.6	30.9 $\pm$ 20.0	36.1 $\pm$ 13.2



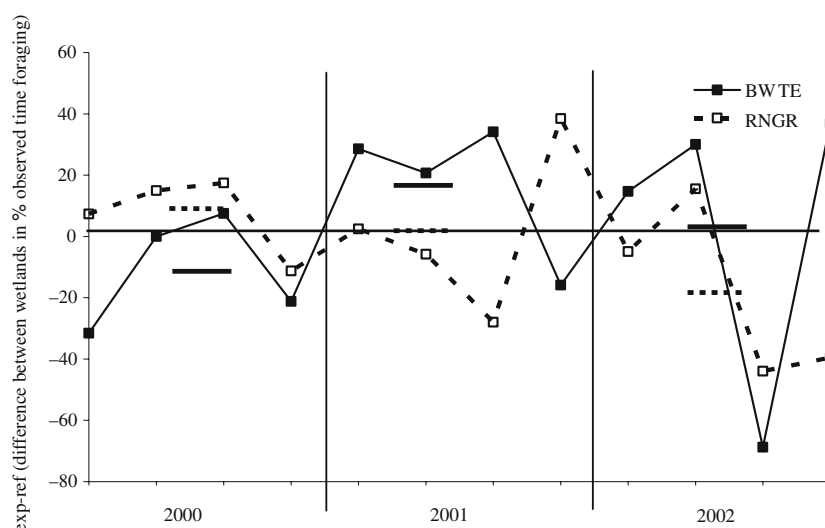
proportion of the observed time foraging in EW than in NW after fish were added to EW (Fig. 3). This difference changed very little between 2001 and 2002, when fish in EW were extirpated ( $|\bar{D}_{pre} - \bar{D}_{post}| = 7\%$ ,  $p = 0.727$ ). Comparing 2000–2002, the years in which the fish status of EW and NW were the same,  $|\bar{D}_{pre} - \bar{D}_{post}|$  was 20% ( $p = 0.290$ ). For red-necked grebes, foraging effort was always very similar between EW and NW (Fig. 3), the largest value of  $|\bar{D}_{pre} - \bar{D}_{post}|$  being less than 8% ( $p = 0.950$ ) for 2000 vs. 2001.

## Discussion

The addition of fish to fishless Aspen Parkland wetlands produced mixed results. We 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). We predicted that, since blue-winged teals consume large amounts of herbivorous and omnivorous invertebrates (Taylor, 1978; Swanson et al., 1979), the presence of fish would trigger increased foraging effort by blue-winged teals. Thus, if they were to maintain similar levels of food intake, teal foraging effort in EW

would be expected to become more similar to FW and diverge from NW. A similar response has been seen in black ducks foraging in lakes with and without fish in eastern Canada (DesGranges & Rodrigue, 1986). We predicted that red-necked grebes would not change their foraging effort since they eat fathead minnow and brook stickleback, and breed successfully on North American wetlands with or without fish (Stout & Nuechterlein, 1999).

Only herbivores responded as predicted within EW itself, decreasing after fish addition and increasing after fishes were extirpated (Table 2). Comparing EW to FW, only herbivore and small predator biomasses in the two wetlands converged in 2001 and diverged in 2002 as expected, and the changes in intersystem differences in biomass of these two invertebrate guilds between 2000 and 2001 were not statistically significant (RIA). Comparing EW to NW, none of the invertebrate biomass values in EW diverged from those of NW between 2000 and 2001 as predicted, nor did the EW invertebrate biomasses converge on NW biomasses post-winterkill (2001/2002). In fact, biomass of large predators and herbivores in EW diverged from NW biomasses 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.



*Figure 2.* Intersystem differences in bird foraging (estimated as % of observation period spent foraging) between experimental wetland (EW) and fish reference (FW). Solid horizontal bars represent average intersystem difference for blue-winged teals foraging in each year, as calculated from the series of intersystem differences (exp-ref). Dashed horizontal bars represent average intersystem difference for red-necked grebes foraging in each year. Zero difference line shown by horizontal bar across entire graph. RIA tests changes in these average intersystem differences ( $|\bar{D}_{pre} - \bar{D}_{post}|$ ) between years.

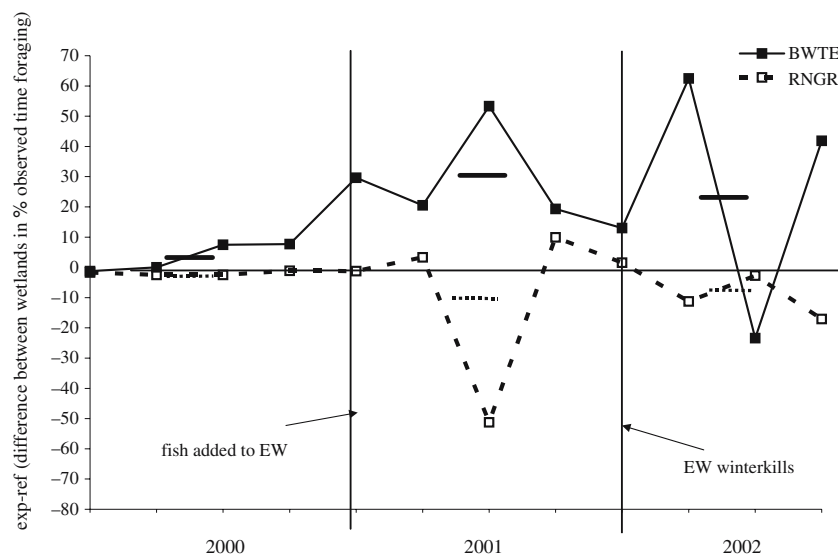


Figure 3. Intersystem differences in bird foraging (estimated as % of observation period spent foraging) between experimental wetland (EW) and fishless reference (NW). Solid horizontal bars represent average intersystem difference for blue-winged teals foraging in each year, as calculated from the series of intersystem differences (exp-ref). Dashed horizontal bars represent average intersystem difference for red-necked grebes foraging in each year. Zero difference line shown by horizontal bar across entire graph. RIA tests changes in these average intersystem differences ( $|\bar{D}_{pre} - \bar{D}_{post}|$ ) between years.

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 our study.

The responses of omnivores (amphipods, chironomids) to fish addition within EW 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* (L.), and brown bullhead, *Ictalurus nebulosus* (LeSuer), 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 predatory invertebrates, 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 our study (Benndorf et al., 2000). If small-bodied fishes were a minor part of the diet the largest predatory invertebrates, 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 within EW except large predators increased over the period 2000–2002 (Table 2b), 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 sticklebacks are very gape-limited even for small fish (Tompkins & Gee, 1983) 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). Thus, fish presence results in reduction in the average sizes of individuals in invertebrate populations in systems that support both large- and small-bodied fishes. The main difference with our study is that the biomasses did not change with respect to fish status, resulting in more and smaller individuals rather than fewer and smaller individuals.

RIA on bird foraging effort data (Table 4, Figs. 2 and 3) supported our prediction that blue-winged teal foraging effort in EW became less like NW when fish were added. When fish were extirpated from EW, there was however no reversal in teal foraging patterns. This suggests that the effect of fish colonization on teal foraging effort was longer-term than we expected, even in a dynamic system like Aspen Parkland (Nicholson & Vitt, 1994), where fish colonizations and extirpations are frequent events. There is little evidence for 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 on birds. The response of teals in EW relative to NW 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 & Rodrigue, 1986; Hunter et al., 1986). In our study, increased teal foraging effort is apparently linked 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* (Eyton), and Buffleheads, *Bucephala albeola* (L.)) 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 teal, being fairly generalist despite their heavy reliance on gastropods (Taylor, 1978), may be responding to changes in the overall invertebrate community that we were unable to detect by examining the guilds we chose. Although not all our 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 & Reinecke, 1992), the increase in foraging effort within EW between 2000 and 2001 (Table 4) and in EW relative to FW and NW was substantial.

Red-necked grebes behaved as predicted, with no major change in foraging effort in EW relative to either FW or NW 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 & Nuechterlein, 1999), this may be due to gape limitation. For example, young black-throated diver, *Gavia arctica* (L.), 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 minnows: 22.14 J/mg dry weight for *Dytiscus* nymphs and 22.37 J/mg dry weight for large leech, *Nepheleopsis obscura* (Verrill), (Driver, 1981; data converted from calories/g), compared to 25.04 J/mg dry weight for fathead minnow (Gingras, 1997).

## Conclusions

Our study suggests that small-bodied fish can reduce 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. At the densities of fish used in this study, the major change in invertebrates seems to lie in relative abundance rather than biomass, with invertebrates generally being smaller and more abundant in the presence of fish than in their absence. In this study, typical fish CPUE values were much lower than in other studies:  $0.39 \pm 0.13$  fish/trap/h 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 h, would be about 1.25 fish/trap/h). Prairie potholes also can have several orders of magnitude more fish in them during wet years than we found in our study (K. Zimmer, pers. comm.). This low density of fish may be behind the limited effects on invertebrate biomasses that we observed.

Although not all our 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 ours deal with very low sample sizes and thus lack power (a point somewhat missed by Murtaugh (2002) in his critique of RIA). Jennions & Møller (2003) recently suggested that meta-analyses of studies in behavioural 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 teals exhibit changes in foraging behaviour in the presence of small-bodied fishes. Our 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.

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