COMMUNITY CONSEQUENCES OF INDIRECT INTERACTIONS BETWEEN WATERFOWL AND TIGER SALAMANDERS IN PRAIRIE POTHOLES

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ABSTRACT

COMMUNITY CONSEQUENCES OF INDIRECT INTERACTIONS BETWEEN WATERFOWL AND TIGER SALAMANDERS IN PRAIRIE POTHOLES

Glenn Arthur Benoy	Advisor:
University of Guelph, 2002	Professor T. D. Nudds

Waterfowl are attracted to prairie wetlands or "potholes" to satisfy nutritional demands for reproduction and brood rearing during the breeding season. Although most potholes in the Minnedosa, Manitoba, area are devoid of native fish populations, many are occupied by tiger salamanders (*Ambystoma tigrinum*). To test the hypotheses that waterfowl influence pothole community structure and indirectly interact with tiger salamanders, I completed a series of observational and manipulative studies.

I determined that tiger salamander occupancy rates of potholes were high (75-80%) but densities ranged widely. Trophic structure varied according to tiger salamander density but greater contrasts in invertebrate abundance and phytoplankton standing crop were obtained between high and low densities rather than simple presence or absence. I interpreted positive relationships between tiger salamander density and phytoplankton standing crop as an indirect effect of nutrient recycling and transfer by tiger salamanders rather than direct consumer-resource interactions between trophic levels. I compared dietary and pothole overlap between ducks (Subfamily Anatinae) and tiger salamanders to estimate the potential for indirect interactions. I found that dabbling ducks had greater overlap in diet with tiger salamanders than diving ducks, but that diving ducks overlapped more among potholes with tiger salamanders than dabbling ducks.

Using exclosures, I determined that invertebrate populations increased and phytoplankton standing crop decreased in the absence of duck, grebe and coot predation. However, the effects of waterfowl exclusion on pothole trophic structure were obscured by the presence of tiger salamanders, especially at high densities. This indirect interaction is an example of compensatory predation and it indicates that either waterfowl or tiger salamanders can control pothole trophic structure. Subsequently, I manipulated tiger salamander densities to test for the effects of food web variation on waterfowl. Within potholes I found that waterfowl preferentially foraged where tiger salamander densities were lower and among potholes I found that American coot (*Fulica americana*) chick growth rates were decreased in the presence of tiger salamanders. These results indicate that waterfowl and tiger salamanders exert trophic control on prairie potholes by competing for shared prey and that community studies of prairie potholes are incomplete without the inclusion of tiger salamanders.

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GENERAL INTRODUCTION

Trophic structure is an abstraction that ecologists use to make sense of complexity in communities. Empirical patterns across many communities imply that such abstractions are useful operational concepts for understanding why communities appear as they do and what to expect of them when they are perturbed. The distinction between direct and indirect effects is one of the most fundamental ways to approach community ecology (Strauss 1991, Wootton 1994, Abrams et al. 1996, Miller and Travis 1996). Direct effects, such as predation and interference competition, typically involve only two species. In contrast, indirect effects are multi-species interactions and they, by definition, involve a minimum of three species. Examples of indirect effects include higher-order interactions, apparent competition and exploitation competition, among others. Exploitation competition, once considered a direct effect, can be more precisely defined as an indirect one because the interaction between the two consumers is mediated by the presence of a third, the resource.

Several models of trophic structure have been developed that incorporate both direct and indirect effects, but they have traditionally been expressed in terms of predation and competition (e.g. Hairston et al. 1960, Oksanen et al. 1981, Menge and Sutherland 1987). Trophodynamic theory states that trophic levels are alternately governed primarily by predation on resources or primarily by competition for resources. Perhaps the most well known formulation of trophodynamic theory is the trophic cascade hypothesis in lakes, itself another type of indirect effect (Carpenter and Kitchell 1993). It predicts that, depending on the presence or absence of top consumers in a pelagic community (i.e. piscivorous or planktivorous fish), algal biomass can be regulated – a practice known to lake managers as biomanipulation.

Though conceptually elegant, there is considerable debate over the generality of trophic cascades across ecosystems and the process of community regulation by top consumers (Brett and Goldman 1996, DeMelo et al. 1992, Pace et al. 1999, Polis et al. 2000). Food web complexity, typically due to multispecies indirect interactions, is most commonly cited as the reason why trophic cascades and "top-down" community regulation are not observed in many comparative and experimental studies (McQueen et al. 1989, Strong 1992, Polis and Strong 1996). However, proponents of top-down control argue that trophic structure underlies all communities and therefore it represents an invaluable null model upon which to base predictions (Oksanen 1991, Hairston and Hairston 1993, 1997, Oksanen and Oksanen 2000). More plainly, this debate may be about "taxonomic sufficiency" in community ecology and the degree of taxonomic resolution that is necessary and meaningful for approaching a particular research question.

The research stage for the trophic cascade hypothesis has traditionally been northern temperate lakes, in large part because of their economic and recreational importance but also because lakes have long enjoyed a tradition as heuristic study systems (e.g. Forbes 1887). More recently, community ecologists working in riverine (e.g. Power et al. 1985, Bowlby and Roff 1986, Flecker and Townsend 1994) and terrestrial (e.g. Spiller and Schoener 1990, 1994, Schmitz 1993, Sinclair et al. 2000, Terborgh et al. 2001) ecosystems have also considered the usefulness of the theory and tested its predictions. In contrast, wetlands have received comparatively very little attention from community ecologists, despite the fact that they cover an estimated 14% of Canada (National Wetlands Working Group 1988) and 12% of the continental United States including Alaska (Dahl 1990) and that the Prairie Pothole Region produces 50-75% of North America's waterfowl (Anatidae) (Batt et al. 1989).

Prairie wetlands or "potholes" have historically been studied either by wetland hydrologists and botanists or by waterfowl biologists, each motivated by distinct research programs (Murkin and Batt 1987). Many patterns relating consumers to resources in prairie wetlands have been published and the idea that waterfowl composition and abundance are affected by wetland spatial and temporal dynamics has been well studied (e.g. Nudds 1992, Murkin and Caldwell 2000). However, the converse of this idea, that waterfowl may exert a degree of control over wetland community structure, is relatively novel (Nudds 1992) in part because estimating it requires integration between processes affecting both waterfowl and wetlands, such as herbivory and predation, and nutrient recycling and transfer, among others. By testing for trophic dynamics in prairie potholes due to the presence of waterfowl, inferences can be made regarding two outstanding issues in waterfowl ecology: whether waterfowl are relatively more regulated by resources or by predators; and whether waterfowl experience greater resource limitation in the breeding or wintering grounds.

Although the influence of waterfowl on prairie wetlands is not well understood, evidence is accumulating that bird predation has significant consequences for community structure in other aquatic systems. In particular, field-based experimental studies in marine intertidal zones have shown that sea ducks, gulls and shorebirds can have significant effects on invertebrate prey, sometimes resulting in variation in community structure (Quammen 1984, Marsh 1986, Wootton 1992, 1997, Hamilton 2000). Similarly, grebe and phalarope predation have also been shown to have significant effects on crustacean densities and size structure (Dodson and Egger 1980, Cooper et al. 1984). Such apparently widespread effects suggest that waterfowl ought to exert comparable effects on prey populations in prairie wetlands. Wrubleski (1989) found that chironomid densities were higher in the absence of diving ducks due to an indirect effect of herbivory by diving ducks on macrophyte tubers. And Pettigrew et al. (1999) showed that variation in algal production was a result of nutrient recycling by waterfowl rather than variation in underlying wetland productivity.

Most studies of wetland community structure involving waterfowl have been comparative and the few that have employed field experiments have either been of short duration or of small scale (Smith et al. 1986, Brönmark 1988, Wrubleski 1989, Peterson et al. 1989, Barnes and Nudds in Nudds 1992) compromising their generality. Prairie potholes represent a unique opportunity for addressing questions of waterfowl ecology because they are relatively manageable and numerous, enabling large-scale manipulations with a high degree of replication. Further, sustained exclosure experiments ("press perturbations") can yield results that include both direct and indirect effects (Bender et al. 1984, Yodzis 1988, 1996, Menge 1997) that may more accurately reflect the responses of communities to natural or anthropogenic disturbances.

The original purpose of this research was to assess whether waterfowl control the trophic structure of prairie potholes (*sensu* Osenberg and Mittelbach 1996). Patterns of trophic control by consumers are consistent with processes of resource limitation. The conventional wisdom regarding trophic structure in many parts of the Prairie Pothole

Region has been that invertebrate populations are governed by nutrient concentrations and primary production and that avian and mammalian predators govern waterfowl populations. Although it has been demonstrated that duck nest success increases under stringent predator control regimes (Garretson and Rohwer 2000), historic trends in declining nest success between 1937 and 1990 were unrelated to predator management (Beauchamp et al. 1996a, b), suggesting that other factors than variation in nest success are related to waterfowl population dynamics. Indeed, in some parts of the prairies, simply the presence or absence of standing water is likely the most important factor affecting regional population dynamics, such as in the relatively more arid shortgrass prairie in western portions of the Prairie Pothole Region. However, eastern portions of the PPR, formerly dominated by tallgrass and mixed-grass prairie, are dominated by more permanent water bodies; thus, questions related to trophic structure are potentially more relevant in these areas for understanding population dynamics of waterfowl.

Pilot studies completed during the first year of field research yielded one overwhelming finding: tiger salamanders (*Ambystoma tigrinum*) seemed ubiquitous among prairie potholes. In the Prairie Pothole Region, waterfowl are evidently not the only vertebrate consumers that may affect wetland community structure. Depending on hydrological conditions, either planktivorous fish or tiger salamanders may coexist with waterfowl and these consumers could have a competitive advantage over waterfowl within wetlands. Many studies have addressed the question of exploitation competition between fish and waterfowl and they have generally concluded that the presence of fish alters the composition of waterfowl, reduces densities of breeding pairs and negatively affects survivorship and growth rates of offspring (Eadie and Keast 1982, Hill et al. 1987, Winfield et al. 1992, Mallory et al. 1994, Bouffard and Hanson 1997, Cox et al. 1998). In contrast, very little is known regarding interactions between tiger salamanders and breeding waterfowl. However, in fishless prairie potholes, tiger salamander densities are comparable to those of fathead minnow (*Pimephales promelas*) (Deutschman and Peterka 1988, Duffy 1998) suggesting that the omission of tiger salamanders from community studies involving potholes and waterfowl may be significant.

As a result of this preliminary finding, the purpose of this research became an assessment of whether tiger salamanders negatively affect coexisting breeding waterfowl and whether they are compensatory predators in prairie potholes. The geographical distributions of different top aquatic consumers in prairie wetlands are relatively predictable in that they follow a hydrological permanence gradient from planktivorous fish in the most stable, permanent, wetlands to predaceous aquatic insects in the most shallow and ephemeral wetlands (Wellborn et al. 1996, Wissinger 1999). Tiger salamanders exist in between these endpoints, presumably because they can make use of semi-permanent wetlands that preclude the existence of fish and they are consumers of aquatic insects (Olenick and Gee 1981, Holomuzki and Collins 1987).

Thus, I initiated a series of studies of consumer-resource interactions in a large number of prairie potholes southeast of Minnedosa, Manitoba, near the northeast edge of the Prairie Pothole Region. This area is specifically known as the Aspen Parkland Continental Prairie Wetland Subregion (National Wetlands Working Group 1988) and under "pristine" conditions it is comprised of mixed-grass prairie dotted with "islands" of deciduous woodlands. European settlement in the area began in the 1870s and most of the land was rapidly converted to agriculture, which remains the dominant economic activity (Leitch 1989). The potholes in this area are mainly semi-permanent (i.e. Class IV, Stewart and Kantrud 1971). Salinity varies widely among potholes according to hydrological permanence and drainage basin geochemistry, but most semi-permanent potholes tend to be low in dissolved solids (i.e. oligosaline, 800 – 8 000 µS/cm, LaBaugh 1989). Except during spring run-off and periods of heavy rainfall, they are basically autonomous. Unless managed for drainage or irrigation, inflow is restricted to the immediate drainage basin and outflow is a function of evaporation. Emergent and submergent vegetation dominate the appearance and physical structure of prairie potholes and their composition and distribution is commonly used as a basis for categorizing potholes. Primary production can be very high in prairie potholes though it is allocated among a variety of forms (Goldsborough and Robinson 1996, Kantrud et al. 1989), some of which are more readily incorporated into the food web than others (Murkin 1989). As a result, secondary production can also be very high but the invertebrates are generally comprised of relatively few ecological generalists, compared to other aquatic ecosystems, that are adapted to the variable environmental conditions, (Euliss et al. 1999). Similarly, the amphibians are limited to just a few frog species and tiger salamanders. In contrast, the diversity of the migratory birds that make use of prairie potholes for breeding is relatively high. Within the waterfowl alone, fourteen species of ducks are commonly observed breeding in the area.

Based on my preliminary findings that tiger salamanders were widely distributed among potholes, in Chapter 1, I tested Zaret's (1980) prediction that tiger salamanders are the "functional equivalents" of fish in fishless wetlands. The effects of tiger salamanders on the trophic structure of prairie potholes are basically unknown though studies from regional baitfish and aquaculture industries anecdotally refer to the potential reduction of fish yields in the presence of high tiger salamander densities (Myers and Peterka 1976, Olenick and Gee 1981). I sampled tiger salamanders, invertebrates and phytoplankton standing crop, and measured pothole morphometry and vegetation distribution across a series of potholes over two years. I compared pothole communities according to tiger salamander densities categorized as absent, low or high. I found that both carnivorous and herbivorous invertebrate abundance was reduced in the presence of tiger salamanders and that phytoplankton standing biomass was positively related to tiger salamander density. I also found that the difference in invertebrate abundance between low and high tiger salamander densities exceeded that observed between absent and low densities. I inferred from these observations that tiger salamanders exert trophic control on invertebrates and primary production and that the consequences of fish coexistence with waterfowl can be extended to include coexisting tiger salamanders and waterfowl.

Breeding ducks exhibit high demands for proteinaceous prey and the presence of coexisting tiger salamanders may reduce invertebrate availability to them. In Chapter 2, I assessed the potential for exploitation competition between tiger salamanders and ducks by examining the gut contents of over 1500 ducks gleaned from the literature and almost 100 tiger salamanders incidentally collected for field work described in Chapter 1. I compared diets between tiger salamanders and ducks in two ways, 1) by overlap in prey type (i.e. taxonomic overlap) and 2) by overlap in prey size. I also compared spatial overlap between tiger salamanders and ducks using estimates of tiger salamander density from Chapter 1 and surveys of ducks from the same set of potholes. I found food and niche complementarity between ducks and tiger salamanders; dabbling ducks had higher diet overlap with tiger salamanders than diving ducks, and dabbling ducks had lower spatial overlap with tiger salamanders than diving ducks. Thus, the presence of tiger salamanders in prairie potholes should have greater consequences for dabbling ducks than diving ducks.

In Chapter 3, I examined the effects of breeding waterfowl (ducks, grebes and coots) on pothole trophic structure. Using a series of large exclosures in 45 potholes over two years, I compared invertebrate populations and phytoplankton standing crop according to the presence or absence of waterfowl and whether observed patterns changed during the course of the breeding season. I also explained the variation in responses obtained as a result of waterfowl exclusion by considering waterfowl and tiger salamander densities from each pothole. From Chapters 1 and 2, I predicted that tiger salamanders should function as compensatory predators in the absence of ducks. I concluded that in the absence of tiger salamanders, waterfowl influenced the trophic structure of prairie potholes, consistent with predictions of the trophic cascade hypothesis. However, in the presence of high tiger salamander densities such effects were nullified. I discussed these results as they relate to indirect pathways that may result in trophic cascades and in terms of population regulation in migratory waterfowl.

In Chapters 1, 2 and 3, I studied the effects of predation by, and competition between, waterfowl and tiger salamanders on invertebrates and phytoplankton standing crop. Instead, in Chapter 4, I examined the effects of variation in pothole food web structure on behaviour, survival and growth of individuals of ducks, grebes and coots in two experiments by exploiting the effects of tiger salamanders on pothole community structure. In the first experiment, I split a series of potholes in half and simultaneously increased tiger salamander density in one half while reducing it in the other. I compared activity budgets of ducks, grebes and coots according to contrasting food web structure. In the second experiment, across a second series of potholes, each with a single breeding pair of American coot, I randomly assigned half the potholes to experimentally increased tiger salamander populations. Like the first experiment, I compared coot chick survivorship and growth rates according to contrasting food web structure. I found that variation in tiger salamander density had significant effects on waterfowl foraging time allocations and offspring growth rates.

This is the first study to consider direct and indirect interactions among vertebrate consumers in prairie potholes and to link them to variation in pothole trophic structure. A combination of methodological approaches was used to clarify the ecological interactions within the system. These results indicate that tiger salamanders exert a degree of trophic control on pothole food webs (Chapter 1) and that they exhibit substantial dietary overlap with dabbling and diving ducks (Chapter 2). They further show that waterfowl are partly responsible for pothole community structure except in the presence of high compensatory predation by tiger salamanders (Chapter 3) and that variation in food web structure, due to the presence of tiger salamanders or otherwise, affects foraging behaviour and offspring growth rates (Chapter 4). In studies concerned with prairie pothole food web structure, waterfowl ought to be considered as influential members of community structure rather than as merely winged-exploiters of apparently superabundant resources. Further, in studies concerned with waterfowl foraging ecology, breeding and brood rearing, it is probably an error to exclude the presence of other vertebrate consumers, such as tiger salamanders.

CHAPTER 1

Tiger salamanders in prairie potholes: a "fish in amphibian's garments?"

Introduction

Only 10-20% of prairie wetlands, or "potholes", in southwestern Manitoba in the Prairie Pothole Region of North America support fish populations (Lawler et al. 1974). Summerkill and winterkill associated with very low dissolved oxygen concentrations are assumed to be the major factors that determine the persistence and extirpation of the most common species of fish, fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*), in potholes. Further, some pothole drainage basins export high concentrations of dissolved solids resulting in salinities that are prohibitively high for fishes. Independent of these various chemical attributes, most pothole drainage basins are closed. Therefore, precipitation patterns and associated water level fluctuations are perhaps the most relevant factors that limit the dispersal of fish among potholes within the Prairie Pothole Region.

Tiger salamanders (*Ambystoma tigrinum*), in contrast, apparently flourish in the variable environmental conditions that characterize prairie potholes. Specifically, some subspecies show evidence of facultative paedogenesis resulting in alternate life history strategies (Sprules 1974, Whiteman 1994, Whiteman et al. 1996). When relatively constant hydrologic conditions prevail, tiger salamanders exhibit the "typical" amphibian life history, metamorphosing from aquatic larvae to terrestrial adults ("metamorphs") that overwinter in self-excavated burrows or small-mammal runway systems followed by redistribution among potholes in the spring (Semlitsch 1983, Madison and Farrand 1998). However, under fluctuating hydrologic conditions, they overwinter in deeper bodies of water by becoming aquatic obligates and reproducing at a larval stage ("paedomorphs"). Given the wide intra- and interannual fluctuations in temperature and precipitation in southwestern Manitoba (National Wetlands Working Group 1988), tiger salamanders should have higher occupancy rates of prairie potholes than fishes that are native to the region. Empirical data from the Cottonwood Lake Study Area in North Dakota indicate that regional population densities of tiger salamanders are coarsely correlated with precipitation patterns (Larson et al. 1998), yet specific wetland occupancy rates are patchy and unpredictable (Madison and Farrand 1998).

Our understanding of tiger salamander ecology in prairie environments is largely due to fish farming initiatives from the 1970's (e.g. Lawler et al. 1974, Myers and Peterka 1976). Annual production estimates for stocked rainbow trout (0-313 kg/ha, Lawler et al. 1974) and native fathead minnows (73-249 kg/ha, Duffy 1998) were found to be comparable to those obtained for larval tiger salamanders (48-564 kg/ha, Deutschman and Peterka 1988) compromising fishery yield estimates for potholes occupied by tiger salamanders. Further, considerable overlap in diet was observed between stocked rainbow trout and tiger salamanders in an aquaculture study area (Olenick and Gee 1981). More recently, tiger salamanders have also been shown to have significant diet overlap with dabbling (*Anas* spp.) and diving (*Aythya* spp., *Oxyura jamaicensis*) ducks and distributed non-randomly with respect to variation in waterfowl assemblages among potholes (Chapter 2). The relative paucity of research on tiger salamander interactions with other important vertebrates of ecological interest and economic importance threatens to undermine our ability to effectively understand and manage pothole ecosystems.

Because tiger salamanders can widely occupy fishless potholes (Euliss et al. 1999), they may similarly affect aquatic community structure as fish (i.e. "a fish in amphibian's garments?" *sensu* Zaret 1980). The objective of this research was to quantify relationships between tiger salamander populations and invertebrate assemblages and phytoplankton standing crop. This was approached in three ways: 1) by comparing interannual patterns of tiger salamander abundance with invertebrate abundance and phytoplankton standing crop over two years, 2) by determining the occupancy and abundance of tiger salamanders (high or low) across a series of potholes to quantify specific relationships between tiger salamanders and invertebrate and phytoplankton components of the pothole food web, and 3) by comparing year-to-year differences in invertebrate abundance and phytoplankton standing crop in a subset of potholes that were common to both study years but were alternately vacant or occupied by tiger salamanders.

Methods

Study area

The geomorphology of the Prairie Pothole Region (PPR) in North America (Fig. 1.1) was largely shaped by glacial advance and retreat during the Pleistocene. Present characteristics of potholes are the result of complex climatic and hydrologic interactions. With a roughly decadal periodicity, potholes undergo periods of drought and periods of

Figure 1.1. The Prairie Pothole Region of North America. The study area is indicated by an asterisk.


Alberta
Saskatchewan
Manitoba
CANADA
*
UNITED STATES
Montana
North Dakota
Minnesota
South Dakota
Iowa

abundant rainfall, commonly known as the wet/dry cycle (Kantrud et al. 1989). Annual temperatures typically range from -40°C to +40°C causing many potholes to completely freeze during the winter and completely evaporate during the summer. The prairie landscape is also remarkably flat and overland flow of water between potholes only occurs when water levels are high or when engineered for drainage and irrigation. Consequently, the vast majority of potholes have very small and isolated drainage basins. Thus, exchange with the groundwater table and inputs from the drainage basin typically determine the chemical attributes and biotic communities of individual potholes. The emergent vegetation communities that are associated with this interaction between climate and hydrology are generally used to classify potholes (Kantrud et al. 1989).

During the ice-free season, potholes are highly productive. The combination of closed drainage basins, low mean depths, and annual inputs of spring snowmelt and fertilizer runoff, results in high concentrations of nitrogen and phosphorus that are bioavailable to primary producers. Secondary production is also very high, but the harsh environmental conditions tend to limit the diversity of aquatic invertebrates to those species that are considered ecological generalists (Euliss et al. 1999). However, all functional feeding groups, as defined for lotic environments (i.e. shredders, collectors-filterers, scrapers and predators), are represented in assemblages of pothole aquatic invertebrates (Murkin and Ross 2000). The majority of North American migratory waterfowl breed in the PPR (Batt et al. 1989) and, in contrast to the aquatic invertebrates, they exhibit relatively high species diversity.

Study potholes used for this research were located in the southwestern Manitoba portion of the PPR (50°16′ N, 99°50′ W; Fig. 1.1) known as the Aspen Parkland

Continental Prairie Wetland Subregion (National Wetlands Working Group 1988), formerly dominated by tallgrass and mixed-grass prairie. Potholes in this area tend to be semi-permanent as they receive higher rates of annual precipitation relative to the rest of the PPR where potholes are more ephemeral. Water levels in semi-permanent potholes vary moderately within the ice-free season, but they rarely completely dry out except during prolonged dry periods of the wet-dry cycle. Twenty-four potholes were sampled in 1998 and twenty-one potholes were sampled in 1999; twelve of these were common to both years.

Field collections and sample processing

In both years, potholes were sampled for gray tiger salamanders (*A. t. diaboli* Dunn), invertebrates and phytoplankton standing crop either eight or nine times, approximately once every seven to ten days, from early May until late July. At each pothole, a cluster of three activity (funnel) traps was randomly located in open water, adjacent to the emergent vegetation. Activity traps are 3.8-l glass jars fitted with modified plastic funnels (opening diameters 15.2 cm at the large end and 2.5 cm at the narrow end) that are horizontally set approximately 30 cm below the surface of the water. Activity traps consistently match or outperform most other invertebrates sampling devices, such as artificial substrates, in that they reasonably represent most invertebrates that exist or pass through the water column (Brinkman and Duffy 1996, Turner and Trexler 1997), benthic invertebrates being a notable exception. Also, one standard-sized wire minnow trap (without bait; mesh size = 0.5 cm) was placed at the sediment-water interface within each cluster of activity traps. Both types of trap are passive samplers in that they are set one day and 24 hours later they are emptied. Analyses of usage of activity traps in Fennoscandian lakes indicated that the presence of invertebrate predators (e.g. Coleoptera, Odonata, etc.) in traps did not affect the overall composition and abundance of catches and that the presence of vertebrates (i.e. fish and amphibians) reduced taxonomic diversity but not abundance (Elmberg et al. 1992). Although the activity traps were intended for macroinvertebrate sampling and the minnow traps were intended for tiger salamander sampling, both types of organism were caught in both types of trap. Sampling locations within each pothole were accessed by canoe so as to minimize disturbance to the sediments and the water column. A total of 648 activity trap and 216 minnow trap samples were collected in 1998 and 567 activity trap and 189 minnow trap samples were collected in 1999. All amphibian and invertebrate abundance estimates are expressed as individuals per sampling effort (i.e. ind./survey).

On each sampling occasion, trapped tiger salamanders were counted, measured and weighed. Live individuals were returned to the same pothole and dead individuals were immediately frozen for future gut contents and tissue analyses. Large macroinvertebrates and tadpoles caught in activity and minnow traps were transferred to large 100-ml vials. In 1999, in one pothole on four occasions, five fathead minnow were found in a minnow trap (mean length 5.2 cm). The rest of the macroinvertebrates caught in the activity traps were concentrated using a plankton net (180 μm), modified to fit 20-ml scintillation vials. At the end of each day of field sampling, usually within six hours of collection, all macroinvertebrates were stored in ~70% ethanol. Before processing with a compound microscope, samples were initially size-fractionated using a 1 mm mesh sieve. Small invertebrates < 1 mm, such as Rotifera, Bosminidae and other small Cladocera and Copepoda, were, therefore, not included in this study. Most invertebrates were then identified, counted and measured to the nearest 0.1 mm. Invertebrates were assigned to one of five taxonomic groups – Insecta, Crustacea, Annelida, Gastropoda and other MIs (other miscellaneous invertebrates, including Acari and Collembola). The remaining invertebrates, herbivorous crustacean zooplankton (including Cladocera and Copepoda) and zoobenthos (including Ostracoda and Conchostraca), were only identified and counted. Appendix 2 details the taxonomic groups assembled for this study.

When activity and minnow traps were retrieved, three 500-ml water samples were also collected from within the cluster of activity traps. Due to occasional mixing following wind events and the variable distribution of submergent vegetation within potholes, some planktonic water samples were partially comprised of resuspended benthic algae and unattached epiphytic algae. Water samples were first strained through a coarse mesh to remove metaphyton. They were then strained through 47-mm Gelman AE filters (1.0-µm porosity) using a vacuum hand pump and stored in a freezer until processing. Frozen filters were digested in 95% ethanol overnight in a refrigerator. Digested samples were centrifuged and the supernatant was decanted and analyzed for reflectance with a spectrophotometer (Hewlett Packard 8452A Diode Array UV spectrophotometer). Chlorophyll *a* concentration was used as a surrogate measure of phytoplankton biomass in each pothole on each sampling occasion (LaBaugh 1995, Bergman and Peters 1980). Concentrations were not corrected for the presence of phaeopigments.

Aerial photographs were taken of all study potholes near the end of both field seasons (late July) to measure pothole area and shoreline length, and to estimate the distribution of emergent and submergent vegetation. The composition of pothole vegetation was further described via canoe-based mapping.

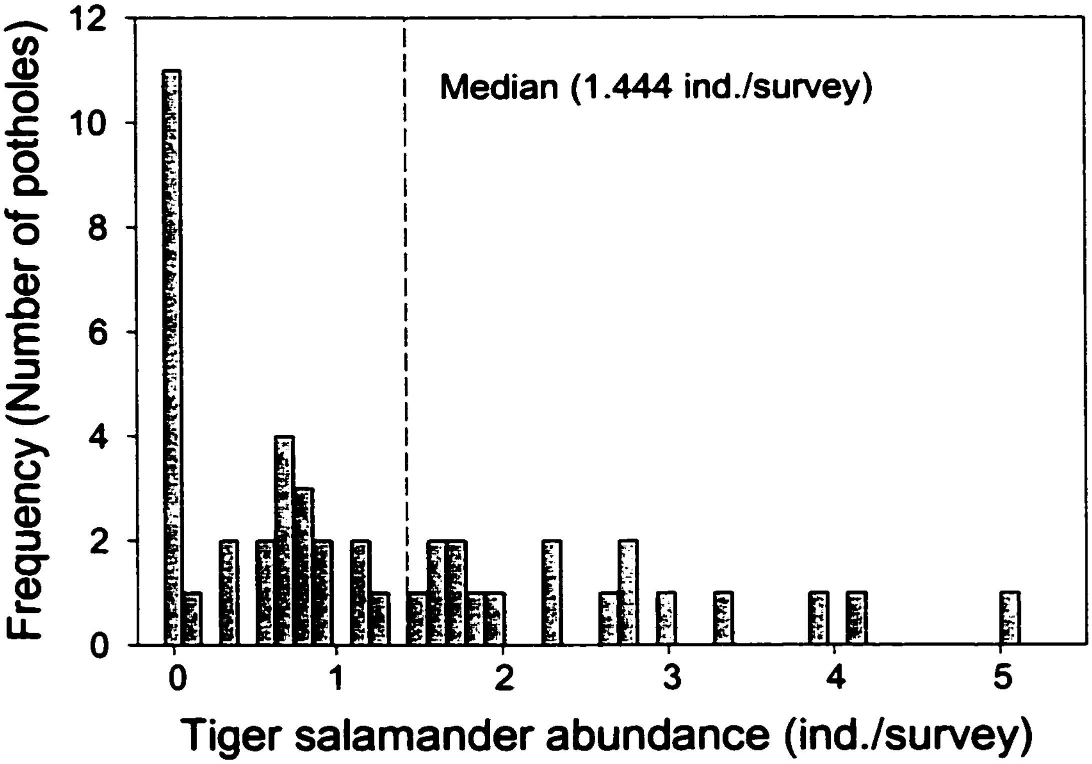
Statistical analyses

Tiger salamanders were found in 34 of the 45 potholes. Potholes were assigned to one of three groups (Absent, Low and High) based on abundance of tiger salamanders and abundance was treated as a categorical variable. The median value (1.44 ind./survey or approximately 13 individuals collected during the sampling time frame) was used to split the set of 34 potholes where at least one tiger salamander was sampled into low and high groups (Fig. 1.2). Multivariate analysis of variance (MANOVA) was used to test the hypothesis that tiger salamander abundance categories and associated independent pothole morphometric variables were related to the abundance of the designated macroinvertebrate groups and phytoplankton standing crop. The data were analyzed using the following model:

$$(X_{1ijk} \ldots X_{9ijk})^T = \mu_k + C_i + Y_j + CY_{ij} + A + D + V^2 + \varepsilon_{ijk} \qquad (1.1)$$

where $(X_{1ijk} \ldots X_{9ijk})$ is the vector of all nine response variables (i.e. tadpoles, Insecta, Crustacea, Annelida, Gastropoda, other macroinvertebrates (Other MIs), zooplankton, zoobenthos, chlorophyll) of the *k*th pothole replicate (n=45) in the *i*th tiger salamander abundance category during the *j*th year and *T* indicates vector transpose. μ is the overall mean for each response variable. *C* refers to the tiger salamander abundance categories (absent, high or low), *Y* refers to year (1998 or 1999) and *CY* is the interaction term between category and year. *A*, *D* and *V* are covariates and they denote pothole area,

Figure 1.2. Distribution of 1998 and 1999 potholes combined according to tiger salamander abundance. The median value of the potholes containing at least one tiger salamander is indicated by the dashed line.


Median (1.444 ind./survey)
Frequency (Number of potholes)
0
2
4
6
8
10
12
0
1
2
3
4
5
Tiger salamander abundance (ind./survey)

maximum depth and vegetation cover, respectively, and ε is the residual error term. Vegetation cover was based on proportions and it was represented as a quadratic term in the statistical model because relatively heterogeneous distributions of vegetation and open water areas have been linked to invertebrate diversity and productivity in a nonlinear fashion (i.e. the "hemi- marsh"; Voigts 1976, Murkin and Ross 2000). Specific differences between categories of Absent, Low and High tiger salamander categories were assessed using General Linear Models-Contrast statements in SAS 8.01 (Littell et al. 1991). Amphibian (i.e. tiger salamanders and tadpoles) and invertebrate abundances, and phytoplankton standing crop were transformed ($\ln x + 1$) to satisfy MANOVA normality assumptions.

Seven of the twelve potholes common to both years had tiger salamanders present during one year and absent during the other (Table 1.1). Area, maximum depth and vegetation structure for each pothole did not differ from year to year, so paired t-tests were used to compare invertebrate abundances and phytoplankton standing crop between years for this subset of potholes.

Results

Overall, 311 tiger salamanders were counted in 1998 and 190 were counted in 1999. In 1998, 79.2% of the study potholes (19 of 24) had tiger salamanders; in 1999, 71.4% did (15 of 21). Of the twelve potholes that were common to both years, tiger salamanders occupied five of them during both years and none were absent of tiger salamanders in both years. Four potholes had tiger salamanders only in 1998 and three had tiger salamanders only in 1999. Pothole occupancy rates also varied from early May

Table 1.1. Tiger salamanders abundance (ind./survey) and categorical designation (Absent, Low, High) for all study potholes. See text and Fig. 1.2 for details as to how categories were assigned.

	1998			1999		
	Area (ha)	Abundance	Category	Area (ha)	Abundance	Category
P1	0.52	1.25	Low			
P2	0.56	0	Absent			
P4	0.72	1.22	Low			
P5	0.53	1.63	High			
P6	0.57	0.38	Low			
P7	0.21	2.38	High			
P9	0.94	2.67	High			
P11	0.53	2.33	High			
P12	1.05	2.00	High			
P15	0.70	0.63	Low			
P16	1.00	0	Absent			
P17	0.85	0.78	Low			
P3P2	0.35	1.00	Low	0.62	0.67	Low
P8P3	0.28	0.75	Low	0.28	0	Absent
P10P5	0.41	0	Absent	0.62	1.67	High
P13P6	0.18	5.13	High	0.20	0	Absent
P14P7	1.06	2.75	High	1.43	0.44	Low
P18P12	0.35	0	Absent	0.60	0.78	Low
P19P9	0.49	0	Absent	0.68	1.33	Low
P20P14	0.61	2.78	High	0.59	0	Absent
P21P15	0.42	4.13	High	0.48	1.78	High
P22P20	0.31	3.00	High	0.27	3.33	High
P23P19	0.44	0.88	Low	0.47	0.22	Low
P25P17	0.42	1.89	High	0.70	0	Absent

P1	0.16	0.89	Low
P4	0.25	1.78	High
P8	0.89	0.78	Low
P10	0.33	0	Absent
P11	0.80	0.89	Low
P13	0.50	1.00	Low
P16	0.91	1.56	High
P18	0.61	0	Absent
P21	0.57	2.89	High

until late July, yet the mean occupancy rate was nearly the same. In 1998, tiger salamanders occupied between 2 and 15 potholes (mean = 8.44) and in 1999, they occupied between 6 and 10 potholes (mean = 8.56). Of the potholes that contained tiger salamanders, in 1998, the number counted per pothole ranged from 1 to 7.57 (mean = 3.67) and in 1999, the number ranged from 1 to 3.75 (mean = 2.44) (Fig. 1.3).

Based on trapping efficiencies, minnow traps sampled 16 times as many tiger salamanders as activity traps did and activity traps sampled almost 2.5 times as many tadpoles as minnow traps did (Table 1.2). However, the specific trapping efficiency of minnow traps for sampling tiger salamanders greatly exceeded all the other trapping efficiencies. On average, at least one tiger salamander was trapped per minnow trap while 15 activity traps were necessary to trap the same number of tiger salamanders and 8 activity traps and 20 minnow traps were necessary to collect the same number of tadpoles. The mean lengths of both tiger salamanders and tadpoles were greater in the minnow trap samples than in the activity trap samples, despite the fact that the diameter of the narrow openings into both types of trap was 2.5 cm. However, amphibians smaller than the mesh size of the minnow traps (0.5 cm) were not retained. Difference in appearance and positioning of the activity and minnow traps may have screened for larger or smaller members of the amphibian populations.

More tiger salamanders and tadpoles were counted per pothole and per sampling effort in 1998 than in 1999 (Table 1.3). In 1998, the greatest number of tiger salamanders was 5.1 ind./survey (mean = 1.56 ind./survey); in 1999 it was 3.9 ind./survey (mean = 1.00 ind./survey). Similarly, the greatest number of tadpoles in 1998 was 2.9 ind./survey (mean = 0.70 ind./survey) and 1.2 ind./survey in 1999 (mean 0.19

Figure 1.3. Average numbers of tiger salamanders trapped per pothole according to week. The number above each of the plots refers to the number of potholes that contained tiger salamanders (n=24 in 1998 and n=21 in 1999). Note that in late June 1998, only 10 potholes were sampled. Error bars are standard errors.

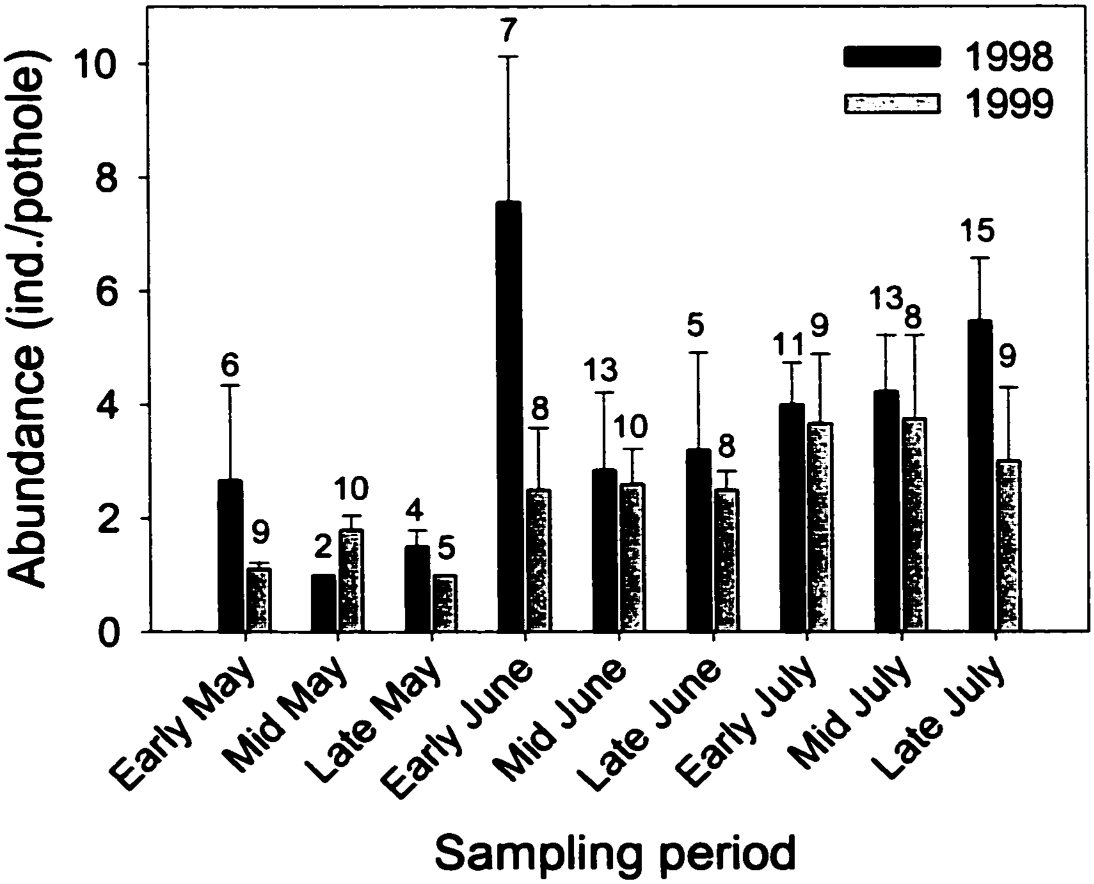

Abundance (ind./pothole)
0
2
4
6
8
10
1998
1999
6
9
2
10
4
5
7
8
13
10
5
8
11
9
13
8
15
9
Early May
Mid May
Late May
Early June
Mid June
Late June
Early July
Mid July
Late July
Sampling period

Table 1.2. Summary statistics and sampling efficiency of activity and minnow traps for collecting tiger salamanders and tadpoles. Years and potholes are pooled. Mean lengths are snout to vent distances.

	Number of traps	Individuals trapped	Trapping efficiency (%)	Mean length and range (cm)
Tiger salamanders				
Activity traps	1215	79	6.50	5.7 (0.5 - 12.6)
Minnow traps	405	422	104.20	6.4 (1.1 - 16.2)
Tadpoles				
Activity traps	1215	153	12.59	1.8 (0.2 - 3.7)
Minnow traps	405	21	5.19	2.1 (1.1 - 3.1)

Table 1.3. Summary statistics for all variables by year. Twenty-four potholes were sampled in 1998 and twenty-one were sampled in 1999. Means and standard errors are calculated among potholes. 'Other MIs' refers to other miscellaneous invertebrates not included under any of the other headings (e.g. Acari). S.E. is the standard error. Vegetation cover refers to the ratio of vegetated to open water areas; in the MANOVA statistical models, this variable is represented as a quadratic term (see text for details).

	1998			1999		
	Mean	Range	S.E.	Mean	Range	S.E.
Abundance (ind./survey/pothole)						
Tiger salamanders	1.56	0 - 5.5	0.28	1.00	0 - 4.3	0.23
Tadpoles	0.70	0 - 2.7	0.15	0.19	0 - 1.2	0.07
Insecta	14.13	5.2 - 36.6	1.67	19.93	9.3 - 28.0	1.24
Crustacea	4.64	0 - 40.6	1.93	11.00	0 - 58.9	3.44
Annelida	0.55	0 - 1.4	0.09	0.74	0 - 2.2	0.19
Gastropoda	1.32	0 - 5.3	0.31	1.20	0.1 - 6.7	0.33
Other MIs	2.34	0.2 - 8.6	0.38	1.37	0.1 - 6.8	0.33
Zooplankton	134.77	19.6 - 920.0	41.18	257.44	34.0 - 1275.2	59.00
Zoobenthos	126.38	1.7 - 1045.8	46.08	5.24	0.3 - 27.4	1.31
Chlorophyll (μg/l)	6.00	1.6 - 12.8	0.61	4.15	0.2 - 52.9	0.38

Pothole morphometric variables						
Vegetation cover (%)	50.63	20-90	5.22	45.00	15-90	5.30
Area (ha)	0.56	0.18-1.06	0.05	0.58	0.16-1.43	0.06
Depth (cm)	110.63	75-100	4.38	116.90	75-160	5.25

ind./survey). Variables used to characterize pothole morphometry (i.e. area, mean depth, vegetation cover) did not differ between years, suggesting that other abiotic or biotic factors are responsible for interannual differences in amphibian populations (Table 1.4).

The most common invertebrates sampled during both years were aquatic insects (i.e. Diptera, Hemiptera, Coleoptera, and Odonata) and crustaceans (i.e. *Hyallela*, zooplankton, zoobenthos). With the exception of Ostracoda, these invertebrates were more numerous in 1999 than in 1998. Phytoplankton standing crop, however, was notably higher in 1998 than in 1999.

Overall MANOVA statistics from the complete set of 45 potholes indicated that pothole invertebrates and phytoplankton were most significantly affected by year, followed by tiger salamanders, and then by pothole area (Table 1.5a). Neither pothole depth nor vegetation cover was significantly related to any of the response variables. Further, the interaction between categories of tiger salamander abundance and year was also not significant. Specific comparisons showed that pothole invertebrates and phytoplankton differed across categories of tiger salamander abundance; the biggest difference being between Absent and High categories; differences between Absent and Low categories and Low and High categories were smaller and more similar (Table 1.5b).

The breakdown of the individual response variables according to univariate ANOVA results is presented in Table 1.6. Invertebrate abundance and phytoplankton standing crop estimates for five of eight (six of eight if Crustacea is included) taxonomic groups were significantly related to the independent variables (Table 1.6a). The sequence of significant variables for the ANOVA results was the same as that for the MANOVA

Table 1.4. Correlation matrix for independent variables used to predict invertebrate abundances and chlorophyll concentrations (n=45 except for correlations involving Length and Biomass, where n=34). Abundance and biomass variables are transformed (ln x + 1). * p <0.05, ** p<0.01, ***p<0.001.

	Tiger salamanders				Pothole variables		
	Abundance	Length	Weight	Biomass	Area	Depth	Veg. cover
Tiger salamanders							
Abundance	1						
Length	-0.254	1					
Weight	-0.387*	0.833***	1				
Biomass	0.549***	0.404*	-0.241	1			
Pothole variables							
Area	-0.070	0.010	0.020	-0.202	1		
Depth	-0.067	-0.278	-0.118	-0.207	0.402**	1	
Veg. cover	-0.142	-0.069	-0.004	-0.168	-0.308*	-0.283	1

Table 1.5. MANOVA results for the full set of potholes (n=45). a) Wilks' Lambdas for all independent variables included in the overall MANOVA model. b) Specific comparison of Wilks' Lambdas using PROC GLM-Contrast procedure to test for differences between categories of tiger salamander abundance (Absent, Low, High). 'Categories' refers to categories of tiger salamander abundance, year refers to 1998 or 1999 and the remaining pothole descriptors are continuous variables.

a) Wilks' Lambdas

Source	df	Value	F	P
Categories	18, 56	0.2898	2.67	0.0026
Year	9, 28	0.3718	5.26	0.0003
Categories*Year	18, 56	0.5931	0.93	0.5497
Area	9, 28	0.5703	2.34	0.0409
Depth	9, 28	0.8232	0.67	0.7301
Vegetation cover	9, 28	0.8232	0.67	0.7301

b) Specific comparisons (Wilks' Lambdas)

Constrast	df	Value	F	P
Absent vs. Low	9, 28	0.6002	2.04	0.0699
Absent vs. High	9, 28	0.3829	5.01	0.0005
Low vs. High	9, 28	0.5949	2.20	0.0593

Table 1.6. Univariate ANOVA results for the full set of potholes (n=45) based on abundance (ind./survey). a) F values and probabilities for each of the response variables. b) Specific comparison of F values using the SAS PROC GLM-Contrast procedure to test for differences between categories of tiger salamander abundance (Absent, Low, High). 'Categories' refers to categories of tiger salamander abundance.

a) F values and probabilities

	Tadpoles		Insecta		Crustacea	
Source	F	P	F	P	F	P
Overall	1.41	0.2245	4.08	0.0015	2.06	0.0660
Categories	0.42	0.6576	6.57	0.0037	3.09	0.0580
Year	7.08	0.0116	5.71	0.0222	5.34	0.0267
Categories*Year	0.61	0.5497	2.75	0.0776	0.09	0.9158
Area	0.36	0.5545	1.72	0.1975	1.01	0.3223
Depth	0.01	0.9141	0.75	0.3916	3.05	0.0895
Vegetation cover	0.02	0.8961	0.76	0.3904	2.71	0.1085

	Annelida		Gastropoda		Other MIs	
Source	F	P	F	P	F	P
Overall	0.70	0.6919	2.54	0.0251	0.87	0.5494
Categories	1.60	0.2155	0.47	0.6287	1.32	0.2805
Year	1.46	0.2350	7.03	0.0118	0.07	0.7998
Categories*Year	0.29	0.7508	0.22	0.8044	0.82	0.4503
Area	0.28	0.6006	4.13	0.0495	0.01	0.9206
Depth	0.17	0.6868	0.46	0.5006	0.72	0.4033
Vegetation cover	0.03	0.8566	3.23	0.0808	1.31	0.2598

	Zooplankton		Zoobenthos		Chlorophyll	
Source	F	P	F	P	F	P
Overall	2.83	0.0152	4.07	0.0016	4.03	0.0017
Categories	0.72	0.4923	0.85	0.4364	5.48	0.0084
Year	5.89	0.0203	19.39	<0.0001	2.58	0.1169
Categories*Year	2.81	0.0734	1.21	0.3115	3.40	0.0443
Area	2.01	0.1646	4.31	0.0452	4.09	0.0505
Depth	0.00	0.9734	0.46	0.5028	0.15	0.6981
Vegetation cover	3.66	0.0637	0.08	0.7790	0.32	0.5739

b) Specific comparison probabilities.

Contrast	Tadpoles	Insecta	Crustacea	Annelida	Gastropoda
Absent vs. Low	0.4693	0.0608	0.1434	0.3551	0.1799
Absent vs. High	0.7100	0.0006	0.4632	0.5748	0.1406
Low vs. High	0.2491	0.0516	0.0233	0.1201	0.8739

Contrast	Other MIs	Zooplankton	Zoobenthos	Chlorophyll
Absent vs. Low	0.4312	0.8507	0.2694	0.1313
Absent vs. High	0.5054	0.5898	0.2730	0.0004
Low vs. High	0.9016	0.7069	0.9998	0.0177

results. Tiger salamander categories were strongly related to aquatic insect abundance, (primarily Chironomidae, followed by Corixidae and Dytiscidae) and phytoplankton standing crop and weakly related to Crustacea abundance (Fig. 1.4). Whether or not the effects of reduced Crustacea abundance (primarily *Hyallela*) was translated into an increase in epiphyton standing crop is unknown, as that source of primary production was not estimated. Pothole size was variously related to other MIs and zoobenthos abundance, as was phytoplankton standing crop. Only phytoplankton standing crop was significantly related to the interaction between tiger salamander abundance and year, and both aquatic insect and zooplankton abundance were weakly so ($p < 0.08$ and $p < 0.08$, respectively). Specific comparisons between categories of tiger salamander abundance were only significant, at $p < 0.10$, for aquatic insect and Crustacea abundance and phytoplankton standing crop (Table 1.6b) where the differences were greatest between Low and High categories, followed by Absent and High categories.

Results from the subset of potholes common to both years were generally consistent with the year-to-year comparisons and the MANOVA and ANOVA results for the entire set of potholes. Several significant differences were found between years (Table 1.7) and, although the sample size was smaller (n=7), the comparisons were between paired potholes that differed only according to the presence or absence of tiger salamanders. Aquatic insect abundance and phytoplankton standing crop differed most according to the presence or absence of tiger salamanders followed by Annelida and zooplankton abundance (Fig. 1.5).

Figure 1.4. Means and standard errors for the invertebrate abundance (ind./survey) and phytoplankton standing crop response variables in relation to categories of tiger salamander abundance (n=45) for 1998 and 1999 potholes combined.

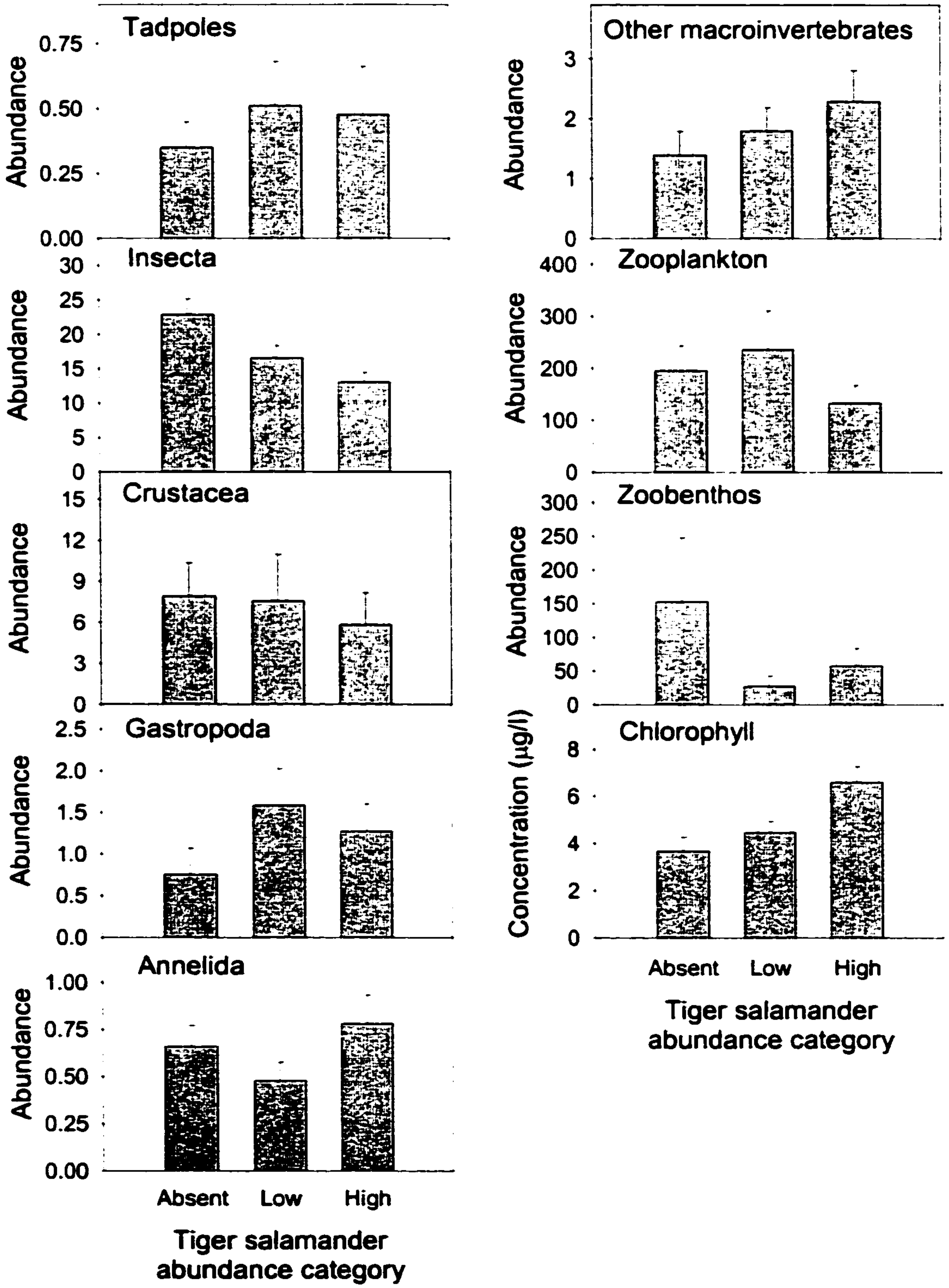
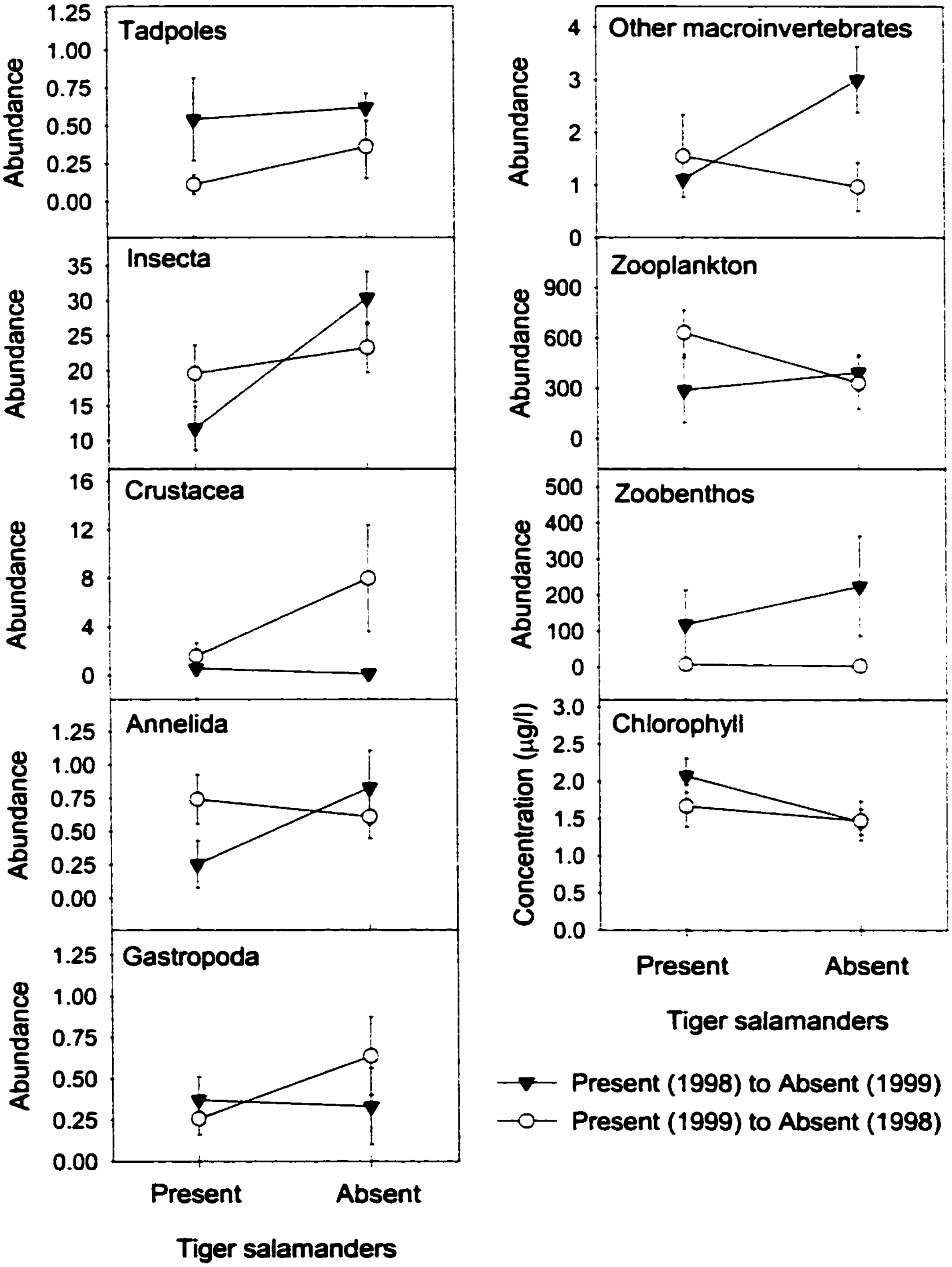

Tadpoles
Abundance
0.75
0.50
0.25
0.00
Other macroinvertebrates
3
2
1
0
Insecta
30
25
20
15
10
5
0
Zooplankton
400
300
200
100
0
Crustacea
15
12
9
6
3
0
Zoobenthos
300
250
200
150
100
50
0
Gastropoda
2.5
2.0
1.5
1.0
0.5
0.0
Chlorophyll
Concentration (µg/l)
8
6
4
2
0
Annelida
1.00
0.75
0.50
0.25
0.00
Absent
Low
High
Tiger salamander abundance category

Table 1.7. Paired t-test comparisons for all of the response variables for the subset of potholes (n = 7) common to both 1998 and 1999 that had tiger salamanders one year (Present) and not the other (Absent). For each pothole, none of the morphometric variables (area, depth, vegetation cover) differed between years (see text). 'Other MIs' refers to other miscellaneous invertebrates.

	Absent		Direction of difference	Present		Paired
	Mean	Standard error		Mean	Standard error	t-test p-value
Abundance (ind./survey/pothole)						
Tadpoles	0.47	0.13	>	0.36	0.17	0.30
Insects	25.55	2.61	>	15.73	2.77	0.0034
Crustaceans	4.63	2.84	>	1.00	0.522	0.15
Annelids	0.70	0.14	>	0.46	0.15	0.040
Gastropods	0.51	0.17	>	0.32	0.09	0.23
Other MIs	1.85	0.54	>	1.31	0.31	0.21
Zooplankton	491.42	171.41	>	236.59	66.39	0.09
Zoobenthos	71.69	55.50	<	98.68	68.94	0.40
Chlorophyll	4.25	0.85	<	6.41	1.36	0.018
Pothole morphometric variables						
Area (ha)	0.46	0.060	~	0.48	0.073	0.82
Depth (cm)	110.0	9.88	~	105.7	8.75	0.67
Veg. cover	38.6	0.093	~	37.9	0.092	0.77

Figure 1.5. Mean abundances of tadpoles and invertebrates (ind./survey) and mean concentrations of phytoplankton standing crop among potholes for 1998 and 1999 (n=7). Potholes are paired according to the presence or absence of tiger salamanders between years. The open circles refer to potholes that were occupied by tiger salamanders in 1998 but not in 1999 and the closed triangles refer to potholes that were absent of tiger salamanders in 1998 but contained them in 1999.


Tadpoles
Other macroinvertebrates
Insecta
Zooplankton
Crustacea
Zoobenthos
Annelida
Chlorophyll
Gastropoda
Abundance
Concentration (µg/l)
Present
Absent
Tiger salamanders
Present (1998) to Absent (1999)
Present (1999) to Absent (1998)

Discussion

The results of this study are consistent with the idea that tiger salamanders are the "functional equivalents" (*sensu* Kurzava and Morin 1998) of fish in fishless wetlands and that tiger salamander densities are related to phytoplankton standing crop in fishless wetlands (Holomuzki et al. 1994, Wissinger et al. 1999). After accounting for a pervasive year-effect, tiger salamander abundance was found to be the most important variable related to the invertebrates and phytoplankton standing crop, followed by an interaction effect between abundance of tiger salamanders and year. Of the remaining independent variables, only pothole size was significantly related to pothole invertebrates and then to just a couple of the invertebrate groups. Pothole depth, size and vegetation cover did not statistically differ between years even though significant interannual differences in the invertebrates and phytoplankton standing crop were observed. Tiger salamanders, however, were inversely correlated with the abundance of several invertebrate groups, including zooplankton, and positively correlated with phytoplankton standing crop. Taken together, these patterns provide strong support for the hypothesis that tiger salamanders are influential members of planktonic prairie pothole communities.

Tiger salamander occupancy in this set of prairie potholes was not related to any of the pothole morphometric variables. Equivalent ranges of area and maximum depth were encountered in both years and most potholes had roughly even distributions of vegetation and open water. Even within the subset of potholes common to both years, no pattern was detected among morphometric variables that could explain why some potholes were occupied by tiger salamanders one year and vacant the other. Slightly fewer potholes were occupied by tiger salamanders in 1999 than 1998 and this difference may be attributable to regional climatic conditions. However, both years were relatively "wet" and no differences in mean, minimum or maximum temperatures, annual precipitation or snow depth were identified between years (National Climate Data Center 2002), suggesting that other smaller-scale factors determine tiger salamander distribution and abundance, such as specific pothole hydroperiod (e.g. Pechmann et al. 1989).

The inverse relationship observed between tiger salamander abundance and aquatic insect and Crustacea abundance reflects a trophic interaction that is corroborated by data on tiger salamander gut contents and it suggests that tiger salamanders forage throughout prairie potholes, across benthic and planktonic habitats. For prairie potholes in southwestern Manitoba, the top five prey types consumed by tiger salamanders were, in descending order, Gastropoda, Diptera, predaceous aquatic insects, Amphipoda, and microcrustaceans (Chapter 2), comprising a wide range of invertebrates with a variety of feeding strategies and trophic positions (Murkin and Ross 2000). Aside from zooplankton and Gastropoda, the dominant invertebrates in this study were aquatic insects (primarily Chironomidae and secondarily Corixidae) and Amphipoda (almost entirely *Hyallela*), suggesting that the invertebrate differences among potholes were at least partly attributable to tiger salamander consumption and that tiger salamanders are opportunistic consumers that forage widely. Zooplankton was variously related to tiger salamander abundance in all three analyses, however the relationship was complicated by an overriding year effect. Gastropoda, a dominant invertebrate in my study potholes and a major prey type of tiger salamanders, were not related to any of the predictor variables though this may have been due to inefficient sampling by the activity traps relative to substrate samplers typically used to estimate abundances of benthic invertebrates (Brinkman and Duffy 1996).

Strong (1992) proposed that top-down forces should be most obvious in simple, low diversity habitats. Prairie potholes would appear to qualify, as most of the invertebrates in these ecosystems are generalists, by dint of having to deal with dramatic temperature and precipitation fluctuations. Trophodynamic theory predicts that the biomass or abundance of non-adjacent trophic levels should be positively correlated (Oksanen et al. 1981). Higher tiger salamander abundance should, therefore, result in a decrease in carnivorous invertebrates (mainly aquatic insects), an increase in herbivorous invertebrates (mainly Gastropoda, Cladocera, Copeopoda and Amphipoda) and a decrease in phytoplankton standing crop. However, phytoplankton standing crop was positively related to tiger salamander abundance, suggesting that this trophic model is inaccurate, most likely because the aforementioned herbivores make use of very different sources of primary production and the rest of the consumers are omnivorous to varying degrees. Further, the number of links between tiger salamanders and phytoplankton varies from two (e.g. tiger salamanders – zooplankton – phytoplankton) to at least three (e.g. tiger salamanders – predaceous aquatic insects – herbivorous invertebrates – phytoplankton) complicating simple predictions of linear trophic interactions.

Whether or not the patterns observed in this study qualify as evidence supportive of the trophic cascade hypothesis depends on how the concept is defined (Pace et al. 1999, Polis et al. 2000) and how trophic aggregations are assembled (Yodzis 1993, 1996). Because the intervening trophic levels, based on taxonomic groups, do not conform to the conventional trophodynamic model, the mechanisms and food web pathways that may link tiger salamanders to phytoplankton standing crop are unclear. Two alternative explanations accounting for this observed pattern are now discussed.

First, it is possible that the distinction between carnivorous and herbivorous invertebrates in prairie potholes is too artificial. While many aquatic invertebrates are carnivorous (e.g. Coleoptera, Odonata), the numerically dominant organisms sampled in this study (e.g. Chironomidae: Diptera, Amphipoda: Hyallelidae) were either herbivorous or omnivorous, representing many functional feeding groups from both planktonic and benthic habitats (Murkin and Ross 2000). Zoobenthos and zooplankton have long been established as primarily herbivorous, especially large-bodied Daphnia that are commonly found in lentic systems (Euliss et al. 1999), and to a lesser extent they are detritivorous and bacterivorous. Thus, the amount of omnivory and, to a lesser extent, herbivory, in prairie potholes may be underestimated because of too convenient trophic aggregations and erroneous preconceived notions regarding invertebrate trophic relations (but see Murkin and Ross 2000).

It is plausible, therefore, that increased phytoplankton standing crop is a response to decreased herbivory as a result of increased tiger salamander consumption of planktonic invertebrates as a whole. This study provides only correlational evidence consistent with this hypothesis though, in Chapter 2, I show that tiger salamander gut contents are dominated by primarily herbivorous invertebrate taxa. Holomuzki et al. (1994) found evidence of trophic interactions between tiger salamanders (*A. t. nebulosum*) and phytoplankton standing crop in enclosures when macroinvertebrates and herbivorous zooplankton were considered as competing trophospecies rather than hierarchical trophic levels. It has generally been assumed that herbivory is relatively unimportant in prairie wetlands because such a small proportion of the total primary production is consumed (Murkin 1989, Euliss et al. 1999). This generalization, though, includes the exceptionally high production of metaphyton (i.e. filamentous algae) and rooted macrophytes, both of which are largely inedible to most invertebrates in prairie potholes (Murkin 1989, Campeau et al. 1994, Robinson et al. 2000). $\delta^{13}C$ stable isotope signatures from invertebrates in a northern prairie marsh were more closely matched with phytoplanktonic and epipelic algae rather than emergent or submergent macrophytes suggesting that the preferred forms of algae are relatively less available (Neill and Cornwell 1992, Wrubleski and Detenbeck in Euliss et al. 1999).

A second potential explanation for the positive relationship between tiger salamander abundance and phytoplankton standing crop avoids invoking direct consumer-resource interactions (i.e. predation and herbivory) as a way to explain apparent top-down influences by focusing on indirect processes of nutrient recycling and transfer. In a series of cylindrical enclosure experiments, Vanni and Layne (1997) found that phytoplankton biovolume was greater in the presence of planktivorous fish than in the absence, though the conventional mechanism of predator-prey interactions was not supported. Direct recycling of nutrients by fish through excretion and fish-induced effects on nutrient recycling through herbivorous invertebrates ("nutrient-mediated effects") were found to be responsible for increased nitrogen and phosphorus in the water column resulting in higher phytoplankton biovolume (Vanni and Layne 1997). Zimmer et al. (2001b) reached a similar conclusion for prairie wetlands. They found that phytoplankton, seston and macrophytes were the dominant pools of nitrogen and phosphorus in a wetland with fathead minnow whereas macrophytes, epiphytes and aquatic invertebrates were the dominant pools in the fishless wetland. As tiger salamanders are ectotherms, like fish, and tiger salamander production approximates that of fathead minnow in similar prairie wetlands, it is conceivable that tiger salamanders could exert a comparable effect on nutrient recycling and planktonic water chemistry. Other prairie pothole vertebrate consumers, such as ducks, grebes and coots, have been shown to affect lake and wetland water chemistry resulting in increased algal biomass (Manny et al. 1994, Pettigrew et al. 1998).

Phytoplankton standing crop may not necessarily reflect processes that occur exclusively in the open water areas of potholes as biotic transfers and physical mixing may also contribute to the composition of the seston. For example, using a simulation model, Schindler et al. (1996) found that planktonic seston (mainly phytoplankton) and SRP (soluble reactive phosphorus) concentrations were subsidized by nutrient transfer and recycling by fish from the littoral zone to the pelagic zone of a lake and that the greatest increase in seston and SRP occurred when the lake was dominated by planktivorous fish. Such may be the case in prairie potholes occupied by tiger salamanders as field studies indicate that they migrate from the shallow to deep areas and from vegetated to unvegetated parts of potholes on a daily basis (Branch and Altig 1981, Holomuzki 1986). A major portion of a tiger salamander's diet is derived from benthic and littoral invertebrates (Chapter 2), which may result in a net transfer of organic matter to open water parts of potholes and planktonic food webs.

In addition, high winds, which are common in prairie environments, can cause resuspension of fine sediments and benthic algae and dislodge epiphytic algae from littoral vegetation through wave action (Haertel 1976, Carper and Bachmann 1984, Hellström 1991). Such events might have potentially inflated estimates of phytoplankton biomass in this study except that the presence of submergent and emergent vegetation has also been shown to reduce disturbance to surficial sediments (Dieter 1990, James and Barko 1990), and resuspended benthic algae (excluding metaphyton) and dislodged epiphytic algae tend to sink in the water column (Robinson et al. 2000).

Across the Prairie Pothole Region, the top consumers in aquatic ecosystems vary according to many different environmental factors, including water chemistry and pothole permanence (the so-called "permanence gradient", Wellborn et al. 1996, Wissinger 1999). In wetter and more productive permanent potholes, planktivorous fish (i.e. fathead minnow, brook stickleback) often assume the position of top consumer while in drier and less productive ephemeral potholes large carnivorous aquatic insects (e.g. Dytiscidae larvae, Odonata nymphs) assume the same trophic position. Between these extremes are semi-permanent potholes where tiger salamanders, possibly enabled through facultative paedogenesis, exist as the top consumer (Wissinger 1999). The extent to which these very different consumers are functional equivalents is unknown. However, they all exert degress of trophic control on their respective wetland ecosystems (Holomuzki et al. 1994, Herwig and Schindler 1996, Zimmer et al. 2001a), indicating that even highly productive aquatic ecosystems in fluctuating environments are generally structured by predation.

The results of this study are qualitatively very similar to those obtained by two earlier studies. Spencer and King (1984) and Hanson and Riggs (1995) found decreased zooplankton and macroinvertebrate abundance, respectively, and increased phytoplankton densities in the presence of brook stickleback and fathead minnow.

Further, in a multivariate analysis, Zimmer et al. (2000) found that the presence or absence of fathead minnow was the single most important factor in explaining variation in invertebrate community structure. Zimmer et al. (2000) also found that the relationship between fathead minnow and invertebrate community structure was nonlinear; even at low fish densities, invertebrates were sensitive to the presence of fathead minnow. A nonlinear relationship was also found between tiger salamanders and some invertebrate taxa in this study. However, contrast comparisons indicated that the more pronounced effects on aquatic insects and Crustacea occurred between High and Low tiger salamander abundance categories rather than Low and Absent categories suggesting that some sort of threshold abundance of tiger salamanders is necessary to have an appreciable effect on pothole communities. Fathead minnow populations are more temporally stable within permanent potholes than tiger salamanders, resident fish populations continuously interact with the invertebrates year-round. In more fluctuating hydrologic environments, semi-permanent potholes are likely more regularly invaded and vacated by tiger salamanders. Thus, only at relatively higher abundances, indicative of longer residency, do tiger salamanders have an appreciable effect on pothole invertebrates and phytoplankton.

Though my study potholes were virtually devoid of fish, other vertebrate consumers, including tadpoles and waterfowl, coexist that also feed on invertebrates (Krapu and Reinecke 1992, Petranka and Kennedy 1999, Chapter 2). Tadpoles were treated as a response variable though the interaction between tiger salamanders and tadpoles is more likely indirect (i.e. exploitation competition) as these amphibians feed on many of the same prey species as tiger salamanders, especially larvae. However, tadpoles, as microphagous suspension feeders, also include various forms of algae in their diets (Robinson et al. 2000) so the link between tiger salamanders and tadpoles is probably weak. Tadpoles never appeared in any tiger salamander gut contents (Appendix 3) yet tadpoles ranged widely in abundance among potholes (Table 1.1).

Migratory birds, especially ducks, coots and grebes, breed in the Prairie Pothole Region and according to gut contents data (Krapu and Reinecke 1992) and morphological variation in body size and lamellar spacing (Nudds and Bowlby 1984) exploit much of the same invertebrate food base and habitat available in prairie potholes. Competition between fish and waterfowl has been widely studied both empirically (e.g. Eadie and Keast 1982) and experimentally (e.g. Cox et al. 1998) and the emerging consensus is that resident fish populations affect waterfowl composition, decrease abundance and reduce reproductive success (Bouffard and Hanson 1997). Given the ecological similarities between tiger salamanders and fathead minnow, these two aquatic consumers should have similar effects on waterfowl. Significant dietary overlap between tiger salamanders and dabbling ducks and significant spatial overlap between tiger salamanders and diving ducks suggests that tiger salamanders and ducks partition habitat and food resources (Chapter 2). It is reasonable, therefore, to predict that migratory waterfowl should be similarly affected by tiger salamanders as they are by resident fish populations.

The goal of this research was to ascertain patterns of pothole community structure in relation to tiger salamanders. Thus, all invertebrate and phytoplankton variables were treated as response variables in the statistical analyses. Within each of the invertebrate groups not all types of organisms behaved similarly. The degree of aggregation of food web members into convenient groups depends on the particular question. For this study, coarse groups of invertebrates were the appropriate for two reasons. First, finer resolution would have greatly increased the number of dependent variables rendering the MANOVAs useless because of the limited number of degrees of freedom. Second, because each group was generally characterized by a few dominant species, the patterns would simply be repeated (Bowman and Bailey 1997). For example, >95% of Crustacea was *Hyallela* and >75% of the aquatic insects were either Diptera or Hemiptera, all of which had similar responses in relation to tiger salamander abundance. This reasoning only applies to issues of taxonomic resolution, as within many insect and crustacean families there often exists a wide variety of trophic functions; subsequent analyses should delve further into these potentially important and informative differences.

Zaret (1980) listed six criteria that arguably qualify *Ambystoma* as a "fish in amphibian's garment" (Appendix 1). Half of them refer to morphological adaptations that are generally in common between planktivorous fish and tiger salamanders, including size, gape limitation and visually dependent foraging. The other half refers to similarity in dietary patterns that have been obtained for both consumers. This study supports two of the three criteria; the exception being that no evidence was found that tiger salamanders in prairie potholes are cannibalistic or that they eat tadpoles. Results from this study, in combination with those obtained in Chapter 2 support the hypothesis that tiger salamanders are the functional equivalents of planktivorous fish in fishless prairie potholes suggesting that the influence of tiger salamanders on prairie pothole communities has been underestimated.

CHAPTER 2

Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes

Introduction

A latent appreciation of indirect interactions in food web ecology has emerged over the past decade (Wootton 1994, Abrams et al. 1996). Predation and interference competition are conspicuous examples of direct interactions that have long been known to affect food web structure in aquatic systems (Zaret 1980). However, both contemporary theory and experimental evidence support the idea that the magnitude of indirect effects rivals those of direct effects (Miller and Travis 1996). Indirect interactions are defined as those effects of one species on another that do not involve physical interaction (Wootton 1994). Detection and estimation of indirect interaction strength are important so that meaningful predictions can be made of ecological communities that are naturally or experimentally perturbed.

Migratory waterfowl use freshwater wetlands of high invertebrate availability during the breeding season to satisfy energetic demands for reproduction and brood rearing. In many of these wetlands, migrants encounter resident fish populations that can affect distribution and abundance of adult waterfowl (Hanson and Butler 1994) and survival and growth rate of waterfowl offspring (Cox et al. 1998, Sjöberg et al. 2000), apparently because of competitive interactions between the two types of consumers (Eadie and Keast 1982, Giles et al. 1990, Winfield and Winfield 1994). However, only

10-20% of wetlands or "potholes" in the Prairie Pothole Region of North America are thought to sustain natural fathead minnow and/or brook stickleback populations (Lawler et al. 1974) and this void appears to have been filled, to some extent, by tiger salamanders (*Ambystoma tigrinum*) (Peterka 1989). Presently, the distribution of tiger salamanders in southwestern Manitoba is only broadly known, but in North Dakota, they are reported to occur widely across prairie wetlands and shallow lakes (Euliss 1999). Although there are analogous effects of fish (Hanson and Riggs 1995, Spencer and King 1984) and tiger salamanders (Holomuzki et al. 1994) on wetland community structure, it is unclear whether or not these two aquatic vertebrates are functional equivalents (Zaret 1980, Kurzava and Morin 1998) and if they have similar effects on breeding waterfowl.

An extensive literature exists on waterfowl diet data and feeding ecology from prairie potholes (reviewed in Krapu and Reinecke 1992), but comparatively little is known about tiger salamanders from the same region (but see Olenick and Gee 1981, Deutschman 1984). In studies of gut and esophageal content from across North America, a wide variety of aquatic invertebrate taxa appear in both waterfowl (Krapu and Reinecke 1992) and tiger salamander (Norris 1989, Olenick and Gee 1981, Collins and Holomuzki 1984) diets, suggesting that there is at least some diet overlap. Within the dabbling ducks (Anatidae), however, diet overlap was assumed to be large, until it was discovered that duck species could be more effectively separated along an axis of prey size rather than prey type (Nudds and Bowlby 1984), so comparisons of diet according to compositional data alone may not reflect actual diet differences.

Using a combination of field surveys, tiger salamander gut contents and published data on duck diets, I examined patterns of invertebrate food (prey type and prey size) and habitat overlap between tiger salamanders and ducks. This is the first study to explicitly compare resource overlap between these two coexisting consumers in prairie potholes. On their own, these patterns do not allow for inferences to be made regarding the type and strength of interactions between tiger salamanders and ducks, but evidence of habitat or dietary overlap means that there is the potential for indirect interactions. If so, this study would be a precursor to subsequent experiments designed to determine if competition exists for common prey.

Methods

Data sources

Gray tiger salamanders (*Ambystoma tigrinum diaboli*) and ten duck species were surveyed in 24 fishless prairie potholes near Minnedosa, Manitoba, during late spring and early summer 1998. Prairie potholes in this area range from ephemeral to permanent and all of the potholes used in this study were semi-permanent (i.e. Class IV, Stewart & Kantrud 1971). In early May, the average pothole size was 0.56 ha and the average pothole depth was 110 cm. Tiger salamanders were sampled using standard minnow traps (mesh size = 5 mm) and 4-l activity traps (Murkin et al. 1983). Both types of trap have maximum diameters of 2.5 cm at the narrow end of the "funnel", effectively preventing trapped individuals from escaping. One minnow trap and three activity traps were set once a week for nine weeks (early May until late July) in 24 potholes. Captured tiger salamanders were counted (to estimate density), measured (snout-vent length) and weighed to the nearest 0.1 g. Any dead tiger salamanders were frozen for later analysis of gut contents immediately following removal from one of the traps. Sampling effort was standardized across potholes and 19 of the 24 potholes had at least one tiger salamander. Relative tiger salamander density in a pothole was calculated by converting total number captured per pothole to number of individuals per hectare per unit of sampling effort.

Breeding birds were also surveyed weekly, including all waterfowl and grebe species and American coot (*Fulica americana*). Only ten duck species, of a possible twelve to fourteen, were included in this study, owing to literature-based restrictions on diet data. For each duck species, relative density on a pothole was calculated by dividing the total number recorded per pothole by the number of surveys and converted to the number of individuals per hectare.

98 of the dead tiger salamanders (49 adult and 49 larval) were randomly chosen for gut contents analysis, representing 42% of the number frozen and 21% of the total number trapped. Tiger salamanders were categorized as adult or larval based on presence or absence of external gills. Consequently, any neotenic tiger salamanders were grouped with larval tiger salamanders. Adult tiger salamanders were 8.2-18.3 cm (mean = 10.5 cm) long and larval tiger salamanders were 4.2-8.2 cm (mean = 6.9 cm) long. The digestive tract, including esophagus and stomach contents, was removed from thawed tiger salamanders. Macroinvertebrates from the gut contents were sorted and stored in 70% ethanol. Prey items were identified generally to family using Merritt & Cummins (1996) and Thorp & Covich (1991), and they were counted and measured in the longest dimension to the nearest 0.01 cm using a compound microscope with a graduated platform.

Duck diet data were obtained through an extensive search of published sources. The following criteria were employed to filter the large pool of sources. First, data had to be collected from the Prairie Pothole Region of North America, during the breeding season, from ducks sampled soon after feeding (and then only from the esophageal contents) (Swanson & Bartonek 1970), and presented as percent volume or percent dry mass (i.e. dry weight). When the same author(s) published more than one study per species, we checked to be sure that the same birds were used only once. Eighteen food habits studies of ten duck species satisfied this criteria, comprising five dabbling duck and five diving duck species, totaling 1508 individuals (Table 2.1).

Analysis of prey type and prey size data

25 types of prey were identified in the guts of tiger salamanders (Appendix 3). Similarly, a wide variety of prey types were reported in the literature for ducks, but the taxonomic resolution used to identify the esophageal contents of the ducks varied among studies. To reconcile discrepancies between the prey lists of the two consumers, some prey types were combined resulting in a broader taxonomic level (e.g. Lymnaeidae, Physidae and Planorbidae identified in tiger salamander diets were subsumed into Gastropoda following several of the published duck prey lists).

For the tiger salamanders, a list of prey types was ranked by calculating the average of volumetric percentages (i.e. aggregate percentage) across all 98 individuals. Under the assumption that volume is proportional to dry weight (Nudds and Bowlby 1984), invertebrate lengths were converted to volumes using regressions published in Smock (1980) for aquatic insects, Mackie & Flippance (1983) for snails, Lawrence et al. (1987) and Culver et al. (1985) for crustacean zooplankton and Panov & McQueen

Table 2.1. Sources of duck diet data used to determine prey type and prey size distributions. Under the column heading "Location", the letters in upper case refer to the location within each province or state where the ducks were collected.

Species	Location	Source	Sample size[a]	Total
Dabbling ducks				
Blue-winged teal	E Saskatchewan	Dirschl 1969	106	257
Anas discors	S North Dakota	Swanson & Meyer 1977	44	
	S North Dakota	Swanson et al. 1974	107	
Gadwall	SW Manitoba	Ankney & Alisauskas 1991[b]	80	115
A. strepera	S North Dakota	Swanson et al. 1979	35	
Mallard	S North Dakota	Swanson et al. 1985	117	132
A. platyrhynchos	S North Dakota	Swanson et al. 1979	15	
Northern shoveler	SW Manitoba	Ankney & Afton 1988[b]	56	71
A. clypeata	S North Dakota	Swanson et al. 1979	15	
Northern pintail	E North Dakota	Krapu 1974a	61	160
A. acuta	E North Dakota	Krapu 1974b	64	
	E North Dakota	Krapu & Swanson 1977	35	
Diving ducks				
Canvasback	SW Manitoba	Austin et al. 1990	62	177
Aythya valisineria	SW Manitoba	Bartonek & Hickey 1969	115	
Redhead	E North Dakota	Woodin & Swanson 1989	59	108
A. americana	SW Manitoba	Bartonek & Hickey 1969	49	
Ring-necked duck	NW Minnesota	Hohman 1985	108	108
A. collaris				
Ruddy duck	E North Dakota	Woodin & Swanson 1989	82	142
Oxyura jamaicansis	SW Manitoba	Siegfried 1973	60	
Lesser scaup	SW Manitoba	Afton & Hier 1991	52	238
Aythya affinis	SW Manitoba	Bartonek & Hickey 1969	39	
	E Saskatchewan	Dirschl 1969	108	
	SW Manitoba	Rogers & Korschgen 1966	39	

[a] Sample size is the number of individuals of each species examined in each study.

[b] Detailed taxonomic composition of diets provided by the first author.

(1998) for amphipods. Although this assumption might overestimate the dry weight of heavy-shelled molluscs, most snails sampled from the study area tended to be very thin-shelled, especially Lymnaeidae and Physidae, the most commonly identified snails. No earthworms or leeches were identified in any of the tiger salamander guts. Algebraically, aggregate percentages equal the proportion of the jth prey type in the ith tiger salamander, where $i = 1$ to 98 and $j = 1$ to 13, averaged across all tiger salamanders. This approach incorporates the contribution of each tiger salamander equally and it is appropriate when the total quantity of gut contents is variable among individuals (Swanson et al. 1974). The same calculation was also applied to the tiger salamander data for adult and larval life stages. Tiger salamander prey-type rankings were supplemented with frequency of occurrence calculations (i.e. the specific number of tiger salamanders that consumed a particular prey type divided by the total number of tiger salamanders). For individual duck species, prey-type rankings were constructed by taking the average of the percentages reported for each prey type by volume or by weight across all applicable studies. For the groups of dabblers, divers and 'all ducks', the number of studies varied for each species. Therefore, the average of the percentages averaged within appropriate sets of species were used to construct prey-type rankings to avoid bias by well-represented species. Although plant matter was found in many tiger salamander guts, it was excluded from the analyses for two reasons. First, the very small amounts that were found were unidentifiable. Second, plant matter is only ingested incidentally by tiger salamanders (Collins & Holomuzki 1984). Accordingly, contributions of plant matter towards duck diets were also excluded from the analyses.

Kendall's coefficient of ranked correlation, *tau* (τ), was used to measure the degree of overlap in prey type between all possible combinations of tiger salamander age classes and duck species. For data sets with many tied ranks, Kendall's τ better approximates Pearson's *r* than Spearman's *r* (Legendre & Legendre 1998). A value for τ of 1.0 indicates complete similarity between two sets of ranks; τ = -1.0 indicates complete dissimilarity. Here we simply use τ as a niche metric; whether a particular value of τ is significant at some arbitrary α-level is not relevant to the purpose of this study.

To compare overlap in prey size between ducks and tiger salamanders, six prey size classes were constructed (1: 0–2.5, 2: 2.6–7.5, 3: 7.6–12.5, 4: 12.6–20.0, 5: 21–40, 6: 41–60 mm; following Nudds & Bowlby 1984). Prey types were assigned to one of the size classes based on average lengths calculated from ambient macroinvertebrate data sampled coincidentally with the tiger salamanders (Chapters 1 and 3) (Table 2.2). Within each size class, prey items were converted to energy, the "lowest common denominator" of resource budgets (Nudds & Bowlby 1984), according to each prey type's specific caloric density (kilocalories/gram dry weight; 1 cal = 4.1868 J). Caloric densities were obtained from the literature and, when necessary, values were averaged across studies (Table 2.2). For the tiger salamanders, prey size-energy distributions were constructed from length measurements of invertebrates identified in the guts. For each duck species, prey size distributions were constructed by pooling the contribution of each prey type across studies and then summing into size classes. When percent volume of prey was reported in the literature, we converted it to energy by multiplying percent volume by caloric density, using the assumption that volume is proportional to dry weight (Nudds &

Table 2.2. Lengths and caloric densities of invertebrate prey of both tiger salamanders and ducks used to construct prey size distributions.

Prey item	Length category	Caloric density (kcal/g dry weight)	Source[a]
Annelida	5	5.3	1,2,3,4
Hirudinea	5	5.4	1,2,3,4
Oligochaeta	6	4.6	4
Coleoptera	3	5.3	1,2,3,4,5
Dytiscidae	4	5.3	1,2
Haliplidae	3	5.3	6
Hydrophilidae	2	5.5	2,4
Diptera	4	5.2	1,2,4,5,7
Ceratopogonidae	3	5.2	8
Chaoboridae	3	5.2	4
Chironomidae	4	5.5	1,4,7
Culicidae	3	5.2	4,5
Ephemeroptera	2	5.5	1,3,4
Hemiptera	2	5.5	1,2,3
Corixidae	2	5.3	1,3
Odonata	4	5.3	1,2,3,4,5
Anisoptera	4	5.2	1,2,3,4,5
Zygoptera	4	5.3	1,3,4,5
Trichoptera	3	5.4	1,2,3,4
Gastropoda	3	1.5	1,4
Lymnaeidae	3	2	1
Planorbidae	2	0.5	4
Physidae	2	1.5	9

Amphipoda	2	3.9	1,2,4,7
Hyalellidae	2	3.9	1,2,4
Gammaridae	3	3.9	1,4
Anostraca	3	5	1,2,4,10
Zoobenthos	1	5.1	1,4
Conchostraca	2	5.3	1,4
Ostracoda	1	5	4
Zooplankton	1	5	4
Cladocera	1	4.8	4,5,7,11
Copepoda	1	6.1	4
Hydracarina	1	5.6	1,2,5

[a] (1) Driver et al. 1974; (2) Driver 1981; (3) Reinecke & Owen 1980; (4) Cummins & Wuycheck 1971; (5) Stockner 1971; (6) based on Coleoptera; (7) Wissing & Hasler 1971; (8) based on Chironomidae; (9) based on Gastropoda; (10) Comita & Schindler 1963; (11) Schindler et al. 1971.

Bowlby 1984). Similar to the prey type comparisons, prey size distributions for sets of species were combined to create composite distributions for groups of dabblers, divers and 'all ducks'.

Kolmogorov-Smirnov two-sample tests (D_{max}), based on cumulative frequency distributions were used to quantify differences in prey size between tiger salamanders and ducks. Unlike other commonly used distribution-free tests, the Kolomogorov-Smirnov two-sample test makes no assumption regarding whether the tiger salamanders or the ducks should be designated as "expected" or "observed". In contrast to Kendall's τ, D_{max} values range from 0 to 1 and values closer to 0 indicate greater similarity between distributions.

Finally, three pairwise discriminant function analyses were used to gauge how well the three indices of overlap (Kendall's *tau*, Kolmogorov-Smirnov D_{max}, and Pearson's r) predicted correct classification of each of the duck species as either a dabbler or a diver (i.e. foraging guild – the grouping variable). Each analysis included two of the three indices of overlap to enable graphical representations in two dimensions.

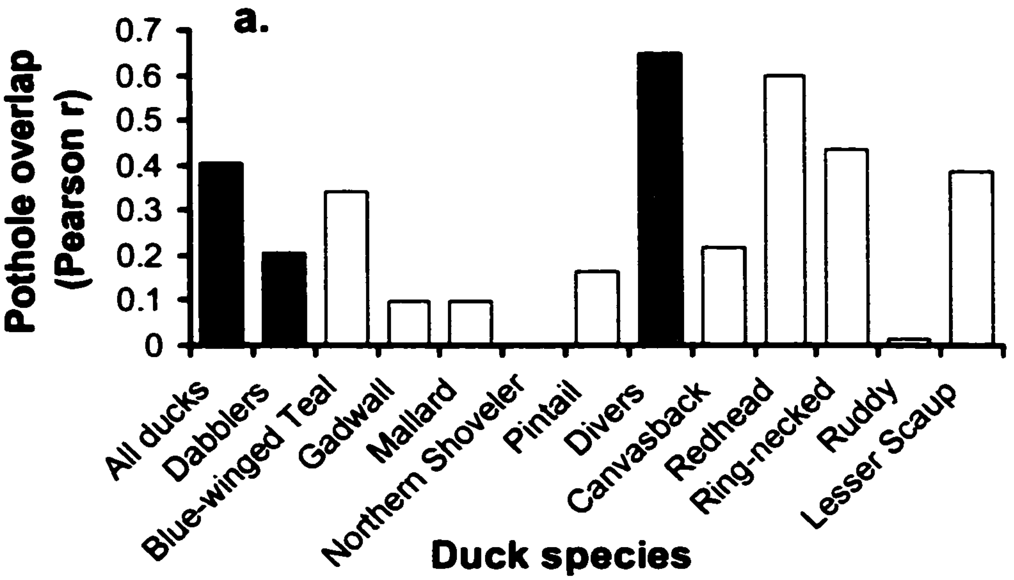
Results

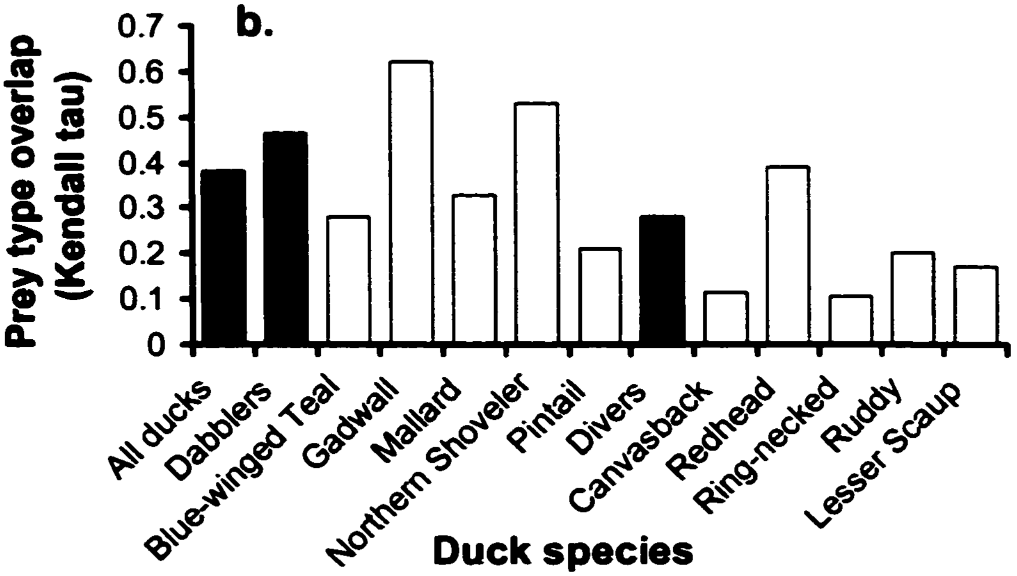
Tiger salamander and duck densities varied widely among the 20 study potholes (Table 2.3). Across potholes, tiger salamander density was most highly correlated with the diving ducks, followed by 'all ducks' and by the dabbling ducks (Fig. 2.1a). Of the individual duck species, Redhead had the highest correlation with tiger salamanders followed by Ring-necked, Lesser scaup and Blue- winged teal. The rest of the species

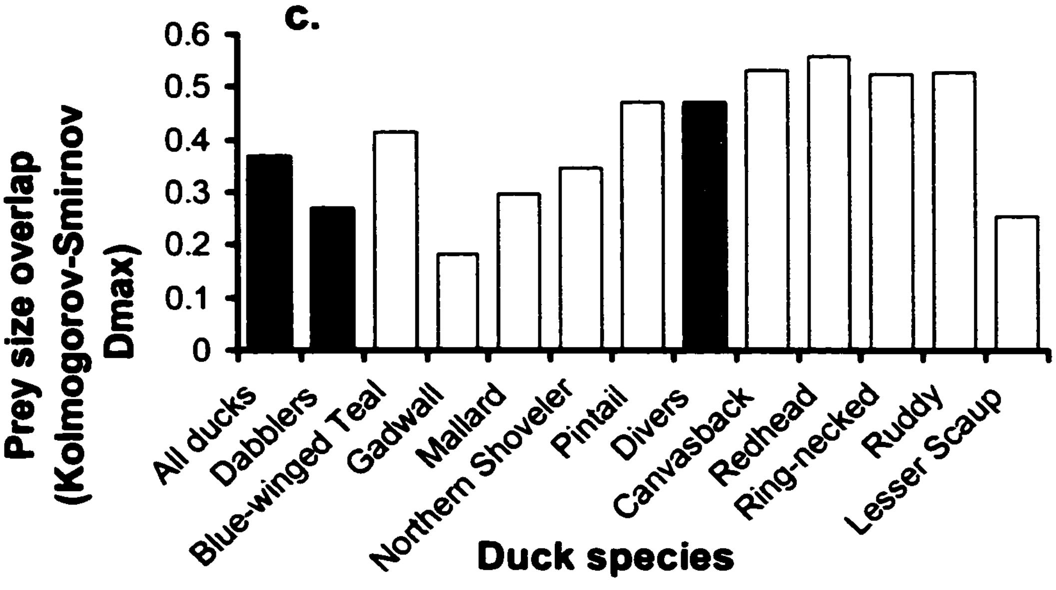
Table 2.3. Densities (ind./ha/survey) of tiger salamanders and ducks surveyed at 20 prairie potholes during 1998.

	Range	Mean	C.V.
Tiger salamanders	6.3 – 306.3	105.6	0.83
All ducks	1.1 – 11.5	6.6	0.47
Dabblers	0.6 – 10.0	5.0	0.54
Divers	0.3 – 4.4	1.7	0.64

Fig. 2.1. Indices of overlap between tiger salamanders and ducks for a. habitat overlap, b. prey type overlap and c. prey size overlap. Note that in c., lower Kolmogorov-Smirnov *Dmax* values indicate higher prey size overlap. The black bars are the overlap measures for 'all ducks' combined and the gray bars are the overlap measures for each of the duck guilds.


a.
Pothole overlap (Pearson r)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
All ducks
Dabblers
Blue-winged Teal
Gadwall
Mallard
Northern Shoveler
Pintail
Divers
Canvasback
Redhead
Ring-necked
Ruddy
Lesser Scaup
Duck species


b.
Prey type overlap (Kendall tau)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
All ducks
Dabblers
Blue-winged Teal
Gadwall
Mallard
Northern Shoveler
Pintail
Divers
Canvasback
Redhead
Ring-necked
Ruddy
Lesser Scaup
Duck species


c.
Prey size overlap (Kolmogorov-Smirnov Dmax)
0.6
0.5
0.4
0.3
0.2
0.1
0
All ducks
Dabblers
Blue-winged Teal
Gadwall
Mallard
Northern Shoveler
Pintail
Divers
Canvasback
Redhead
Ring-necked
Ruddy
Lesser Scaup
Duck species

were weakly positively correlated with tiger salamanders except Ruddy and Northern shoveler, which were unrelated to tiger salamander density (r = 0.014 and r = -0.016, respectively).

At the level of taxonomic resolution we used, the number of prey types common to both consumers was 13 (Table 2.4). Gastropoda and Diptera comprised just over 60% of the total weight of gut contents averaged across tiger salamanders. Numerically, zoobenthos and zooplankton were the most commonly identified organisms in tiger salamander gut contents, but they accounted for only about 7% of the total weight. However, not all prey types were consumed by all tiger salamanders. Although Gastropoda accounted for 34% of the gut contents by aggregate weight, it occurred in only 41% of the tiger salamanders. In contrast, Diptera also comprised a major portion of the gut contents and it was consumed by almost 90% of the sampled tiger salamanders. Other invertebrates that were well represented among tiger salamanders but did not contribute substantially to the total weight of the gut contents included Hemiptera, zoobenthos and zooplankton and to lesser extents Odonata and Amphipoda.

Dabbling duck prey types were more similar to those of tiger salamanders than were the prey types of diving ducks, and the strength of the overall similarity with dabbling ducks appears to be partly because of the high degree of similarity with Gadwall and Northern shoveler (Fig. 2.1b). Among the diving ducks, the only other species to overlap to any important degree with tiger salamanders with respect to prey type ranking was Redhead. The overall pattern of ranks for prey type overlap was maintained when the tiger salamanders split into adult and larval groups and compared with the duck diets (Table 2.5). Gadwall, Mallard, Northern shoveler and Redhead had the highest overlap

Table 2.4. Prey types common to both tiger salamanders and ducks (n = 13) used in the calculation of Kendall's rank correlation coefficient (*tau*), ranked from 1 to 13 according to those prey types most consumed by tiger salamanders and compared with, for example, all ducks. Supplementary information on tiger salamander gut contents is also included.

Prey type	Tiger salamanders % occurrence	Tiger salamanders Aggregate %	Rankings Tiger salamanders	Rankings All ducks	Rankings Dabblers	Rankings Divers
Gastropoda	40.8	34.0	1	2	1	4
Diptera	88.9	26.1	2	1	2	1
Coleoptera	55.1	10.6	3	6	4	8
Hemiptera	75.5	7.7	4	8	8	3
Odonata	39.8	7.1	5	9	9	11
Amphipoda	39.8	5.7	6	11	11	6
Zoobenthos	69.4	3.7	7	4	5	9
Zooplankton	58.2	3.4	8	7	3	12
Ephemeroptera	20.4	1.0	9	12	12	7
Trichoptera	11.2	0.5	10	3	6	2
Hydracarina	4.1	0.2	11	13	13	10
Anostraca	1.0	0*	12	10	10	13
Annelida	0*	0*	13	5	7	5

* <0.1% identified.

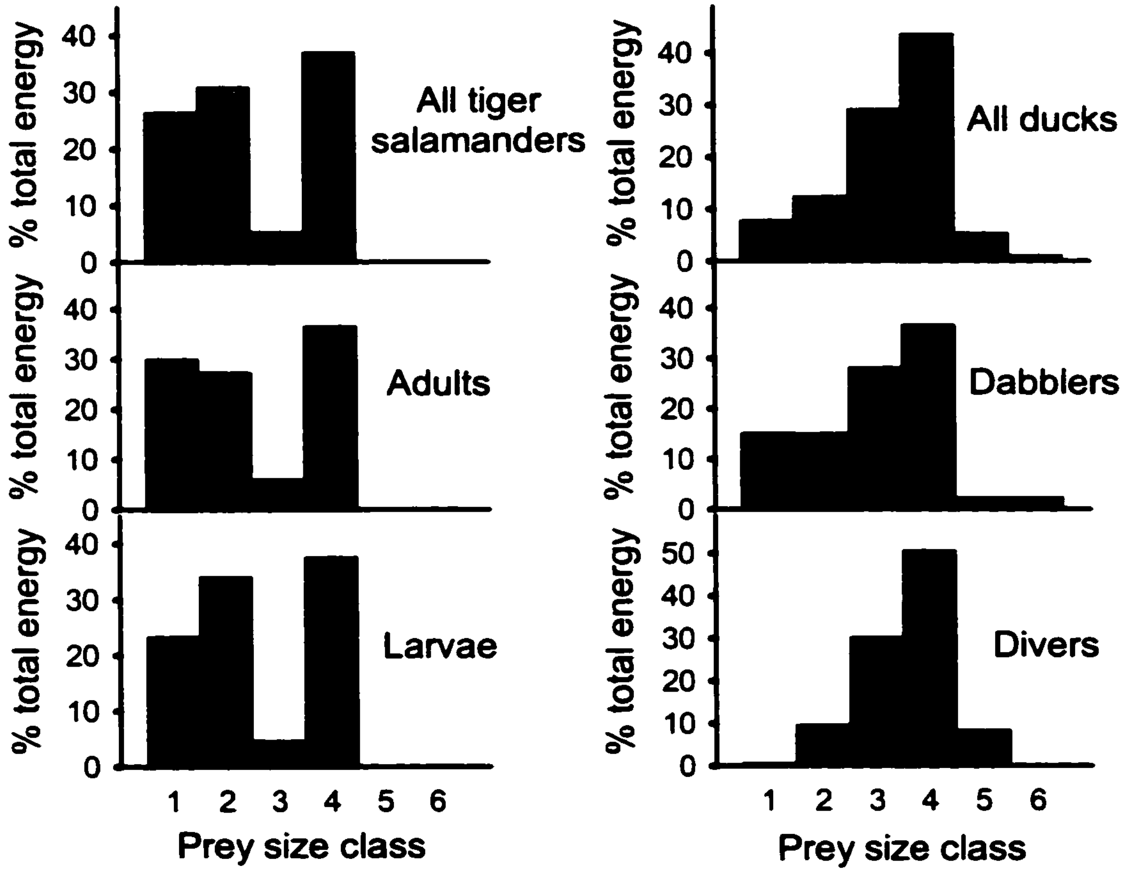
Table 2.5. Indices of diet overlap between adult (n = 49) and larval (n = 49) tiger salamanders and ducks. Note that high *tau* values correspond to high prey type overlap whereas low D_{max} values correspond to high prey size overlap. Groups of duck species are in bold.

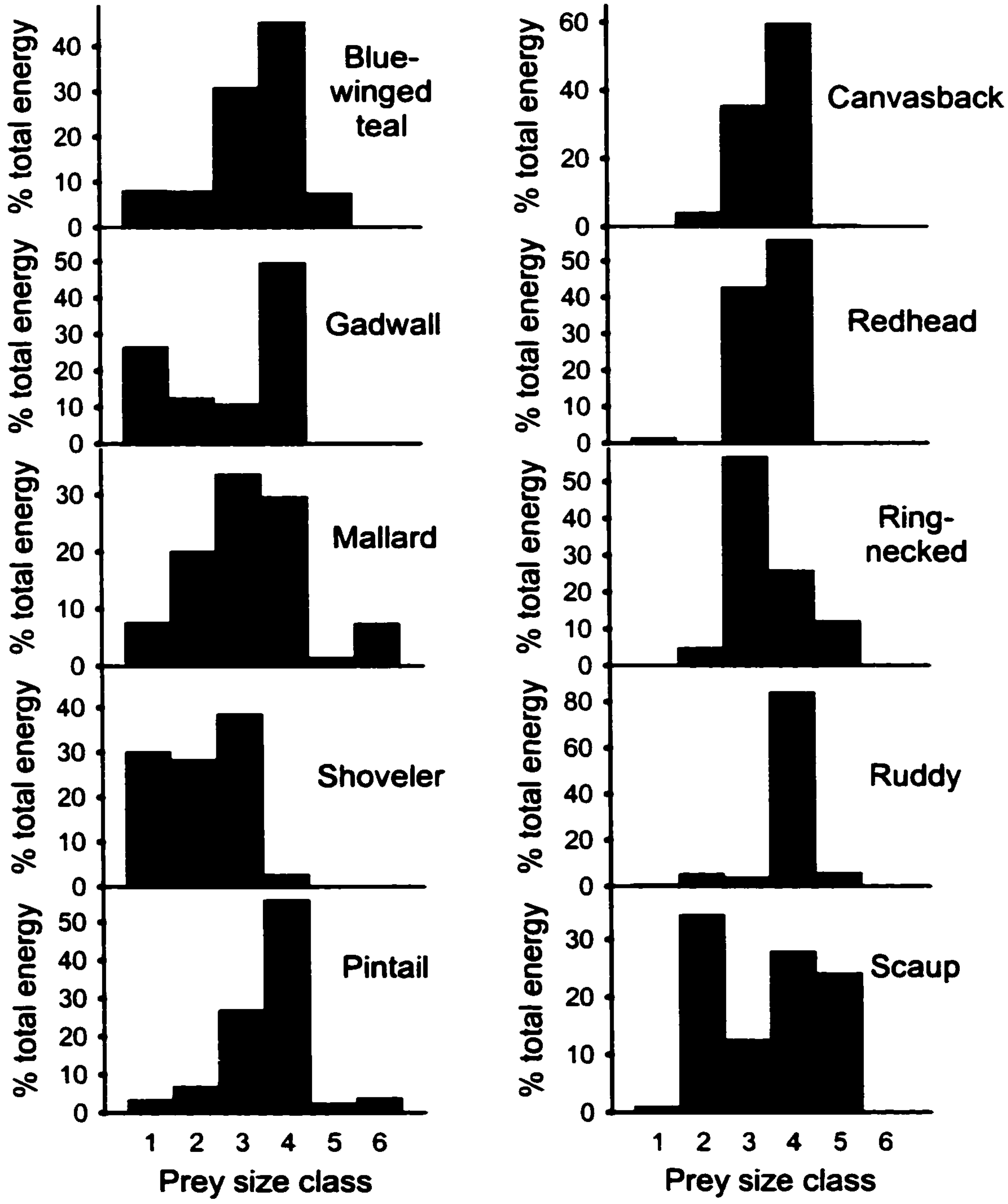
	Prey type (*tau*)		Prey size (D_{max})	
	Adults	Larvae	Adults	Larvae
All ducks	**0.334**	**0.294**	**0.369**	**0.371**
Dabblers	**0.468**	**0.431**	**0.269**	**0.271**
Blue-winged teal	0.232	0.290	0.412	0.414
Gadwall	0.667	0.493	0.181	0.183
Mallard	0.384	0.276	0.296	0.298
Northern shoveler	0.417	0.388	0.338	0.350
Pintail	0.238	0.140	0.469	0.471
Divers	**0.181**	**0.258**	**0.469**	**0.471**
Canvasback	0.164	0.114	0.532	0.533
Redhead	0.392	0.353	0.556	0.561
Ring-necked	0.164	-0.013	0.522	0.524
Ruddy	0.169	0.149	0.533	0.522
Lesser scaup	0.054	0.208	0.290	0.224

with both adult and larval tiger salamanders. Across each of the tiger salamander developmental stages, the lowest dietary overlap occurred with one of the diving duck species.

The proportions of total energy among prey size classes for the tiger salamander and duck groups as well as the 10 duck species are shown in Fig. 2.2. None of the tiger salamander diets included any macroinvertebrates that were longer than size class four (7.6–12.5 mm), whereas several of the duck species consumed leeches from size class five (21–40 mm) and two dabbling ducks, Mallard and Pintail, consumed earthworms from size class six (41–60 mm). Consequently, all of the Kolmogorov-Smirnov comparisons are based on four tiger salamander prey size classes and three to six duck prey size classes, depending on diet variation among duck species. Overall, prey size differed more between diving ducks and tiger salamanders than it did between dabbling ducks and tiger salamanders (Fig. 2.1c). Size class four, dominated by Chironomidae and Odonata, was particularly important to both adult and larval tiger salamanders and all ducks, except Northern shoveler and Ring-necked. Again, adult and larval life stages of tiger salamanders had almost identical prey size distributions, resulting in trivial differences when compared with any of the duck species or group (Table 2.5). Among dabbling ducks, Gadwall diets were most similar to tiger salamander diets but the prey sizes of the remaining four duck species were divergent from tiger salamanders. In contrast, prey-size distributions of diving ducks, with the exception of Lesser scaup, were all more dissimilar from the tiger salamanders than any of the dabbling ducks. Furthermore, Canvasback, Redhead, Ring-necked and Ruddy prey size distributions were almost equally dissimilar from tiger salamanders.

Fig. 2.2. Prey size distributions expressed as percent total energy for tiger salamanders, including adults and larvae, and ducks, including dabbling ducks, diving ducks and each of the 10 species used in the analysis.


% total energy
0
10
20
30
40
All tiger salamanders
Adults
Larvae
1
2
3
4
5
6
Prey size class
All ducks
Dabblers
Divers
50

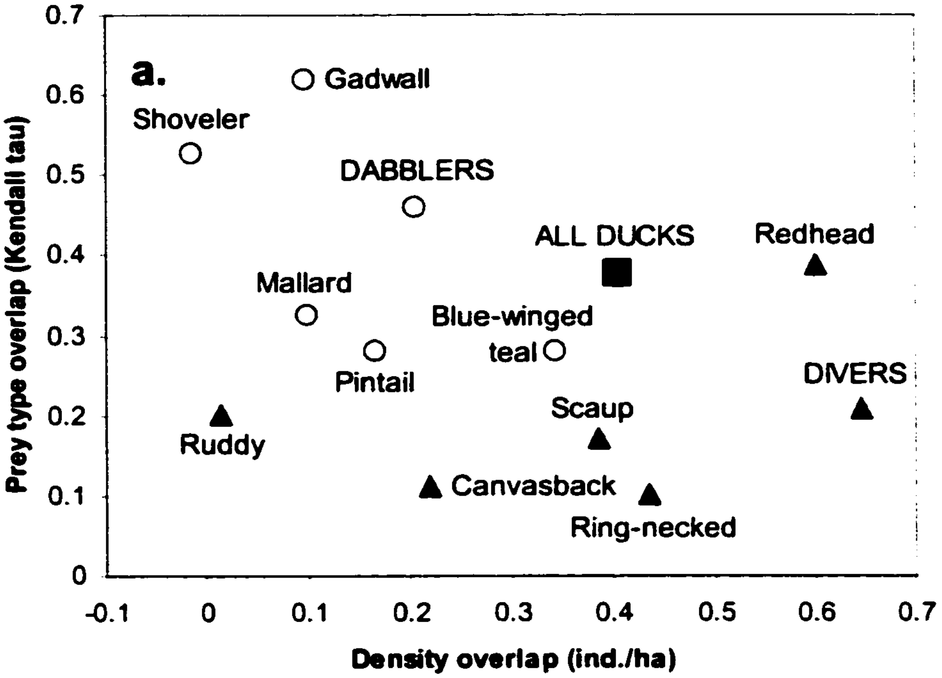

% total energy
Blue-winged teal
Canvasback
Gadwall
Redhead
Mallard
Ring-necked
Shoveler
Ruddy
Pintail
Scaup
0
10
20
30
40
50
60
80
1 2 3 4 5 6
Prey size class

When tiger salamanders and ducks were combined in multivariate analyses, an interesting pattern emerged. In other words, individual duck species with high prey type and prey size overlap with tiger salamanders tended to have reduced overlap across potholes. Both measures of diet overlap, prey type and size, appear to be weakly correlated with overlap in density (Fig. 2.3a, $r = -0.36$, df = 9, $P = 0.23$; Fig. 2.3b, $r = -0.36$, df = 9, $P = 0.23$, respectively) and when the two indices of diet overlap alone were compared there was a positive correlation between prey type and prey size (Fig. 2.3c, $r = 0.62$, df = 9, $P = 0.03$). Furthermore, pairwise discriminant function comparisons with foraging guild (dabbler or diver) as the grouping variable showed similar patterns of group membership (prey type × density, $F_{2,7} = 3.73$, $P = 0.079$; prey size × density, $F_{2,7} = 2.44$, $P = 0.16$; prey type × prey size, $F_{2,7} = 3.14$, $P = 0.11$). Based on Mahalanobis distances, 60-80% of all duck species were correctly classified as either a dabbler or a diver, according to all combinations of diet overlap and pothole overlap with tiger salamanders. Only Blue-winged teal were misclassified in all three comparisons; Pintail and Ruddy were miscalssified in two of three comparisons and Lesser scaup was misclassified is one of three comparisons.

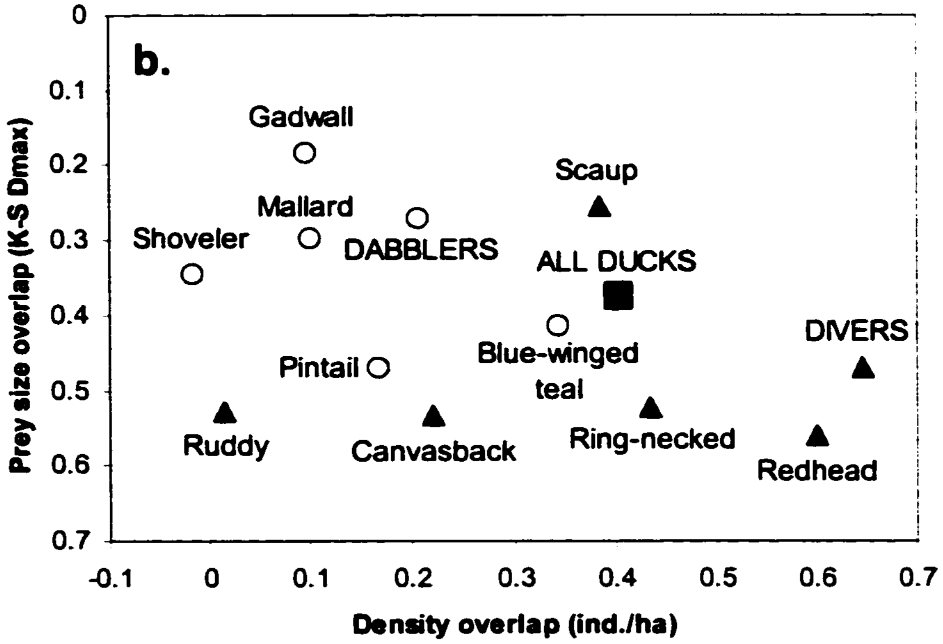
Discussion

Traditionally, waterfowl biologists and managers in the Prairie Pothole Region have focused on the effects of intraspecific and interspecific interactions within the Anatidae, or predators (i.e. mammalian, avian, human), on duck populations. Recently, interactions between waterfowl and other vertebrate consumers that may live below the water surface have received attention (Bouffard and Hanson 1997). I hypothesized that

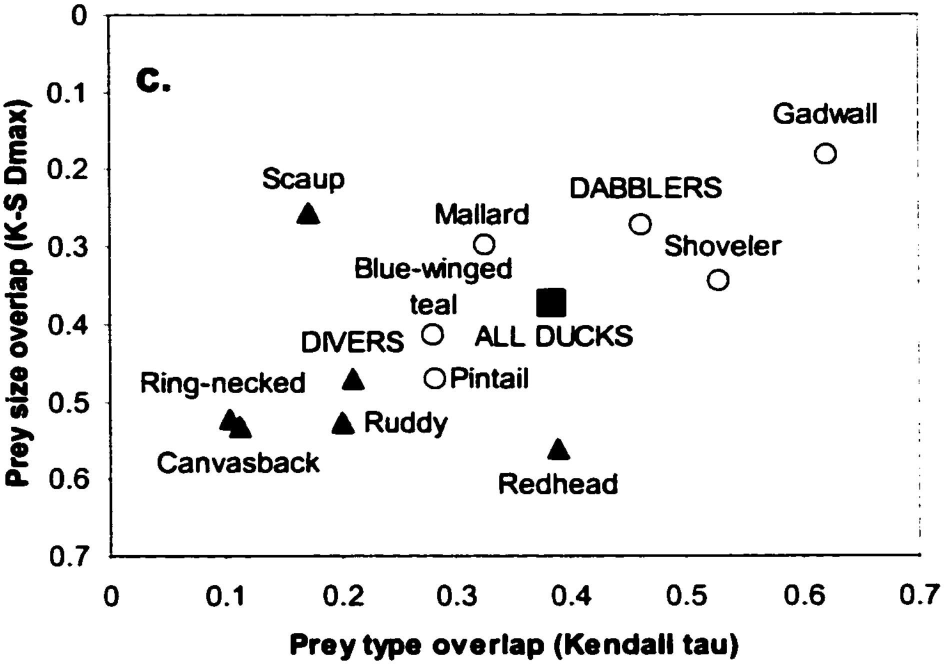
Fig. 2.3. Bivariate plots of indices of overlap between tiger salamanders and ducks. In a. and b., individual points refer to intersections between density overlap and prey type or prey size overlap and in c., points refer to intersections between prey type overlap and prey size overlap. 'K-S *Dmax*' refers to Kolmogorov-Smirnov *Dmax*. Note that in b. and c., lower Kolmogorov-Smirnov *Dmax* values indicate higher prey size overlap; the y-axes in these plots are flipped to be consistent with a. (i.e. duck species in the top right corners of all plots have the greatest overlap with tiger salamanders). The open circles are dabbling duck species, the closed triangles are diving duck species and the closed square is the composite value for 'all ducks' combined.



a.
Prey type overlap (Kendall tau)
Density overlap (ind./ha)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Gadwall
Shoveler
DABBLERS
ALL DUCKS
Redhead
Mallard
Blue-winged teal
Pintail
DIVERS
Scaup
Ruddy
Canvasback
Ring-necked



b.
Prey size overlap (K-S Dmax)
Density overlap (ind./ha)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
-0.1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Gadwall
Scaup
Mallard
Shoveler
DABBLERS
ALL DUCKS
DIVERS
Blue-winged teal
Pintail
Ruddy
Canvasback
Ring-necked
Redhead


c.
Prey size overlap (K-S Dmax)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Prey type overlap (Kendall tau)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Gadwall
Scaup
DABBLERS
Mallard
Shoveler
Blue-winged teal
ALL DUCKS
DIVERS
Ring-necked
Pintail
Ruddy
Canvasback
Redhead

tiger salamanders and ducks might share prey resources and, possibly, interact with one another. This study is the first to consider both these vertebrate consumers and it is an initial step towards an appreciation of higher-order interactions that may govern the distribution and abundance of waterfowl in prairie potholes.

All three measures of resource overlap – consumer density, prey type and prey size – indicated a high degree of use of common resources between tiger salamanders and all ducks combined. More specifically, dabbling ducks overlapped with tiger salamanders in prey type and prey size more than did diving ducks, but less in space. Interestingly, the highest overlap in prey with tiger salamanders occurred with Gadwall and Northern shoveler, the two dabbling duck species for which gut contents data were specifically available in southwestern Manitoba. Conversely, diving duck density among prairie potholes was positively correlated with tiger salamander densities, but these ducks demonstrated less overlap in prey type and prey size. Four of five diving duck species, excepting Ring-necked, were well represented by gut contents data from the study area, suggesting that indices of overlap involving these species are particularly informative. Substantive differences were not found between adult and larval tiger salamander developmental stages for any of the indices of overlap. This was likely because gut contents from very young tiger salamander larvae were not obtained for this study and the feeding behaviour of small larvae tends to be constrained by gape limitation (Dodson and Dodson 1971, Shaffer and Lauder 1988) and interactions with potential predators (Holomuzki and Collins 1987).

At this stage, it would be tempting to infer that these results, consistent with early niche theory (*sensu* MacArthur and Levins 1967), indicate that tiger salamanders and ducks strongly interact. However, it would be premature to infer species interactions from these patterns. Nevertheless, this study is an important precursor to subsequent manipulative experiments testing for species interactions directly. If, in such experiments, and in light of these results, there was evidence of tiger salamander-duck interaction, then the strong inference would allow that tiger salamanders and ducks indirectly interact through common prey (i.e. interspecific exploitation competition).

Relatively little is known about tiger salamanders in prairie wetlands. The densities of adult and larval tiger salamanders estimated for these study potholes in southwestern Manitoba are comparable to those estimated in other studies. At one extreme, Deutschman and Peterka (1988) calculated that in two North Dakota prairie lakes, larval tiger salamander densities reached 5000 ha^{-1} in late July, but by mid-September the density decreased to approximately 400 ha^{-1}. More modestly, Tavarutmaneegul (1978) and Meyers (1973) reported adult tiger salamander densities of 100 to 364 ha^{-1} for southwestern Manitoba and other North Dakota prairie lakes. My tiger salamander diet data are quite different from those reported by Olenick and Gee (1981) who found, for example, that in potholes near Erickson, Manitoba, *Gammarus* was the dominant prey item (>87% aggregate weight). Potholes in their area are more permanent relative to the semi-permanent ones in this study's area and amphipod species distributions are correlated with wetland permanence (Swanson 1984, Lindeman and Clark 1999). Accordingly, *Hyallela azteca* was the only amphipod identified in any of the tiger salamander gut contents, but they were never the top ranked prey item by type, accounting for only 5.7% of the total aggregate weight, on average. Though there are reports that tiger salamanders exhibit prey type and prey size preferences within potholes

(Olenick and Gee 1981, Deutschman 1984), the species is apparently widespread enough and in different wetland classes at a variety of stages in the wet-dry cycle that their diets appear to generally reflect prey availability (Euliss et al. 1999, Zerba and Collins 1992).

The reciprocal effects, if they exist, of these two consumers may be asymmetric and vary seasonally. Tiger salamanders would appear to have some advantages over ducks for exploiting invertebrate prey. First, during much of the ice-free season, tiger salamanders are almost obligately aquatic organisms, and second, they have a facultatively paedomorphic life history strategy enabling them to reproduce within a breeding season and without leaving a pothole. For example, enclosure experiments in fishless Arizona ponds revealed that the presence of larval tiger salamanders resulted in decreased herbivorous zooplankton biomass and increased chlorophyll *a* concentrations (Holomuzki et al. 1994). Alternatively, although the evidence for waterfowl effects on invertebrate food webs is less obvious, ducks may have advantages at some times. Certainly, in other aquatic systems, experiments have tested the hypothesis that birds are important agents of food web structure (e.g. Hurlbert and Chang 1983, Quammen 1984, Hamilton 2000), but, this notion has received only occasional attention in research on migratory waterfowl and never in prairie potholes. During the breeding season, Wrubleski (1989) found that densities of Chironomidae was higher where ducks were prevented from feeding and disturbing the rooted vegetation, whereas, during the wintering season, Smith et al. (1986) found that diving ducks had little overall impact on benthic food resources. Furthermore, flying birds can subsidize competitive ability on any particular pothole by acquiring resources away from it. Perhaps any competitive effect of tiger salamanders on ducks is greater during the flightless, brood-rearing period when movement is more restricted.

By comparing duck diet data with ambient invertebrate size distributions, Nudds and Bowlby (1984) showed that dabbling duck species can be separated along an axis of prey size differences that correlate with lamellar density; 18 of 21 pairwise comparisons between species were significantly different. Similarly, there was an overall effect of interspecific diet separation among diving ducks and 10 of 10 pairwise comparisons between species were significantly different (Nudds and Prescott, unpublished manuscript). However, diving ducks have reduced variation in lamellar spacing relative to dabbling ducks, suggesting that they partition prey along a different axis (e.g. prey type, feeding behavior) than do dabbling ducks. In this study, tiger salamander prey types and prey sizes were found to overlap more with dabbling ducks than with diving ducks, suggesting that in prairie potholes, tiger salamanders foraged more in habitats common to dabbling ducks, such as planktonic and inshore habitats rather than in benthic habitats typically associated with diving ducks.

Nudds and Bowlby (1984) and Nudds and Prescott (unpublished manuscript) ranked dabbling duck species and diving duck species, respectively, from generalist to specialist according to log-likelihood ratios (*G* statistics) of each duck species' prey size distribution compared to ambient invertebrate size distribution. By converting prey size overlap between tiger salamanders and each duck species from cumulative frequency distributions created in this study to log-likelihood distributions, these two indices can be compared (Table 2.6). The prey size overlap rankings of the five dabbling duck species common to both studies are almost the same, with only Blue-winged teal and Mallard

Table 2.6. Comparison of prey size overlap between tiger salamanders and ducks in this study and between ducks and ambient size distributions reported in Nudds and Bowlby (1984) and Nudds and Prescott (unpublished manuscript). Values are *G*-statistics and, in parentheses, ranks are listed according to foraging tactic (1 = "generalist"; 5 = "specialist") with respect to either tiger salamander prey size or ambient invertebrate size distributions.

A. Dabbling ducks

	This study	Nudds and Bowlby
Gadwall	21.1 (1)	30.0 (1)
Mallard	106.9 (2)	95.7 (3)
Blue-winged	114.2 (3)	46.1 (2)
Pintail	115.2 (4)	167.9 (4)
Shoveler	130.7 (5)	289.8 (5)

B. Diving ducks

	This study	Nudds and Prescott
Ruddy	129.0 (1)	251.6 (4)
Canvasback	159.8 (2)	46.4 (2)
Scaup	163.0 (3)	245.2 (3)
Redhead	195.1 (4)	12.6 (1)
Ring-necked	275.8 (5)	372.2 (5)

reversed between ranks two and three. Because tiger salamander diets are more similar to dabbling duck species, it can be inferred that tiger salamanders are not as selective on prey size as previously suggested (Olenick and Gee 1981, Deustschman 1984). In contrast, there is less similarity between diving duck prey size overlap rankings in this study and those reported in Nudds and Prescott (unpublished manuscript), as ranks one and four, Redhead and Ruddy, respectively, are reversed. This is largely because prey size consumption by 4 of the 5 diving duck species fell mainly into size classes 3 (7.6-12.5 mm) and 4 (12.6-20.0 mm); Lesser scaup being the exception. Prey size consumption of tiger salamanders, on the other hand, fell mainly into size classes 1 (0-2.5 mm), 2 (2.6-7.5 mm) and 4 (12.6-20 mm). Reduced invertebrate length variability is characteristic of benthic and planktonic habitats relative to vegetated, littoral habitats (Mittlebach 1981; Armstrong and Nudds 1985). This pattern is also consistent with early theory on diving duck feeding behavior, which purported that, among species pairs, selection for different foraging sites within a pothole was important in segregating those species with the greatest dietary overlap (Siegfried 1976). In other words, for diving ducks, space was more easily partitioned than food.

Much of the difference between the dabbling and diving duck diets is attributable to variation in prey type rankings and proportions of large prey (Gastropoda, Amphipoda and Hemiptera) and zooplankton (Cladocera, Copepoda and Ostracoda) in the dabbling ducks compared to the high ranks of Diptera and Trichoptera in the diving ducks. Trichoptera differed most between tiger salamanders and all groups of duck species but their contribution to tiger salamander diets was very small (~0.5%). Dabbling ducks were more similar to tiger salamanders in that they also had high proportions of Gastropoda in their diets, but unlike tiger salamanders and dabbling ducks, tiger salamander and diving duck densities were positively correlated among potholes. Across the surveyed potholes there were three times as many dabbling ducks observed as diving ducks, suggesting that, numerically, the probability of an interaction occurring with dabbling ducks was also much greater.

These results appear contradictory in light of the fact that salamanders and diving ducks are usually assumed to share foraging habitats (i.e. benthic). However, habitat overlap between these animals is likely for several reasons. First, shallow planktonic and inshore habitats may cover a larger area than benthic habitats resulting in greater invertebrate availability. Saucer-shaped semi-permanent potholes common to the Prairie Pothole Region often have a maximum depth of less than 1 m, resulting in a wide, shallow littoral zone that is accessible to dabbling ducks. Ambient invertebrate size distributions are wider within the littoral zone of aquatic habitats than the benthic zone (Mittlebach 1981), which is consistent with the breadth of prey size that both tiger salamanders and dabbling ducks consume. Second, tiger salamanders and dabbling ducks may forage within the same habitat, but at different times of the day. For instance, to possibly avoid avian predation (Wiedenheft 1983, Euliss et al. 1999), tiger salamanders may move into the more protected, vegetated, areas during the day to feed on large macroinvertebrates and only forage in the potentially more exposed, planktonic, areas at night (Anderson and Graham 1967, Branch and Altig 1981, McWilliams and Bachmann 1989). Dabbling duck peak foraging typically occurs in the morning, coincident with diurnal chironomid emergence (Sjöberg and Danell 1982, but see Swanson and Sargeant 1972). Third, we cannot rule out direct interference between tiger salamanders and diving ducks in deeper, benthic habitats. Though tiger salamander and duck densities were correlated among potholes, interference competition may maintain partitioned foraging habitats.

The potential for competition exists between tiger salamanders and ducks for prey resources, as both consumers co-occur across prairie potholes and have varying degrees of dietary overlap. Testing the hypothesis that competitive interactions structure tiger salamander and duck populations requires further investigation involving manipulative experiments with unequivocal response variables (i.e. survivorship, growth rates). Also, considering that the estimated mean annual production of larval tiger salamanders (48-564 kg ha^{-1}, Deutschman and Peterka 1988) approximates that of fathead minnows (73-249 kg ha^{-1}, Duffy 1998) and stocked rainbow trout (0-313 kg ha^{-1}, Lawler et al. 1974), it is reasonable to predict comparable effects of indirect interactions between tiger salamanders and waterfowl as have been reported between fish and waterfowl.

CHAPTER 3

Exclosure experiments reveal trophic control of prairie potholes by waterfowl and compensatory predation by tiger salamanders

Introduction

A primary goal of ecology is to understand and predict the determinants of community structure. Through the use of conceptual dichotomies, communities have often been characterized as shaped by competition or predation, top-down or bottom-up forces, and abiotic or biotic factors, among others. Although these dichotomies are convenient, they belie the fact that multiple processes probably affect most communities. Thus, research that simultaneously considers multiple factors is likely to provide a more realistic account of what determines community structure (Osenberg and Mittelbach 1996, Batzer 1998).

Such an approach has only recently made its way into investigations of community structure in prairie wetlands (or "potholes"). The tacit assumption in the literature is that waterfowl are simply consumers of seasonally abundant resources during the breeding season (Krapu and Reinecke 1992). A corollary to this is that competition during the wintering season regulates annual waterfowl population dynamics (DuBowy 1988, Owen and Black 1990). However, over the past 20 years evidence has been mounting that during the breeding season waterfowl assemblages may be, at least partly, affected by intraspecific and interspecific competitive interactions (reviewed in Nudds 1992). Furthermore, the hypothesis that predators of waterfowl (i.e. avian, mammalian, human) are responsible for observed patterns in duck nest success and, hence, population dynamics, has recently been challenged. A literature review by Beauchamp et al. (1996a, 1996b) revealed that a decline in nest success among prairie-nesting ducks between 1935 and 1992 existed independent of predator control initiatives, suggesting that other factors were relatively more important in explaining year-to-year variation in duck populations. Such a factor might be resource limitation (i.e. food limitation) during the wintering season, but an exclosure study by Smith et al. (1986), for example, found that invertebrate densities were similar regardless of the presence or absence of waterfowl. These studies are instructive in that they question specific hypotheses purported to explain variation in waterfowl distribution and abundance. They also point towards resource limitation during the breeding season as an alternate hypothesis worthy of attention. To date, relevant experimental studies during the breeding season have yielded equivocal results (Wrubleski 1989, Barnes and Nudds in Nudds 1992).

Trophodynamic theory (*sensu* Oksanen et al. 1981) provides a useful framework for addressing questions of resource limitation. It accepts that predators and resources can simultaneously affect abundance (or biomass, etc.) at a particular trophic level. If a trophic level is relatively more resource limited than predator limited, then in the absence of predators, that trophic level should remain unchanged. Although this approach has been applied to a number of disparate communities, including temperate lakes (Carpenter and Kitchell 1993), the rocky intertidal zone (Menge and Sutherland 1987, Wootton 1992, Hamilton 2000) and rivers (Bowlby and Roff 1986, Power et al. 1985), few studies on prairie wetlands have adopted it (Arruda 1979, Spencer and King 1984, Zimmer et al. 2001) and even fewer have explicitly considered birds (but see Hanson and Butler 1994).

Perhaps one of the reasons why broad integrative models have not been applied to prairie potholes is the apparent cleavage between traditions of researchers interested in processes that exclusively involve wetland hydrology, biogeochemistry and vegetation, and those interested in processes that exclusively involve higher order consumer interactions between waterfowl, their mammalian predators and their potential competitors (e.g. fish).

Waterfowl and their predators are not the only vertebrate predators that interact in pothole food webs. Depending on regional climatic and local hydrologic conditions, planktivorous fish and/or tiger salamanders can also occupy prairie potholes. As a consequence of baitfish harvesting and fish-farming industries, the effects of fathead minnow on wetland invertebrates have been relatively well studied. Generally, densities of fathead minnow or stocked rainbow trout are inversely related to aquatic invertebrate production, biomass and diversity (Hanson and Riggs 1995, Zimmer et al. 2000, 2001a). Similarly, the presence of tiger salamanders in prairie potholes has also been shown to decrease the abundance of aquatic invertebrates (Chapter 1). Thus, predation appears to be an important factor structuring pothole communities. Aquatic vertebrate predators, like fathead minnow and tiger salamanders, may have a competitive advantage over waterfowl (Bouffard and Hanson 1997), suggesting that direct predator-prey interactions between vertebrates and invertebrates in prairie potholes may be complicated by indirect interactions between waterfowl and other vertebrate consumers. Across a wide variety of aquatic habitats, resident fish populations have been shown to the composition of waterfowl assemblages and to vary inversely with densities of breeding pairs (Eadie and Keast 1982, Winfield et al. 1990, Mallory et al. 1994). Under experimental circumstances, fish populations have also been shown to reduce duckling survivorship and growth rates (Hunter et al. 1986, Hill et al. 1987, Cox et al. 1998). It is unclear, however, if waterfowl similarly affect pothole community structure and whether waterfowl predation itself is at all mitigated by the presence of other aquatic consumers. Most studies on the effects of waterfowl on shallow lakes and wetlands have been concerned with the importation of nutrients and resultant effects on water quality (Manny et al. 1994, Pettigrew et al. 1999) or the increases in turbidity as a result of herbivory on rooted plants (Wrubleski 1989, Lodge 1991).

Though the influence of birds on prairie pothole food webs has possibly been under appreciated, a growing body of evidence from other aquatic ecosystems indicates that they can have substantial effects on prey resources. Reduction in invertebrate abundance or biomass has been associated with eared grebes (Cooper et al. 1984), red phalaropes (Dodson and Egger 1980), shorebirds (Quammen 1984), gulls and oystercatchers (Marsh 1986, Wootton 1992), common eiders (Hamilton 2000) and assemblages of waterfowl (Brönmark 1988). There are several reasons why waterfowl, including dabbling and diving ducks, American coots and grebes, in prairie environments may yield comparable effects. First, although bird numbers may appear to be relatively small relative to other aquatic consumers in prairie potholes, per unit biomass, endothermic waterfowl have a relatively higher metabolic rate than fish or salamanders. Second, waterfowl tend to augment primarily herbivorous diets during the wintering season with greater quantities of proteinaceous invertebrates during the breeding season (Krapu and Reinecke 1992). Third, waterfowl are relatively mobile compared to other vertebrate predators in prairie potholes so they can frequent multiple potholes. Fourth, waterfowl comprise a diverse group of consumers that, through a combination of ecomorphological traits (i.e. lamellar spacing, neck length, body size, etc.) and habitat preferences (i.e. vegetated, nonvegetated, benthic, planktonic, etc.), can potentially exploit most prey resources in prairie potholes.

Predictions derived from trophodynamic theory are readily amenable to experimentation, provided that adequate replication and appropriate controls are in place. A "press" perturbation is defined as a sustained alteration of species densities or a complete elimination of a particular species (Bender et al. 1984). In the context of testing for the influence of waterfowl predation on prairie pothole communities, the removal of waterfowl constitutes a press perturbation. While so-called "pulse" experiments reveal information only on direct interactions within food webs, "press" experiments yield information on direct interactions mixed with indirect interactions mediated through other species in the community (Bender et al. 1984). If waterfowl are excluded from portions of prairie potholes, then all consumers of ducks, grebes and coots are also excluded. The focus of this study therefore is on the influence of waterfowl on pothole trophic structure.

To assess the relationships between waterfowl and prairie pothole trophic structure, large waterfowl exclosures were constructed in a series of potholes over two years. The objectives of this research were to: 1) examine changes in aquatic invertebrate populations and phytoplankton standing crop according to the presence or absence of waterfowl predation, 2) assess if any observed relationships vary over time within the breeding season, and 3) determine if interactions between waterfowl and other vertebrate consumers, namely tiger salamanders, mitigate responses to the exclusion of waterfowl.

Methods

Study area

Field experiments were conducted southeast of Minnedosa, Manitoba, Canada (50°16′ N, 99°50′ W), in the Prairie Pothole Region (PPR), from early May until late July in 1998 and 1999. One of the key defining features of this landscape is the mosaic of agricultural activities and shallow surface waters. Prairie potholes are the result of Pleistocene glacial advance and retreat. Specifically, this study area was located in the Aspen Parkland Continental Prairie Wetland Subregion (National Wetlands Working Group 1988), formerly dominated by tallgrass and mixed-grass prairie. 40% of this geomorphological subregion consists of ground or hummocky moraines and it is in this particular area that pothole densities range from approximately 20 to 30 per square kilometre (National Wetlands Working Group 1988), depending on how wetlands are precisely defined. Another key defining feature of this landscape is the variable climate. The PPR is considered to be semi-arid. Temperature extremes range from -40°C to +40°C and, on average, half of the annual precipitation (~250 mm) falls from April through July (National Wetlands Working Group 1988). The climate is also characterized by high winds that greatly increase evaporation during the warm summer months.

The interaction between climate and hydrology results in a distribution of potholes that ranges from seasonal to permanent. Annual fluctuations in water depth are linked to climate-induced 10- to 20-year wet-dry cycles (Kantrud et al. 1989). Within years, water levels typically decrease during the ice-free season in potholes reflecting the important contribution of spring snowmelt runoff and precipitation to annual water budgets. 1998 and 1999 are considered to be "wet" years in that they were preceded and succeeded by "dry" years (National Climate Data Center 2002). Accordingly, most of the potholes tended to be semi-permanent and all were close to maximum area and depth. Unless engineered for drainage or irrigation, potholes are generally autonomous, except during periods of high runoff when channeling can temporarily connect those in close proximity. Limited topographic relief, characteristic of the area, also contributes to pothole autonomy since most have a very low drainage basin to surface area ratio. External loading into potholes, therefore, is typically a function of adjacent land uses. Also, semi-permanent potholes in the less arid parts of the PPR, such as southwestern Manitoba, tend to have low dissolved solid concentrations (i.e. 800 - 8 000 µS/cm, LaBaugh 1989).

Vegetation dynamics are superimposed on the interaction between climatic history and annual water level variation in prairie potholes. Emergent and submergent vegetation stands are highly productive and most potholes are also highly heterogeneous. Although macrophytes tend to have the highest biomass of any primary producer in prairie potholes, they experience little direct herbivory (Wrubleski and Detenbeck in Euliss et al. 1999). Potholes also experience dramatic metaphytic blooms of filamentous algae, but it too is largely inedible (Goldsborough and Robinson 1996). Instead, prairie pothole food webs are usually based on benthic, epiphytic and planktonic algae (Murkin 1989, Neill and Cornwell 1992, Wrubleski and Detenbeck in Euliss et al. 1999). While these primary producers may have low standing crop at any given time, they exhibit high turnover rates that may result in significant annual production (Murkin 1989, Shamess et al. 1985).

Relatively little is known about herbivory in prairie potholes and even less about detritivory. Generally, the overall diversity of aquatic invertebrates in prairie potholes relative to other aquatic ecosystems is low because the harsh environmental conditions of the PPR are thought to select for ecological generalists (Euliss et al. 1999). Within the existing assemblage of invertebrates, however, are representatives from all functional feeding groups, including shredders, collectors-filters, scrapers and predators (Murkin and Ross 2000). Regardless of aquatic invertebrate diversity, one of the reasons why waterfowl are attracted to the PPR is high aquatic invertebrate availability and production. Unlike the invertebrates, the waterfowl assemblage is relatively diverse in the PPR. The PPR is home to an estimated 50-75% of all of North America's breeding waterfowl (Batt et al. 1989) and the densities of waterfowl in the immediate area of this study are estimated to be among the highest. Seven species of dabbling duck and five species of diving duck are common to the study area. Dabbling ducks tend to forage and nest in all types of potholes whereas diving ducks are more restricted to deeper, more permanent, potholes (Nudds 1983). In addition, American coot (*Fulica americana*), Horned grebe (*Podiceps auritus*) and Pied-billed grebe (*Podilymbus podiceps*) are also commonly encountered in prairie potholes. For the purposes of this study, all ducks, grebes and coot are simply described as waterfowl.

Among the other vertebrate consumers present in the PPR, fish (i.e. fathead minnow *Pimephales promelas* and brook stickleback *Culaea inconstans*), do not widely inhabit prairie potholes in this study area. Summerkill and winterkill, due to very low dissolved oxygen concentrations, and summertime evaporation and wintertime freeze-up, likely causes local extirpations of resident fish populations. This apparent void appears to have been, to some extent, assumed by tiger salamanders (*Ambystoma tigrinum*), that, in many respects, appear to be the functional equivalents of planktivorous fishes (Chapter 1, Zaret 1980). Several frog species also make use of prairie potholes for breeding and large numbers of tadpoles are occasionally observed in the spring.

Finally, mammals and raptors and some other birds are usually the top predators in prairie pothole food webs. Coyote and red fox occasionally consume adult waterfowl, but most of the mortality is due to depredation of clutches of eggs and consumption of prefledged young by other mammals, such as raccoon, striped skunk and mink, and birds, such as hawks, owls, crows and magpies (Sargeant and Raveling 1992).

A summary of the invertebrate and vertebrate consumers encountered in this study is provided in Appendix 1.

Waterfowl exclosures

24 potholes in 1998 and 21 potholes in 1999 were randomly selected from a subset of available potholes. The subset included all semi-permanent potholes that were not connected to any other potholes during spring run-off. The study area (1980 Forest Inventory maps TWP 14 RGE 17 W and TWP 13 RGE 17 W) covered 24 square miles. In 1998 and 1999, approximately 50 semi-permanent potholes occurred per square mile resulting in an average of one study pothole per square mile or 2% of all available potholes. Twelve potholes were common to both 1998 and 1999.

For both years, one 5.5 m × 11 m exclosure was randomly placed along the perimeter of each pothole (Fig. 3.1, 3.2a). For the twelve potholes common to both years, exclosures were dismantled in August 1998 and reconstructed in May of 1999 (but not necessarily in the exact previous location). Exclosures were framed with

Figure 3.1. Diagram of an idealized prairie pothole with exclosure infrastructure. In the detailed exclosure diagram at the bottom of the page, the smaller rectangles within the exclosure and control zones indicates where invertebrate and phytoplankton sampling should be unaffected by fence effects.

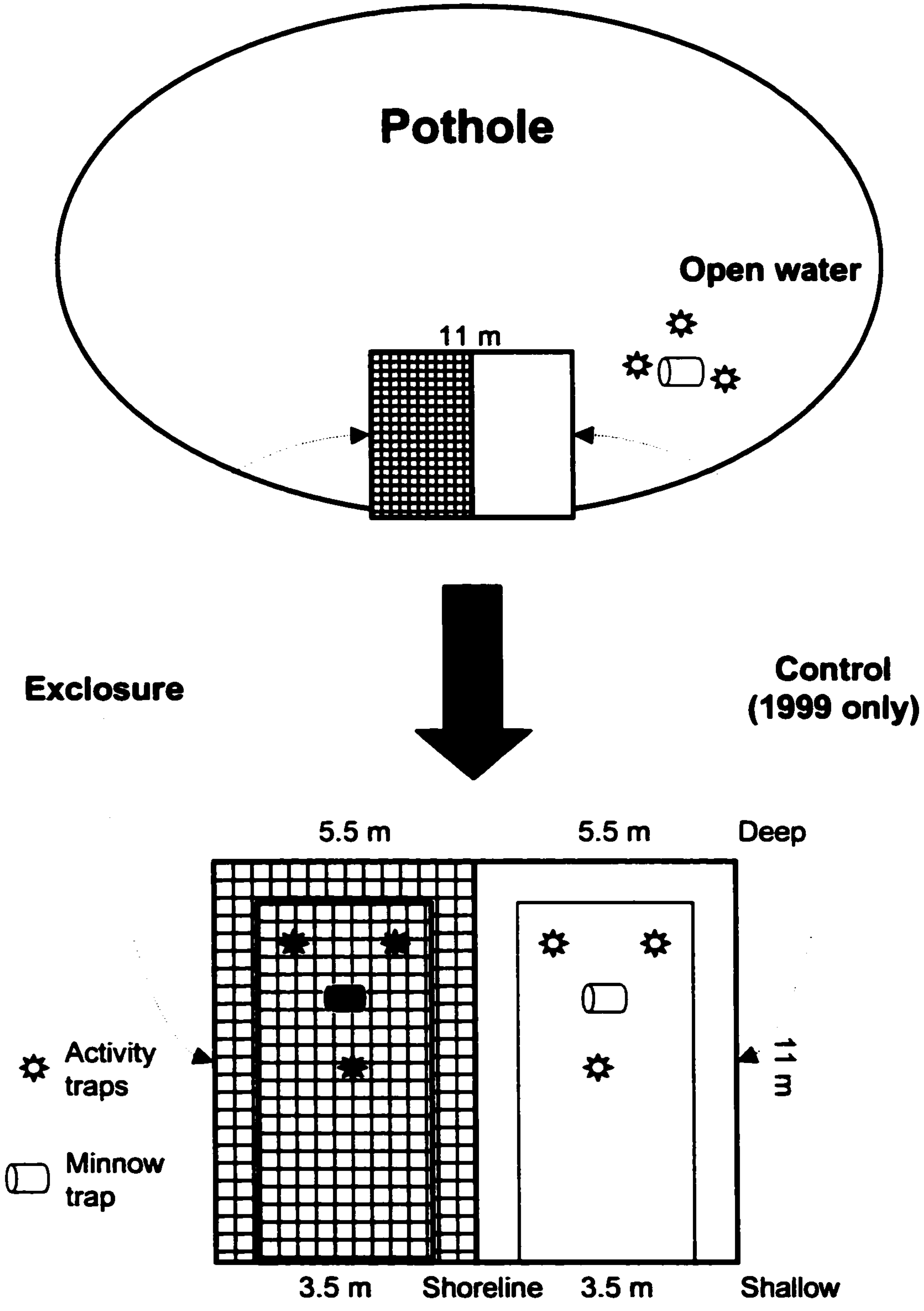
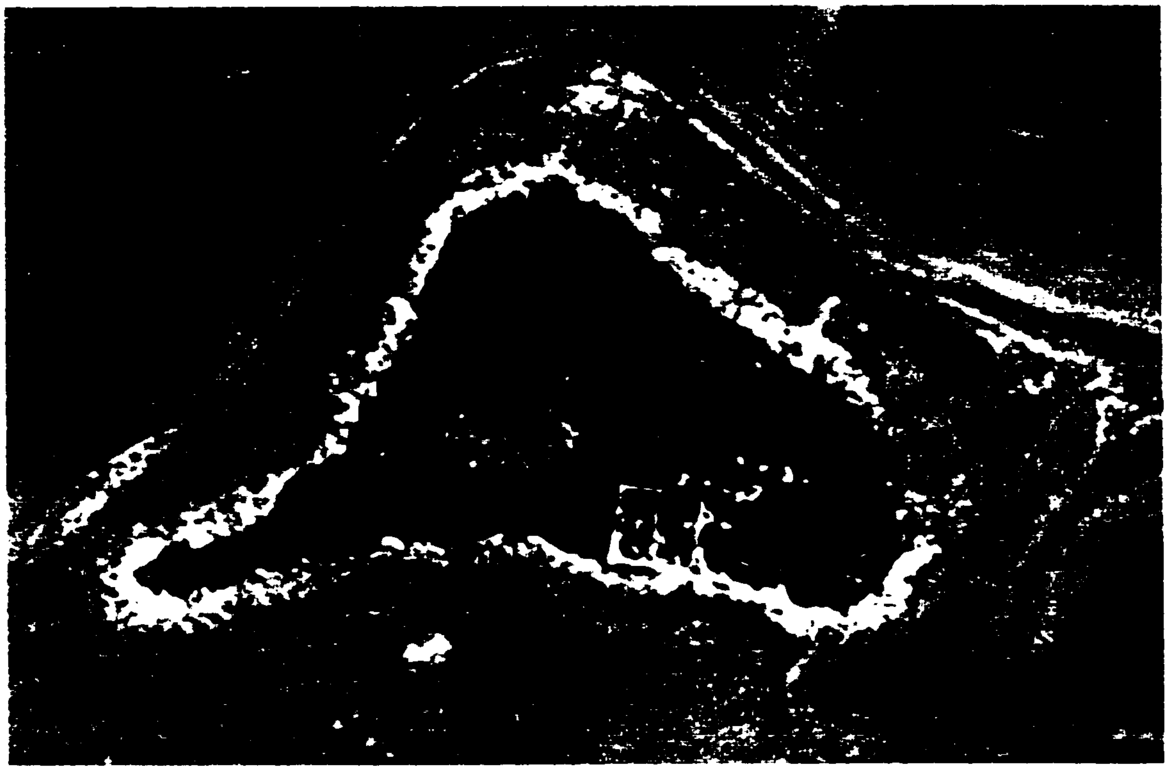

Pothole
Open water
11 m
Exclosure
Control
(1999 only)
5.5 m
5.5 m
Deep
Activity traps
Minnow trap
11 m
3.5 m
Shoreline
3.5 m
Shallow

Figure 3.2. Aerial (a) and landscape (b) photographs of an exclosure.

a)



b)

5 cm × 5 cm wood beams and positioned within each pothole using wood stakes pounded into the sediment (Fig. 3.1, 3.2b). The frames floated and were not attached to the stakes, only guided, so as to adjust to water level fluctuations. At the beginning of each year for all potholes, the inner edge of the exclosure (i.e. towards the middle of the pothole) was never in water shallower than 0.5 m and the outer edge (i.e. towards the emergent vegetation surrounding the pothole) was never in water deeper than 0.5 m. Most exclosures, therefore, traversed a depth gradient that spanned more littoral, vegetated habitats to more planktonic, open water habitats. By the end of each field season, several potholes developed extensive beds of submergent vegetation but the distribution of the vegetation was similar among zones within each pothole.

Exclosures were constructed to prevent waterfowl occupation and foraging activities. 5 cm × 5 cm polypropylene netting (Aquatic Eco-Systems Inc., Apopka, Florida) was suspended across each exclosure and fastened to the frame. To prevent sagging within the exclosure area, additional stakes were used to support the netting. Polyethylene plastic sheeting was fastened to three sides of the exclosure and it was draped to the sediment-water interface. Sheeting was weighted with lead line excised from freshwater gill nets and taped to the bottom. Approximately 20 cm of extra sheeting was allowed to sag on the bottom in case of water level fluctuations. Considering that nearly all potholes were close to maximum depth, it was assumed that only under exceptional circumstances would water levels increase more than 20 cm. The fourth side of the exclosure, along the outer edge (i.e. shallower end of the exclosure), was left open primarily for one reason: Tiger salamanders were initially, on occasion, seen inside the exclosures. Tiger salamanders were not originally intended as a treatment effect for this experiment and there was a concern that they might perish and decompose within the confined space, potentially confounding the outcomes. The outer edges for all exclosures were butted up against thick emergent vegetation or in shallow water (0.5 cm) so although tiger salamanders were able to enter and exit exclosures, invertebrates and algae were largely unaffected by the open edge. Periodic heavy rains and high winds meant that the experimental infrastructure had to be regularly checked and sometimes repaired. Over the course of the field experiments, potholes were observed or visited at least twice weekly and only four birds were ever found inside the exclosures (one Green-winged teal and three Ruddy ducks) over the two years of the study across all potholes.

In 1999 only, paired controls were constructed adjacent to each exclosure (Fig. 3.1). Controls were identical to the exclosures in every respect except that they lacked suspended netting. Although the size of the exclosures, 60.5 m^2, was large enough to minimize specific "edge effects" (Stephenson et al. 1984), it was considered prudent to determine if broader "cage effects" might be a complicating factor in the experimental design relative to ambient, non-experimental conditions. In a subset of potholes observed in 1998, waterfowl proportionately occupied and foraged in control areas relative to total pothole areas (Appendix 4). Thus, the controls were deemed to be relevant to the exclosures with respect to the hypothesized waterfowl treatment effect.

Field and laboratory protocols

Potholes were sampled and surveyed once every seven to ten days on nine occasions, beginning in mid-May and ending in late July. This 10-12 week period bracketed the earliest opportunity to initiate field experiments after ice-out until the time most waterfowl had completed breeding. Because of heavy rainfall during late June

1998, 14 potholes could not be visited on one occasion. In 1998, there were two sample zones (exclosure and open water) and in 1999 there were three zones (exclosure, control and open water). To avoid disturbance of sediments and emergent and submergent vegetation, all sampling activities in potholes were carried out from a canoe.

A cluster of three activity traps and one minnow trap were randomly located in each experimental zone. Activity traps, or funnel traps, followed the design of Murkin et al. (1983); 3.8-l glass jars were positioned approximately 30 cm below the surface of the water. Activity traps inside the exclosures were suspended on ropes while activity traps in the control and open water areas were hung from posts pounded into the sediment. Compared to other passive wetland invertebrate sampling devices (e.g. artificial substrates), activity traps are very effective at collecting planktonic invertebrates (Brinkman and Duffy 1996), though they are biased against benthic invertebrate (Turner and Trexler 1997). The standard-sized aluminum minnow trap used in each experimental zone was tossed into the area within the three activity traps. Both activity and minnow traps are passive sampling devices in that the traps are set one day and retrieved 24 hours later. Activity traps were intended to sample invertebrates and minnow traps were intended to sample tadpoles and tiger salamanders, however, both invertebrates and vertebrates were collected in both types of trap. Analyses of usage of activity traps in Fennoscandian lakes indicated that the presence of invertebrate predators (e.g. Coleoptera, Odonata, etc.) in traps did not affect the overall composition and abundance of catches and the presence of vertebrates (i.e. fish and amphibians) reduced taxonomic diversity but not abundance (Elmberg et al. 1992).

Upon retrieval, large macroinvertebrates were manually removed from the activity and minnow traps and transferred to large 100-ml vials. Dead tadpoles and tiger salamanders were also transferred to large vials or, when necessary, to freezer bags, while live amphibians were identified, measured for length and released back into the pothole. Dead amphibians were immediately frozen for subsequent gut contents and tissue analysis. The rest of the activity trap sample was emptied into a modified 180-µm zooplankton net fitted with a 20-ml scintillation vial. At the end of each field sampling day, amphibians and invertebrates were preserved in ~70% ethanol. Before processing, scintillation vial samples were size-fractionated with a 1-mm mesh sieve. Thus, especially small microinvertebrates, such as Rotifera, Bosminidae and other small Cladocera and Copepoda, were not included in the composition of the invertebrates. Most invertebrate taxa were identified, counted and measured to the nearest 0.1 mm using a compound microscope fitted with a graduated platform. Dry weight biomass for each organism was calculated using published length-weight regressions as in Chapter 2 (pulmonate snails, Mackie and Flippance 1983; amphipods, Panov and McQueen 1998; aquatic insects, Smock 1980; leeches, Collins 1992). The remaining invertebrates were only identified and counted and included Cladocera, Copepoda, Ostracoda, Conchostraca and Hydracarina (water mites). All organisms were identified to family or genus using Preston (1982), Pennak (1989), Thorp and Covich (1991) and Merritt and Cummins (1996). For convenience, the assemblage of larger invertebrates is hereafter referred to as macroinvertebrates and the assemblage of zooplankton, zoobenthos and water mites is hereafter referred to as microcrustaceans.

At the same time as the activity and minnow traps were being retrieved, three 500-ml water samples were collected from each of the experimental zones at a depth of 20 to 30 cm. Due to mixing following wind events and the variable distribution of submergent vegetation among potholes, planktonic water samples likely partly comprised of resuspended benthic algae and unattached epiphytic algae. Samples were immediately stored in a cooler and prepared for subsequent analysis on the same day. Using a vacuum hand-pump, water samples were filtered through 47-mm Gelman AE filters (1.0-µm porosity). Filters were then wrapped in aluminum foil and stored in a freezer. Before analysis, filters were digested in 95% ethanol and refrigerated for at least 12 hours. After centrifuging, the supernatant was decanted into quartz cuvettes and analyzed with a spectrophotometer (Hewlett Packard 8452A). Estimates of chlorophyll *a* concentration are surrogate measures of phytoplankton standing crop (LaBaugh 1995, Bergman and Peters 1980). Phytoplankton standing crop was considered a response variable with respect to the experimental treatments rather than an indicator of baseline pothole fertility, which might also affect food web structure, for several reasons. First, turnover and reproductive rates of algae are very short (Goldsborough and Robinson 1994). Consequently phytoplankton populations respond relatively quickly to changes in water chemistry or changes within the planktonic herbivores. Second, planktonic chlorophyll *a* concentrations were generally low, indicating either extremely high phytoplankton turnover or simply low primary planktonic production (Robinson et al. 2000). Third, planktonic primary production is not reliably a good estimate of overall pothole primary production (Goldsborough and Robinson 1994).

Roughly corresponding to the sampling occasions, the waterfowl assemblage of each pothole was surveyed at some point between 06 00 h and 10 00 h. Potholes were surveyed, usually about 10 minutes, until I considered that most of the resident birds had been identified; full flush surveys were avoided because persistent flushes and visits might negatively affect the resident birds. All ducks, grebes and coots found at a pothole were recorded. Other bird species, such as American bittern and Great-blue heron, were observed very rarely so they were not included. As waterfowl broods appeared, young were also identified and tallied.

Maximum water depth was measured in the centre of each pothole at the beginning and end of each field season. Pothole area was estimated from aerial photographs taken towards the end of the field season with a planimeter, using exclosure dimensions as reference points. The composition and distribution of emergent and submergent vegetation was estimated from both aerial photographs and canoe-based vegetation mapping. The importance of these variables in explaining variation in invertebrate populations for the study potholes is provided in Chapter 1.

Statistical analyses

All analyses were performed using SAS version 8.01 (SAS Institute Inc., Cary, North Carolina). Univariate normality was assessed using the Shapiro-Wilk statistic W and homoscedasticity was assessed using Bartlett's test. Variables that violated assumptions of parametric tests were remedied by transformation ($\ln x + 1$). Statistical significance of results was set at $\alpha = 0.05$. Interactions between variables were noted when P 0.15, because, when statistical power is low, main effects are not always apparent unless interactions are considered (Winer et al. 1991). When interactions were detected, reduced models were analyzed separately for each level of one of the interacting variables to facilitate interpretation of main effects (Keppel 1982).

The statistical model underlying the primary analyses in this study was a randomized-block mixed-model analysis of variance (ANOVA) with two treatment (fixed) factors. Variables associated with the experiment included zone (the first fixed factor; exclosure, open water and, in 1999, control), and date (the other fixed factor; nine sampling occasions roughly corresponding to once every seven to ten days). Pothole, the random factor, was the unit of replication. The data were analyzed separately for each year using the following model:

$$X_{ijk} = \mu_k + E_{k(i)} + D_{k(j)} + ED_{k(ij)} + \varepsilon_{k(ij)} \tag{3.1}$$

where X_{ijk} represents each of the response variables of the kth pothole (n=24 in 1998, n=21 in 1999) in the ith treatment on the jth date. μ is the overall mean for each response variable. E refers to the exclosure zone (compared to either open water or control zone), D refers to the date (maximum of nine sampling periods between early May and late July), ED is the interaction term between zone and date, and ε is the error term. Table 3.1 lists specific error terms for testing statistical hypotheses in a mixed model, as residual error terms are inappropriate. This model is analogous to a two-factor repeated measures experiment where the treatment factors are typically referred to as the within-subjects factors (Zar 1996). The inclusion of a repeated factor (time) in the model necessitated also testing for the presence of compound symmetry. Mauchly's Criterion was used to test for this additional assumption (SAS PROC GLM, REPEATED statement).

Table 3.1. Effects tested in mixed model ANOVAs used in this chapter.

Effect	Analyzed by	Error term
Exclosure		Exclosure × Pothole
Date		Date × Pothole
Exclosure × Date		Exclosure × Date × Pothole
Exclosure	Date	Pothole

Notes: The use of a mixed model involving fixed and random factors precluded the use of residual error terms in testing specific statistical hypotheses. Error terms for particular tests are therefore indicated. When significant interactions occurred (P 0.15), data were analyzed separately for each level of the interacting variables.

Owing to attributes of the experimental design, the major analyses performed in this study were broken down in two ways, yielding four distinct groups of invertebrate response variables. First, years were kept separate because the exclosures constructed in 1999 included a paired control to test for cage effects whereas in 1998 they did not. Thus, in 1998, statistical analyses were performed comparing exclosure and open water zones and in 1999, the comparisons were between exclosure and control zones. Amphibian, invertebrate and water samples were also concurrently collected from the open water zone in 1999. Differences among zones in 1999 were compared to assess how well the control zones in the experiment mimicked the ambient pothole environmental conditions (SAS PROC GLM, CONTRAST statement). Second, macroinvertebrate and microcrustacean groups were kept separate because they were processed differently; mean lengths and biomasses were not calculated for the microcrustaceans.

This first set of analyses comprised combined datasets of all macroinvertebrates and microcrustaceans. Several dependent variables were used to describe the invertebrates, all expressed per sample per week. Quantitative measures included abundance (total number), mean length (mean invertebrate length along the longest dimension in mm) and biomass (total dry weight in g). Taxonomic descriptors included richness (total number of species), diversity (Shannon-Wiener index *H*) and evenness (Pielou's *J*). The only dependent variable used to describe the microcrustaceans was abundance. Finally, phytoplankton standing crop, also with the dimensions per sample per week, was also analyzed as a response variable.

Because taxonomic descriptors only described coarse patterns, a second set of analyses was carried out to assess more specific responses to the experimental treatments. Species-abundance relationships for aquatic invertebrates tend to exhibit lognormal distributions (Mittelbach 1981) and prairie potholes have relatively low overall invertebrate diversity (Euliss et al. 1999). Consequently, a few species tend to dominate pothole food webs. Seven taxonomic groups, describing >95% of the macroinvertebrates and five groups describing >99% of the microcrustaceans were analyzed separately for patterns of association with the exclosure treatment, date and the interaction therein.

Several other variables were also measured during the course of the study, but for logistical reasons, they were not sampled according to zone. Amphibians (tiger salamanders and tadpoles) and birds (ducks, grebes and coots) were sampled without consideration of experimental treatment; amphibians because they could relatively easily enter and exit the exclosure and control zones and birds because of the exclosures. To gauge the relationships between these covariates and the "effect size" of the waterfowl exclosures on pothole community structure, analyses of covariance (ANCOVA) were performed. Effect size, the response variable, was calculated as the simple difference between the exclosure zone and either the open water (1998) or control (1999) zone, averaged over the course of the study. For each effect size, the associated open water or control zone value was added as a covariate to the statistical model to adjust the magnitude of the effect size for each pothole. For these analyses, the following statistical model was used:

$$X_k = \mu_k + C_k + T_k + W_k + TW_k + \varepsilon_k \tag{3.2}$$

where X_k is the effect size for the selected response variables for each year. μ is the overall mean for each response variable. C refers to the covariate (open water zone in 1998 and control zone in 1999), T refers to tiger salamander abundance and W refers to waterfowl abundance, both continuous variables, TW is the interaction term between tiger salamanders and waterfowl, and ε_k is the error term. This ANCOVA approach to handling indices of effect sizes is superior to the use of either ratios or residuals primarily because error rates become unreliable when either of these other techniques are employed (Packard and Boardman 1988, Jackson et al. 1990, García-Berthou 2001). Effect sizes were then averaged over the entire sampling period and compared with average tiger salamander abundance and average waterfowl abundance.

Results

Waterfowl abundance and composition

A wide variety of waterfowl were observed on the study potholes during both years of the study. In 1998, a total of 1629 birds were counted across 24 potholes on nine surveys (15.1 birds/survey/pothole/ha). Dabbling ducks were the most commonly observed group of birds (50.2%; 7 spp.), followed by American coots (23.9%), diving ducks (18.2%; 5 spp.), grebes (6.8%; 2 spp.) and Canada geese (0.9%). Only two potholes on one surveying occasion were empty of waterfowl. Slightly fewer birds were observed in 1999, 1365 (14.4 birds/survey/pothole/ha). The most common group of birds observed were American coots (40.8%), followed by dabbling ducks (30.8%; 6 spp.), diving ducks (22.0%; 5 spp.) and grebes (6.4%; 2 spp.). No Canada geese were observed in 1999 and on nine surveys no birds were observed.

In 1998 the total number of birds observed ranged from 21.3 to 22.4 birds/pothole/ha for the first four surveys and dropped for the remaining five surveys ranging from 6.5 to 12.8 birds/pothole/ha (date effect: $F_{8,174} = 2.40$, $P = 0.018$). A reverse trend was observed in 1999 (Fig. 3.3). The number of birds observed ranged from 7.4 to 17.1 birds/pothole/ha during the first through eighth surveys and then sharply rose to 26.4 birds/pothole/ha, but it should be noted that the final survey in 1999 included a high number of American coot broods (date effect: $F_{8,174} = 3.45$, $P = 0.0010$).

Effects of waterfowl predation on pothole communities

Waterfowl exclusion generally altered macroinvertebrates and microcrustaceans in both 1998 and 1999 (Table 3.2). The inclusion of a paired control in 1999 did not result in qualitatively different results from those obtained in 1998, indicating that the exclosures were sufficiently large and that the environmental conditions that occurred in the exclosures approximated those of the surrounding open water areas. Macroinvertebrate abundance, biomass, richness and diversity were all elevated in the absence of waterfowl predation (Table 3.2a, b; Fig. 3.4a-l). The remaining microcrustacean variables were variously related to the exclosure treatment but they, too, were generally elevated in the absence of waterfowl (Table 3.2c; Fig. 3.4m, n). In contrast, phytoplankton standing crop exhibited the opposite pattern; chlorophyll concentrations tended to be higher in the control and open water zones relative to the exclosure zones (Table 3.2d; Fig. 3.4o, p).

Figure 3.3. Average number of waterfowl observed per pothole plotted by week. The number above each of the plots refers to the number of potholes that were surveyed during that sampling period (n=24 in 1998 and n=21 in 1999). Note that in late June 1998, only 10 potholes were sampled. Error bars are standard errors.

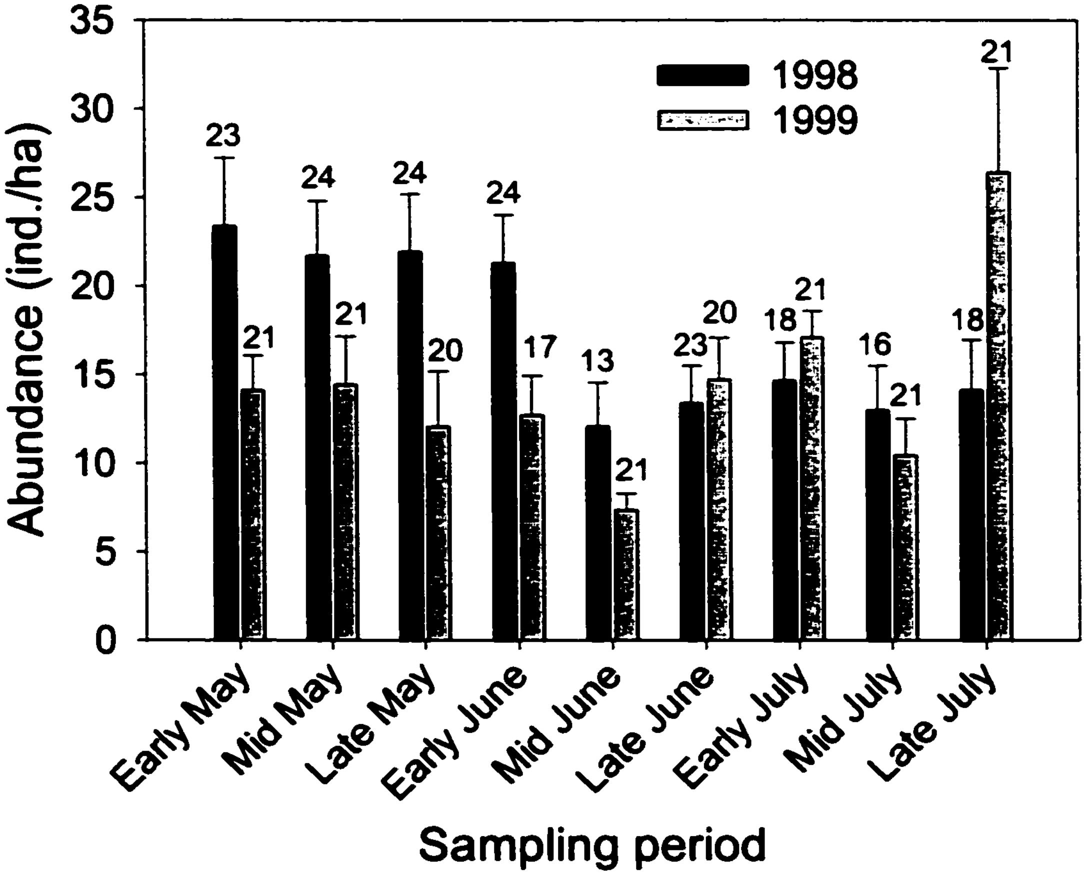

35
30
25
20
15
10
5
0
Abundance (ind./ha)
1998
1999
23
21
24
21
24
20
24
17
13
21
23
20
18
21
16
21
18
21
Early May
Mid May
Late May
Early June
Mid June
Late June
Early July
Mid July
Late July
Sampling period

Table 3.2. Results of ANOVAs for macroinvertebrate and microcrustacean response variables and phytoplankton standing crop. For 1998, "Exclosure" refers to comparisons between exclosure zones and open water zones and in 1999 it refers to comparisons between exclosure zones and control zones. Abundance and biomass were transformed ln ($x + 1$). For 1998, the degrees of freedom are as follows: Exclosure – 1, 23; Date – 8, 184; Exclosure × Date – 8, 184. For 1999, the degrees of freedom are as follows: Exclosure – 1, 20; Date – 8, 160; Exclosure × Date – 8, 160.

a) Coarse macroinvertebrate variables

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	23.10	<0.0001	9.87	0.0051	1.72	0.20	3.05	0.096	8.16	0.0089	5.56	0.029
Date	7.32	<0.0001	4.64	<0.0001	2.21	0.03	3.12	0.0027	6.18	<0.0001	7.95	<0.0001
Exclosure × Date	2.13	0.036	1.63	<0.0001	1.94	0.06	0.33	0.95	0.68	0.71	0.65	0.74

b) Taxonomic macroinvertebrate variables

	Richness				Diversity				Evenness			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	23.60	<0.0001	17.18	0.0005	21.35	0.0001	24.16	<0.0001	0.11	0.74	4.01	0.059
Date	12.14	<0.0001	10.54	<0.0001	8.19	<0.0001	7.91	<0.0001	4.49	<0.0001	1.20	0.30
Exclosure × Date	2.81	0.0060	1.71	0.10	1.64	0.12	1.95	0.056	2.36	0.020	0.94	0.48

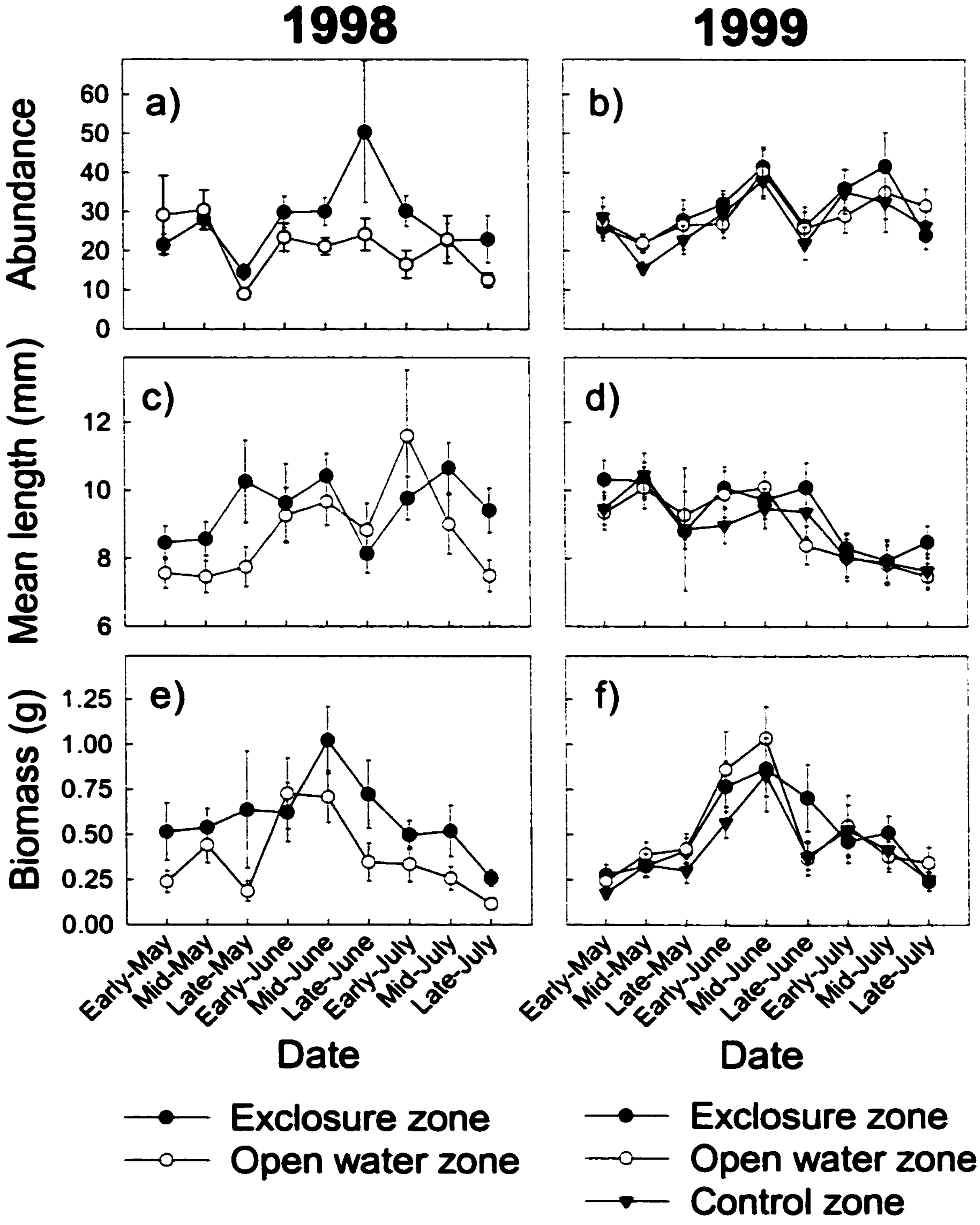
c) Microcrustaceans

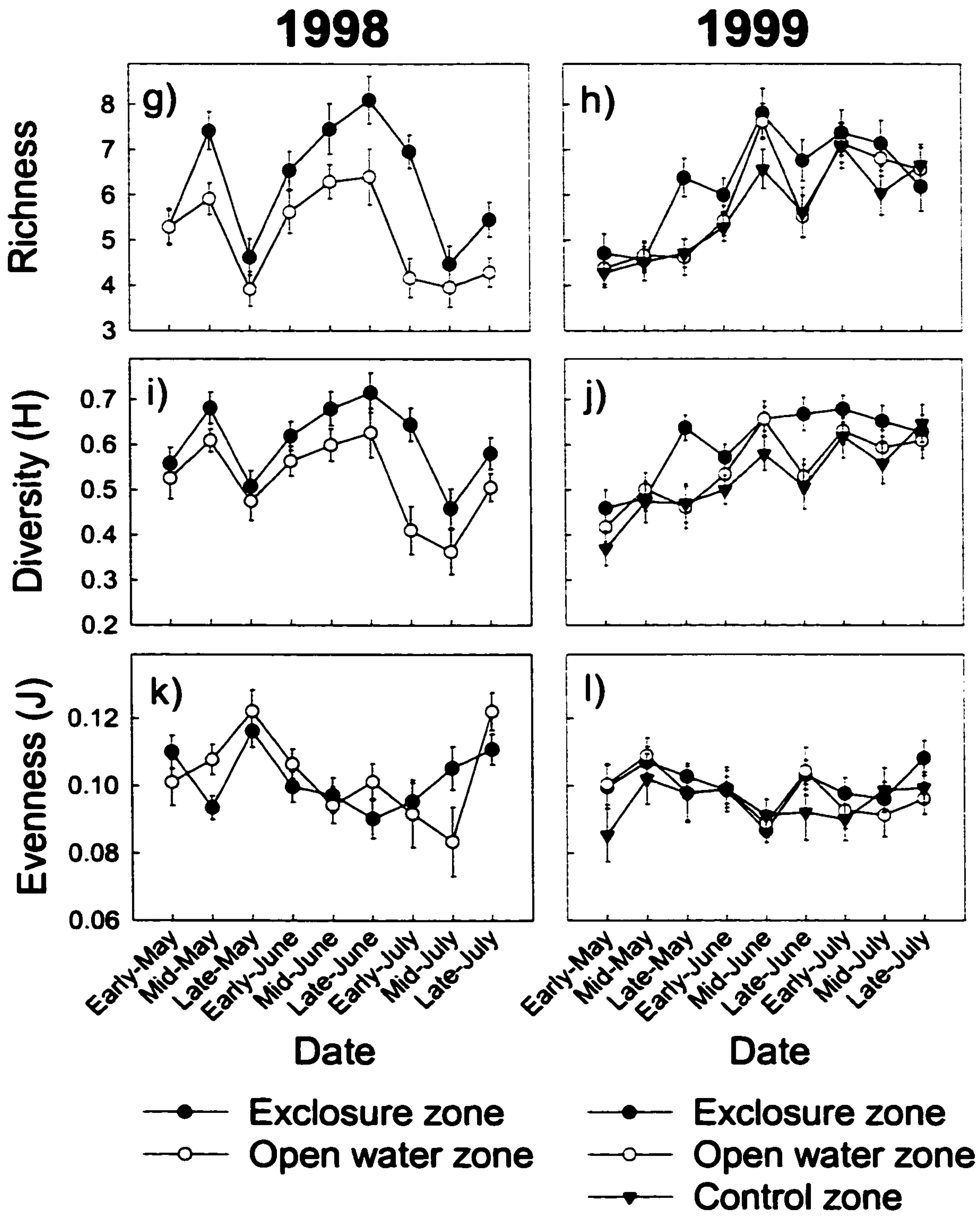
	Abundance			
	1998		1999	
	F	P	F	P
Exclosure	5.31	0.031	7.02	0.015
Date	13.75	<0.0001	9.52	<0.0001
Exclosure × Date	2.64	0.0096	0.53	0.83

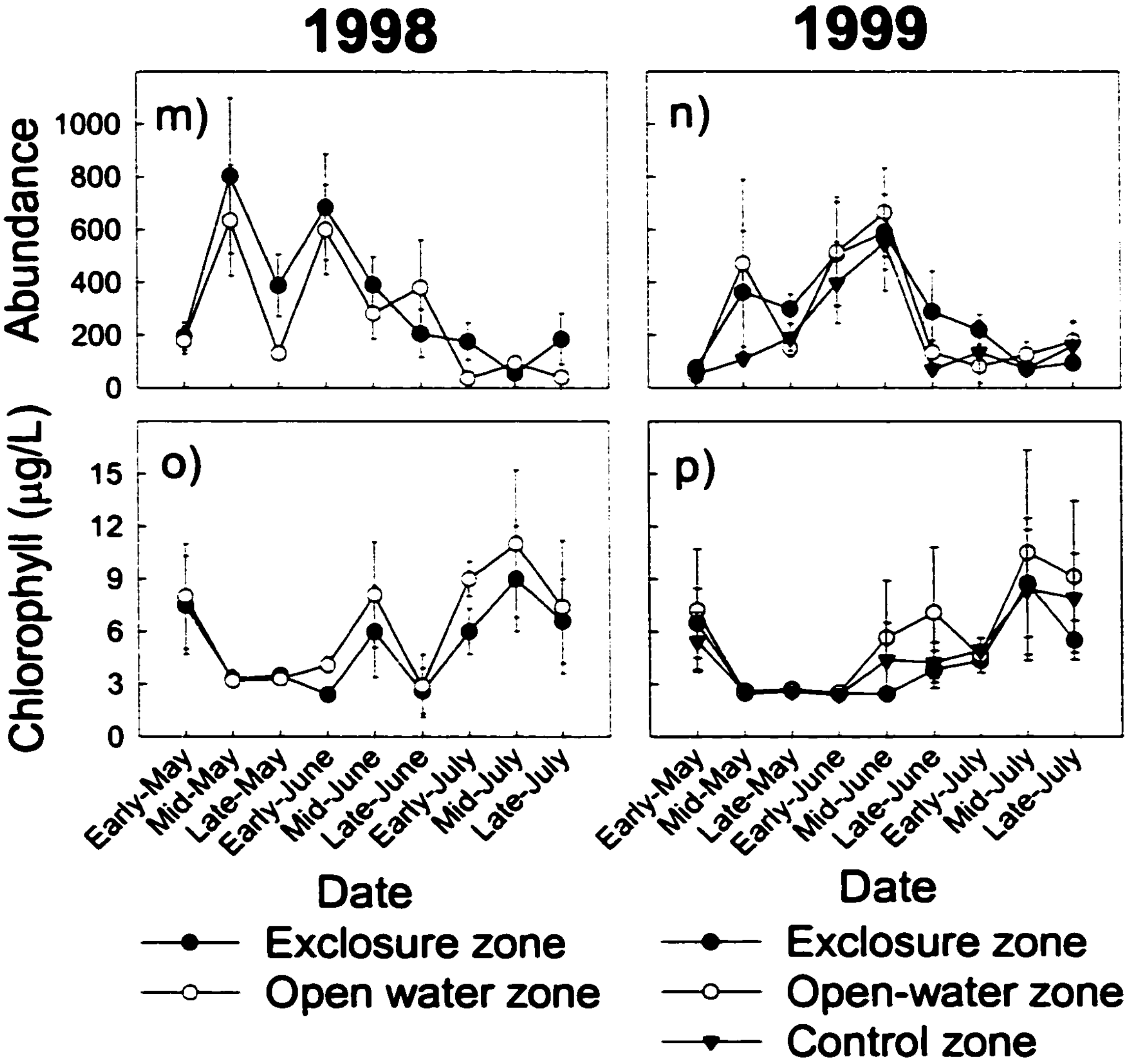
d) Phytoplankton standing crop

	Chlorophyll			
	1998		1999	
	F	P	F	P
Exclosure	4.04	0.052	2.68	0.12
Date	14.88	<0.0001	4.35	<0.0001
Exclosure × Date	0.97	0.44	1.18	0.31

Figure 3.4. Response variables plotted according to date and separated by year. Note that all three sampling zones are included in the 1999 plots. Error bars are ± 1 standard error. Panels a-l show the macroinvertebrate variables, panels m and n show the microcrustacean variables and panels o and p show phytoplankton standing crop.


1998
1999
a)
b)
c)
d)
e)
f)
Abundance
Mean length (mm)
Biomass (g)
0
10
20
30
40
50
60
6
8
10
12
0.00
0.25
0.50
0.75
1.00
1.25
Early-May
Mid-May
Late-May
Early-June
Mid-June
Late-June
Early-July
Mid-July
Late-July
Date
Date
Exclosure zone
Open water zone
Exclosure zone
Open water zone
Control zone


1998
1999
g)
h)
i)
j)
k)
l)
Richness
8
7
6
5
4
3
Diversity (H)
0.7
0.6
0.5
0.4
0.3
0.2
Evenness (J)
0.12
0.10
0.08
0.06
Early-May
Mid-May
Late-May
Early-June
Mid-June
Late-June
Early-July
Mid-July
Late-July
Date
Exclosure zone
Open water zone
Control zone


1998
1999
m)
n)
o)
p)
Abundance
Chlorophyll (µg/L)
0
200
400
600
800
1000
0
3
6
9
12
15
Early-May
Mid-May
Late-May
Early-June
Mid-June
Late-June
Early-July
Mid-July
Late-July
Date
Date
● Exclosure zone
○ Open water zone
● Exclosure zone
○ Open-water zone
▼ Control zone

To better assess the importance of the control zones in relation to the interpretation of the exclosure effects, contrasts, averaged over date, were performed between exclosure, control and open water zones for 1999. Among all contrasts, the greatest differences were observed between exclosure and control zones, followed by exclosure and open water zones and finally the least by control and open water zones (Table 3.3a-d). None of the comparisons between control and open water zones were significant (P 0.15), indicating that the exclosures adequately represented ambient pothole conditions. Across all response variables in 1999, the difference between exclosure and control zones was greater than the difference between exclosure and open water zones. Thus, 1998 results should be considered as conservative with respect to the impacts of waterfowl predation on pothole community structure during that year.

The similarity in results between macroinvertebrate abundance and biomass, but not mean length, indicates that size-selective predation by waterfowl consumers was not detected, if it even existed, for these species. Similarly, the consistent effects of waterfowl predation on macroinvertebrate species richness and diversity, but not evenness, indicates that consumption occurred relatively evenly across all prey taxa and that in the absence of waterfowl, a few, rare, taxa "emerged". Richness and diversity in 1998 and 1999 were all significantly affected by waterfowl exclusion, date and the interaction therein, but the effect on species evenness was equivocal. In the absence of waterfowl, additional species appeared (richness differed by approximately one species as a result of the exclosures) that increased diversity but not evenness (Fig. 3.3i-l). For both 1998 and 1999, the species that specifically tended to appear in the absence of

Table 3.3. Linear a prior contrasts by pothole (i.e. averaged over dates) between the three zones in 1999. EX = exclosure, CO = control, OW = open water. The degrees of freedom are 1, 23 for all the contrasts.

a) Coarse macroinvertebrate variables.

	Abundance		Mean length		Biomass	
	F	P	F	P	F	P
EX vs. CO	8.51	0.0058	3.23	0.080	4.70	0.036
EX vs. OW	2.86	0.098	2.79	0.10	3.76	0.060
CO vs. OW	1.50	0.23	0.002	0.90	0.05	0.82

b) Taxonomic macroinvertebrate variables.

	Richness		Diversity		Evenness	
	F	P	F	P	F	P
EX vs. CO	18.65	0.0001	32.42	<0.0001	3.93	0.054
EX vs. OW	8.68	0.0053	15.96	0.0003	0.86	0.36
CO vs. OW	1.88	0.18	2.88	0.098	1.11	0.30

c) Microcrustaceans.

	Abundance	
	F	P
EX vs. CO	7.13	0.010
EX vs. OW	1.48	0.23
CO vs. OW	2.11	0.15

d) Phytoplankton standing crop.

	Chlorophyll	
	F	P
EX vs. CO	3.22	0.074
EX vs. OW	1.99	0.20
CO vs. OW	0.10	0.75

waterfowl were dragonflies (Odonata: Aeshnidae, Libellulidae), large-bodied beetles (Coleoptera: Dytiscidae) and large leeches (Erpobdellidae).

Date had a strong effect on all response variables except for macroinvertebrate evenness in 1999, which is consistent with known chronologies of invertebrate ontogeny for prairie potholes and aquatic ecosystems in general (Armstrong and Nudds 1985, Bataille and Baldassarre 1993). The exclosure by date interaction was significant ($P < 0.15$) for nine of the sixteen invertebrate year-by-variable comparisons (Table 3.2). Thus variables including macroinvertebrate abundance, richness and diversity, and to a lesser extent, macroinvertebrate mean length varied significantly with time over the course of the waterfowl breeding season. For microcrustacean abundance and phytoplankton standing crop, in particular, and the rest of the variables to a lesser degree, the date effect dominated the observed patterns of abundance and the exclosure effect, when significant, was superimposed on this underlying temporal variation.

Temporal patterns were not, however, consistent between years for the macroinvertebrate variables (Table 3.4a, b; Fig. 3,4a-l). If the third sampling rotation is excluded from 1998, there is an overall trend for all the macroinvertebrate variables (except evenness) to increase until the fourth of fifth sampling rotation, and then decrease to values near the first rotation. In 1999, the temporal patterns were more unidirectional, excepting biomass, which closely resembled the biomass pattern for 1998. Macroinvertebrate abundance, richness and diversity all increased during the course of the study while mean invertebrate length decreased and evenness was essentially unchanged.

Table 3.4. Results of ANOVAs, analyzed by date. Abundance and biomass were transformed $\ln(x + 1)$. For 1998 the degrees of freedom are 1, 23 and for 1999 they are 1 ,20. Late June in 1998 has reduced degrees of freedom (1, 9) because heavy rains prevented access to just over half of the potholes.

a) Coarse macroinvertebrate variables

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Early May	0.02	0.89	0.05	0.82	2.34	0.14	3.80	0.066	2.70	0.11	2.46	0.13
Mid May	0.80	0.38	5.74	0.026	3.83	0.063	0.09	0.77	1.35	0.26	0.00	0.97
Late May	10.92	0.0031	5.16	0.034	3.26	0.084	0.00	0.97	3.21	0.087	1.66	0.21
Early June	3.75	0.065	1.55	0.23	0.20	0.66	3.89	0.063	0.09	0.76	1.02	0.32
Mid June	6.32	0.019	0.85	0.37	0.97	0.33	0.12	0.73	2.09	0.16	0.30	0.59
Late June	7.58	0.022	4.46	0.048	0.61	0.45	0.62	0.44	6.14	0.035	3.66	0.070
Early July	18.52	0.0003	0.39	0.54	0.97	034	0.31	0.58	4.44	0.046	0.16	0.69
Mid July	1.34	0.26	7.86	0.011	1.94	0.18	0.01	0.92	3.04	0.095	1.02	0.33
Late July	11.36	0.0026	0.46	0.50	10.88	0.0031	3.24	0.087	10.16	0.0041	0.08	0.78

b) Diversity macroinvertebrate variables

	Richness				Diversity				Evenness			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Early May	0.00	1.00	0.95	0.34	0.49	0.49	5.31	0.032	2.15	0.16	2.93	0.10
Mid May	9.55	0.0052	0.01	0.92	3.26	0.084	0.05	0.83	6.76	0.016	0.44	0.52
Late May	2.45	0.13	13.16	0.0017	0.59	0.45	13.28	0.0016	0.71	0.41	0.50	0.49
Early June	3.02	0.096	2.09	0.16	2.23	0.45	4.63	0.044	1.32	0.26	0.00	0.97
Mid June	3.85	0.062	10.42	0.0042	2.79	0.11	6.40	0.020	0.14	0.71	0.94	0.34
Late June	18.45	0.0020	6.34	0.021	3.10	0.11	15.62	0.0008	4.89	0.054	1.82	0.19
Early July	23.39	<0.0001	0.20	0.66	13.30	0.0013	1.15	0.30	0.12	0.73	2.61	0.12
Mid July	0.88	0.36	3.55	0.074	2.22	0.15	5.37	0.031	4.76	0.040	0.21	0.65
Late July	13.10	0.0014	0.53	0.47	3.93	0.060	0.10	0.76	2.88	0.10	2.30	0.15

c) Microcrustaceans

	Abundance			
	1998		1999	
	F	P	F	P
Early May	0.71	0.41	0.64	0.45
Mid May	0.50	0.61	6.83	0.017
Late May	11.56	0.0032	2.13	0.16
Early June	0.28	0.75	3.75	0.067
Mid June	0.63	0.48	0.02	0.90
Late June	0.78	0.38	1.78	0.20
Early July	9.85	0.0073	0.05	0.82
Mid July	4.05	0.051	0.23	0.64
Late July	8.81	0.0092	0.15	0.70

d) Phytoplankton standing crop

	Chlorophyll			
	1998		1999	
	F	P	F	P
Early May	0.16	0.85	3.53	0.039
Mid May	0.30	0.74	0.43	0.65
Late May	0.48	0.69	0.36	0.70
Early June	12.03	0.0028	0.08	0.93
Mid June	0.52	0.61	0.94	0.40
Late June	0.22	0.78	1.68	0.20
Early July	3.01	0.099	0.59	0.56
Mid July	2.40	0.10	2.23	0.13
Late July	1.55	0.26	5.01	0.024

In contrast, between years, both microcrustacean abundance and phytoplankton standing crop followed similar trajectories (Table 3.4c, d; Fig. 3.4m-p). Microcrustacean abundance increased early in the study period and then tapered off to very low abundances. Phytoplankton standing crop was highly variable early in the study period but then rapidly diminished to very low, almost oligotrophic conditions, for almost a month before gradually increasing to values approximating those at ice-out. The high degree of variation in phytoplankton standing crop at the ends of both study periods was likely the result of metaphytic blooms that periodically appeared and disappeared. The intense summer storms that occurred during late June of 1998 and early July of 1999 are reflected in the dramatic collapse of the differences between zones in both 1998 and 1999 in chlorophyll concentrations.

Effects of waterfowl predation on pothole invertebrate taxa

Similar to the all-inclusive macroinvertebrate and microcrustacean variables, variation in specific taxonomic groups tended to be most strongly related to date. Superimposed on this seasonal variation, either the exclosure treatment or the interaction between the exclosure treatment and date, were significantly related to abundance, mean length and/or biomass (Table 3.5a-g). Waterfowl exclusion resulted in increased Diptera (primarily Chironomidae) abundance in both years, while length and biomass were significantly increased in alternate years. Coleoptera (primarily Dytiscidae) only differed according to the length variable where they were longer in the exclosure zones. Waterfowl exclusion had no effect on Hemiptera (primarily Corixidae). All measurements for Odonata were strongly related to sampling date but they were also significantly related to waterfowl exclusion where they were more numerous, larger and

Table 3.5. Results of ANOVAs according to abundance, mean length and biomass for the macroinvertebrate taxonomic groups. Abundance and biomass were transformed ln $(x + 1)$. For 1998, the degrees of freedom are as follows: Exclosure – 1, 23; Date – 8, 184; Exclosure × Date – 8, 184. For 1999, the degrees of freedom are as follows: Exclosure – 1, 20; Date – 8, 160; Exclosure × Date – 8, 160.

a) Diptera

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	5.62	0.027	19.70	0.0003	0.48	0.49	3.70	0.069	3.61	0.070	0.64	0.43
Date	3.89	0.0003	6.61	<0.0001	6.45	<0.0001	1.90	0.063	1.95	0.056	3.87	0.0003
Exclosure × Date	2.76	0.0069	2.55	0.012	1.18	0.32	1.31	0.25	0.74	0.66	1.46	0.18

b) Coleoptera

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	0.00	0.99	0.94	0.34	6.46	0.018	4.44	0.052	0.35	0.56	2.14	0.16
Date	7.57	<0.0001	4.45	<0.0001	3.07	0.0030	4.32	<0.0001	2.41	0.017	7.38	<0.0001
Exclosure × Date	2.61	0.010	1.21	0.30	1.10	0.37	0.97	0.47	3.34	0.0014	0.46	0.88

c) Hemiptera

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	1.80	0.19	1.56	0.23	1.13	0.30	0.54	0.47	0.00	0.96	1.16	0.30
Date	3.20	0.0021	8.55	<0.0001	3.53	0.0010	5.50	<0.0001	2.39	0.018	1.00	0.44
Exclosure × Date	2.72	0.0076	0.99	0.44	1.56	0.16	1.14	0.34	2.31	0.022	1.17	0.32

d) Odonata

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	2.74	0.11	4.70	0.042	5.71	0.038	3.52	0.091	3.86	0.062	3.63	0.071
Date	5.52	<0.0001	5.52	<0.0001	3.35	0.0019	2.58	0.014	1.73	0.094	6.22	<0.0001
Exclosure × Date	1.56	0.14	1.18	0.31	0.83	0.59	0.21	0.99	1.44	0.18	1.58	0.13

e) Amphipoda

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	0.63	0.44	3.19	0.089	0.66	0.44	0.93	0.35	0.32	0.58	6.50	0.019
Date	2.39	0.18	8.66	<0.0001	10.03	<0.0001	20.73	<0.0001	1.26	0.27	2.09	0.040
Exclosure × Date	1.01	0.43	0.67	0.71	0.42	0.90	1.13	0.35	1.31	0.24	1.56	0.14

f) Gastropoda

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	45.07	<0.0001	10.30	0.0044	1.51	0.23	0.98	0.33	14.45	0.0009	3.20	0.089
Date	11.43	<0.0001	4.43	<0.0001	3.27	0.0022	3.58	0.0011	5.13	<0.0001	1.97	0.53
Exclosure × Date	4.10	0.0002	0.52	0.84	3.06	0.010	0.92	0.51	3.58	0.0007	1.18	0.31

g) Annelida

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Exclosure	24.49	<0.0001	7.69	0.012	0.01	0.93	0.15	0.70	3.43	0.077	0.00	0.96
Date	5.99	<0.0001	21.04	<0.0001	1.67	0.12	1.82	0.084	2.72	0.0076	3.40	0.0012
Exclosure × Date	2.09	0.04	2.52	0.013	0.97	0.49	1.48	0.22	0.68	0.71	1.56	0.14

longer. Amphipoda length and biomass were greater in the exclosures only in 1999. And finally, Gastropoda and Annelida abundance was greater in 1998 and 1999 but mean length was not; Annelida biomass differed only in 1999, when it, too, was greater.

For the five taxonomic groups that comprised microcrustacea, while they nearly all varied with date, there was no consistent pattern within taxa among years; variation was significantly related to the exclosure treatment in 1998 or 1999 but not both (Table 3.6a-e). Both groups of planktonic microcrustaceans, including Cladocera and Copepoda, and benthic microcrustaceans, including Ostracoda and Conchostraca, responded similarly to the absence of waterfowl foraging. Benthic microcrustaceans tended to be affected by date more in 1998 while planktonic microcrustaceans tended to be affected more in 1999, though this difference was not apparently related to either the exclosure effect alone or the exclosure by date interaction.

Amphibian abundance and composition

In 1998, tiger salamanders were found in 83.3% of the potholes (20 of 24) and in 1999 occupancy were found in 76.2% (16 of 21). The total number of tiger salamanders found in 1998 was 527, or 3.1 salamanders/survey/pothole for the potholes containing tiger salamanders. In 1999, that number also dropped slightly to 375 or 2.8 salamanders/survey/pothole. Unlike waterfowl, tiger salamander abundance was not adjusted per unit area (hectares) because they were sampled using the standardized sampling protocol based on a fixed area per pothole. The rest of the amphibians sampled were tadpoles and they exhibited similar pothole occupancy rates as tiger salamanders; in 1998, 268 were found in 20 of 24 potholes while in 1999, 101 were found in 15 potholes.

Table 3.6. Results of ANOVAs according to abundance for the microcrustacean taxonomic groups. Abundance was transformed ln ($x + 1$). For 1998, the degrees of freedom are as follows: Exclosure – 1, 23; Date – 8, 184; Exclosure × Date – 8, 184. For 1999, the degrees of freedom are as follows: Exclosure – 1, 20; Date – 8, 160; Exclosure × Date – 8, 160.

a) Hydracarina

	1998		1999	
	F	P	F	P
Exclosure	23.66	<0.0001	0.01	0.94
Date	9.47	<0.0001	1.87	0.067
Exclosure × Date	3.88	0.0003	1.44	0.19

b) Cladocera

	1998		1999	
	F	P	F	P
Exclosure	1.33	0.26	5.22	0.033
Date	6.78	<0.0001	9.55	<0.0001
Exclosure × Date	2.27	0.0247	0367	0.71

c) Copepoda

	1998		1999	
	F	P	F	P
Exclosure	2.97	0.098	0.97	0.36
Date	2.79	0.0063	7.52	<0.0001
Exclosure × Date	1.05	0.40	0.48	0.87

d) Ostracoda

	1998		1999	
	F	P	F	P
Exclosure	0.18	0.67	3.36	0.082
Date	21.12	<0.0001	3.99	0.0002
Exclosure × Date	1.33	0.23	0.45	0.89

e) Conchostraca

	1998		1999	
	F	P	F	P
Exclosure	4.35	0.048	0.25	0.62
Date	5.80	<0.0001	1.14	0.34
Exclosure × Date	1.17	0.32	1.28	0.26

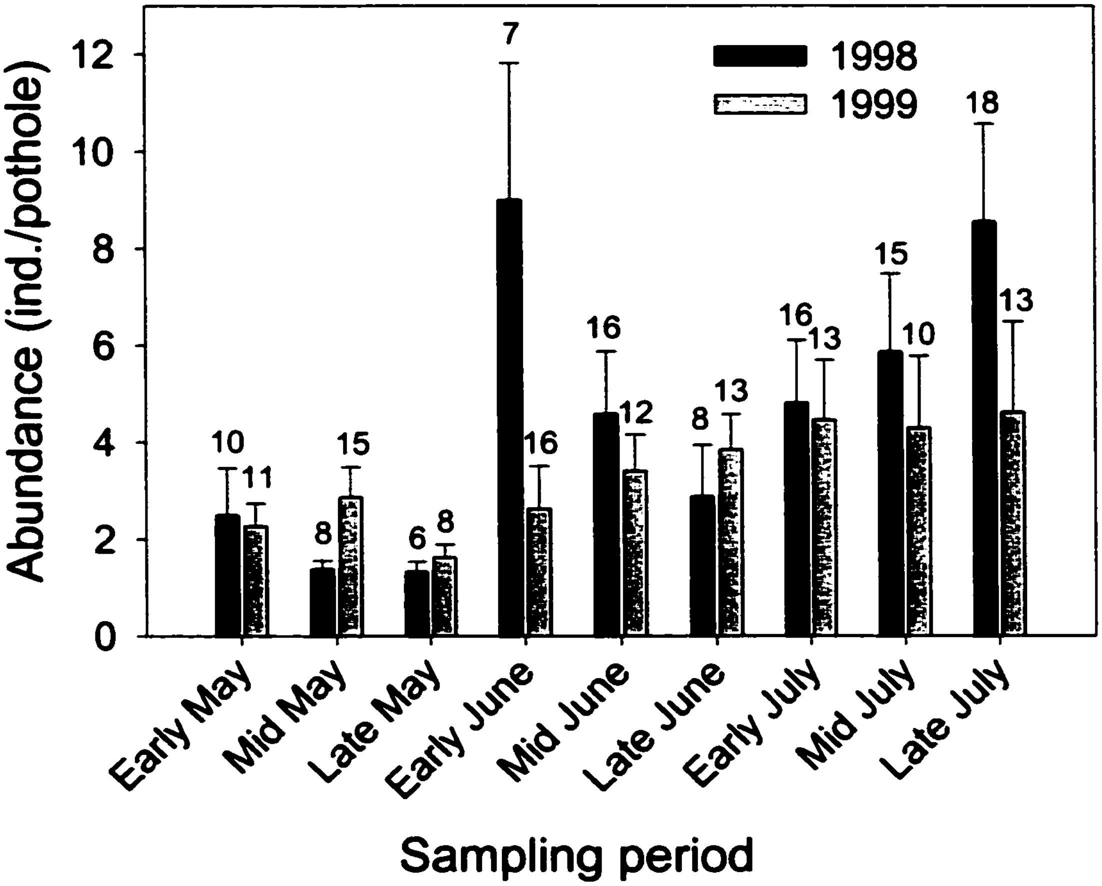
Finally, five fathead minnow were found in one pothole in 1999 over four sampling occasions.

Over the course of the study period, tiger salamanders increased from early May until late July in 1998 (date effect: $F_{8,96} = 2.46$, $P = 0.018$) possibly reflecting the progression of egg-laying and recruitment of young-of-the-year into the population, but the same pattern was not evident in 1999 (date effect: $F_{8,102} = 0.87$, $P = 0.55$) (Fig. 3.5). Tiger salamanders were subdivided into larval and mature developmental stages. Mature tiger salamanders comprise both metamorphic and paedomorphic life history forms. In 1998, the ratio of larval to mature tiger salamanders was approximately three to one (394 larval, 133 mature), while in 1999 the ratio was nearly one to one (199 larval, 176 mature). In both years, the number of larval individuals was very low during the month of May. In 1998, the number steadily increased towards the end of July (date effect: $F_{8,73} = 2.34$, $P = 0.027$). A qualitatively similar pattern was observed in 1999, however, it was not significant (date effect: $F_{7,67} = 0.80$, $P = 0.59$). Mature tiger salamanders, in contrast, did not monotonically increase or decrease during the course of the field season, but they did exhibit significant abundance fluctuations in 1998 (1998 date effect: $F_{8,47} = 2.92$, $P = 0.0099$; 1999 date effect: $F_{8,63} = 0.99$, $P < 0.45$).

Influence of covariates on exclosure effect sizes

The difference between the exclosure zones and the control or open water zones for most response variables varied widely among potholes. To account for some of this "effect size" variation further statistical analyses were performed using the simple difference (i.e. the mean over all dates) between the exclosures and either the control or open water zones, depending on the year, as the dependent variable. The independent

Figure. 3.5. Average numbers of tiger salamanders trapped per pothole according to week. For 1998, exclosure and control zones are combined and for 1999, exclosure and open water zones are combined. The number above each of the plots refers to the number of potholes that contained tiger salamanders (n=24 in 1998 and n=21 in 1999). Note that in late June 1998, only 10 potholes were sampled. Error bars are standard errors.



Abundance (ind./pothole)
0
2
4
6
8
10
12
1998
1999
10
11
8
15
6
8
7
16
16
12
8
13
16
13
15
10
18
13
Early May
Mid May
Late May
Early June
Mid June
Late June
Early July
Mid July
Late July
Sampling period

variables were comprised of a covariate (either the control or open water zone), waterfowl abundance, tiger salamander abundance and the interaction between the two groups of consumers. If the interaction term was insignificant (P 0.15), then that term was removed from the model and the reduced model was run again to achieve more exact estimates of main effects.

Inclusion of the covariate term in the model was significant for all macroinvertebrate variables except biomass in 1999 (Table 3.7a). In contrast, the covariate term was not statistically significant for either of the microcrustacean variables (Table 3.7b), and it approached significance for phytoplankton standing crop in both years (Table 3.7c). Generally, relationships between waterfowl abundance and effect size were more statistically significant than those between tiger salamander abundance and effect size. In 1998, waterfowl abundance was strongly related to all dependent variables except mean length, whereas in 1999, waterfowl abundance was only strongly related to macroinvertebrate abundance and mean length. The remaining dependent variables were variously related to waterfowl, except phytoplankton standing crop. A similar pattern characterized the relationship between the dependent variables and tiger salamander abundance but they were uniformly weaker. Finally, only microcrustacean abundance in 1998, macroinvertebrate mean length in 1999 and macroinvertebrate abundance in 1998 were significantly related to the interaction term between waterfowl and tiger salamanders.

These statistical outcomes were illustrated with bivariate plots of untransformed variables (Fig. 3.6). Effect sizes due to the exclosures were plotted as a function of waterfowl abundance and tiger salamander abundance. The intercepts and slopes for the

Table 3.7. Effect size relationships between response variables and waterfowl abundance ("Birds") and tiger salamander abundances ("Tigers"). Full models were initially run. Where interactions were not significant (F and P values in parentheses), models were rerun without the interaction term to determine the correct level of significance for the main effects. "Covariate" refers to the response variable measurement in either the open water (1998) or control (1999) zones (see text for further details). "Birds" and "Tigers" are the only variables that are logged. For 1998 the degrees of freedom are 1, 19 and the degrees of freedom for 1999 are 1, 16.

a) Coarse macroinvertebrate variables

	Abundance				Mean length				Biomass			
	1998		1999		1998		1999		1998		1999	
	F	P	F	P	F	P	F	P	F	P	F	P
Covariate	23.12	0.0001	6.17	0.024	6.01	0.024	15.32	0.0012	6.62	0.018	0.74	0.40
Birds	29.34	<0.0001	8.00	0.012	0.20	0.66	11.70	0.0035	16.70	0.0006	3.78	0.069
Tigers	14.62	0.0011	3.91	0.065	2.13	0.16	6.41	0.022	8.84	0.0075	2.24	0.15
Birds × Tigers	18.91	0.0003	(0.95)	(0.35)	(0.39)	(0.54)	7.50	0.015	(0.54)	(0.47)	(0.19)	0.67

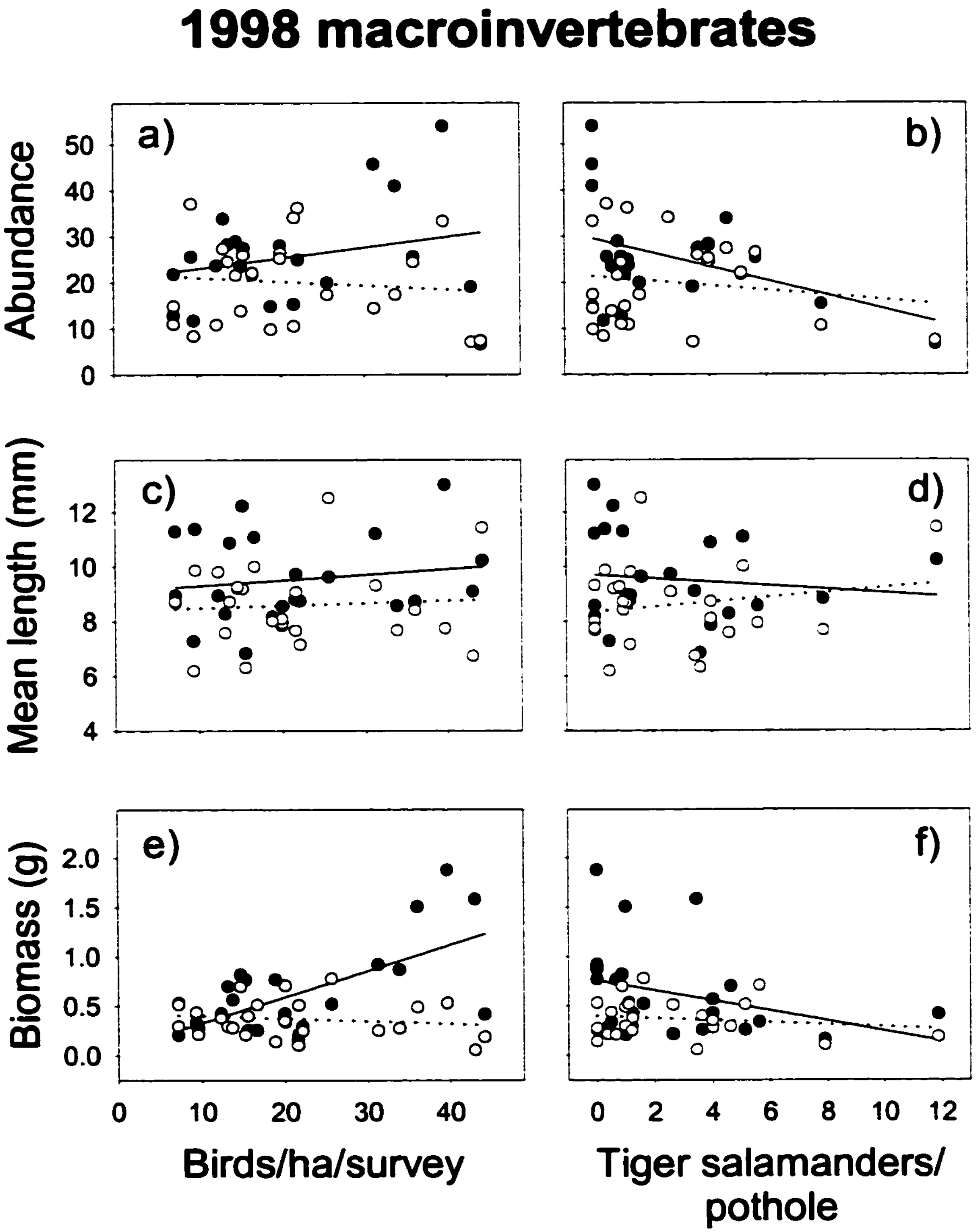
b) Microcrustaceans

	Abundance			
	1998		1999	
	F	P	F	P
Covariate	1.49	0.24	0.88	0.36
Birds	7.25	0.014	7.62	0.013
Tigers	3.34	0.083	3.78	0.069
Birds × Tigers	4.42	0.049	(0.35)	(0.56)

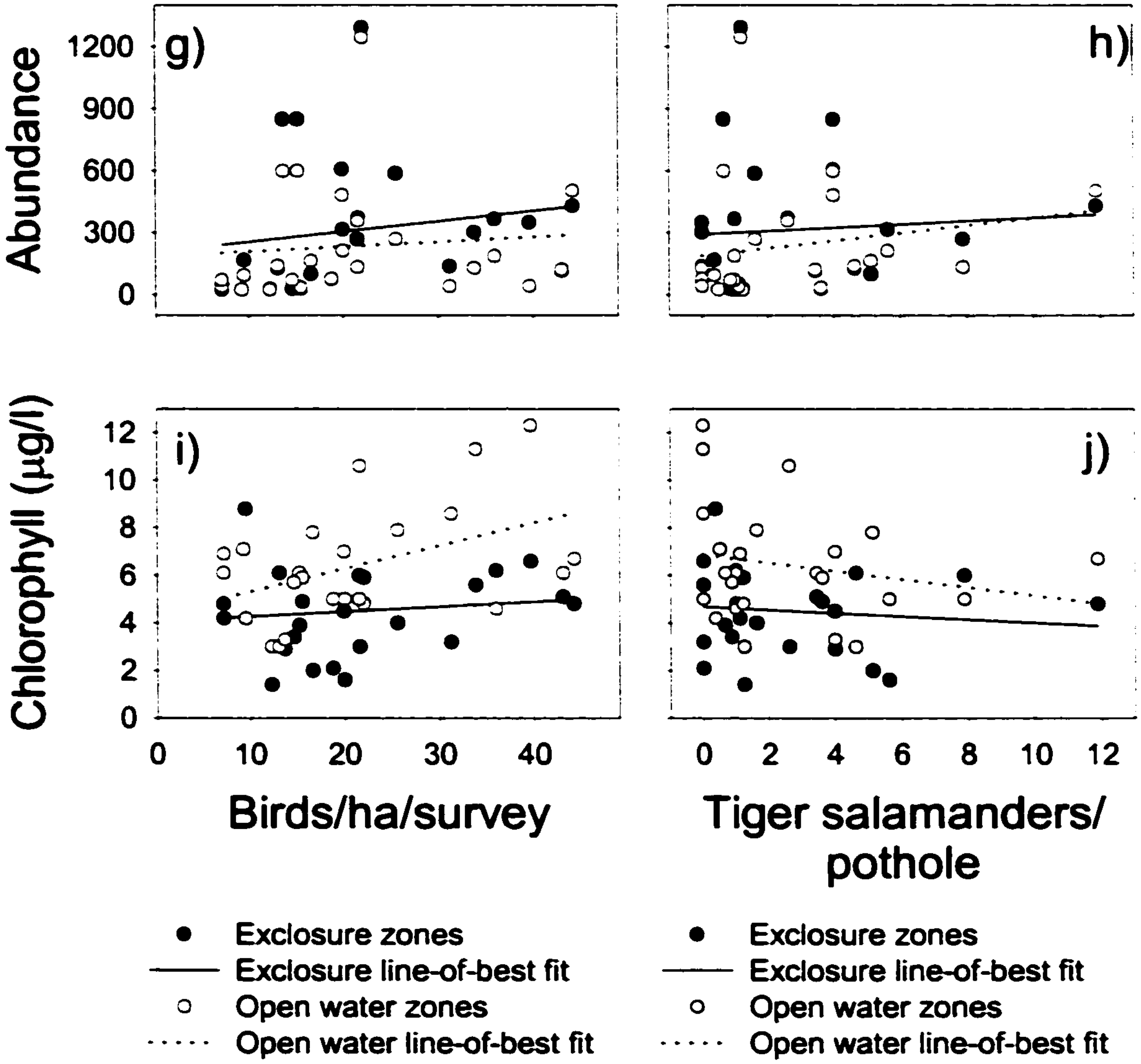
c) Phytoplankton standing crop

	Chlorophyll			
	1998		1999	
	F	P	F	P
Covariate	3.16	0.094	4.08	0.054
Birds	4.73	0.042	1.50	0.24
Tigers	4.01	0.069	0.29	0.60
Birds × Tigers	(1.98)	(0.18)	(1.50)	(0.24)

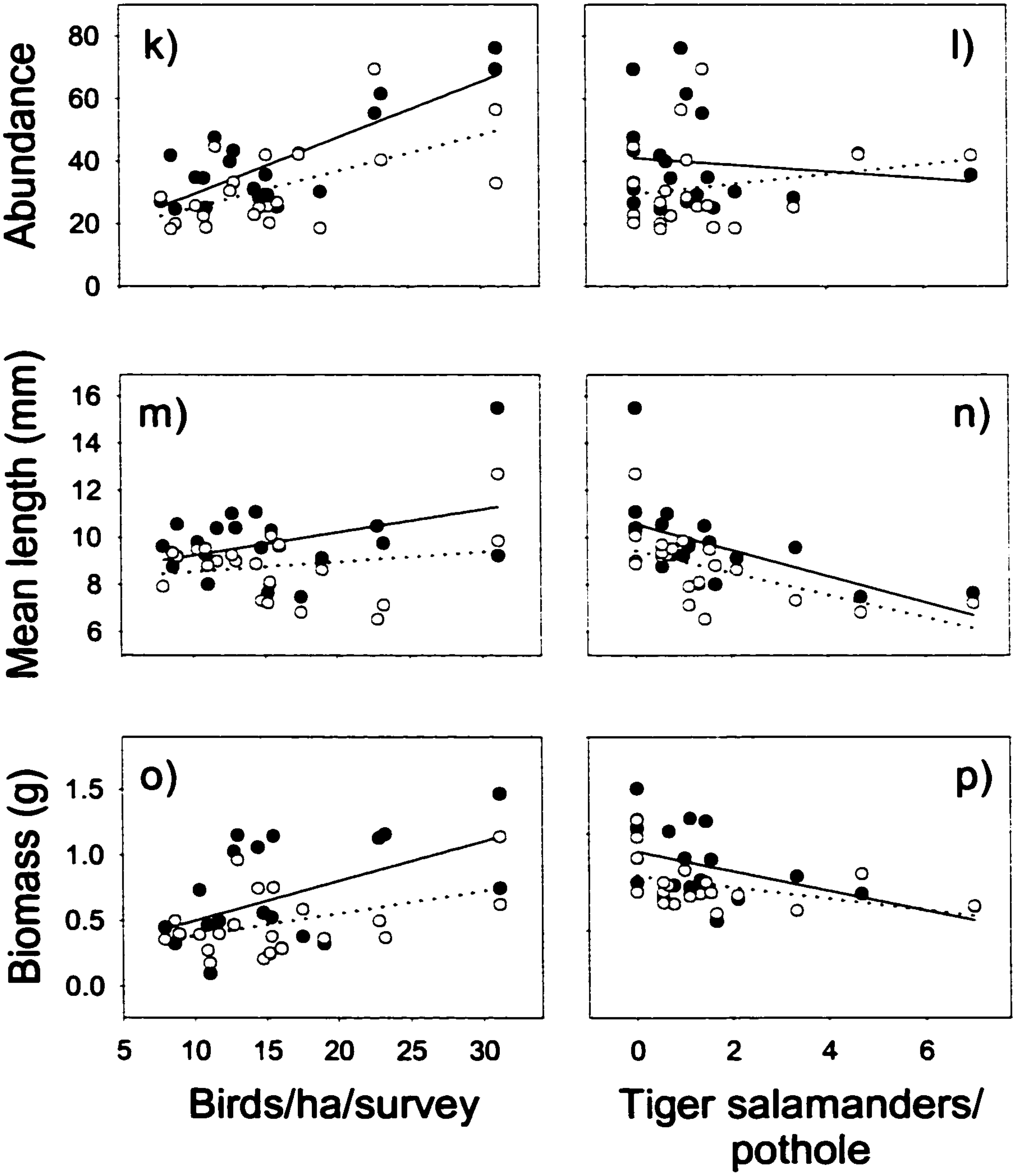
Figure 3.6. Comparison of coarse macroinvertebrate variables, microcrustacean abundance and phytoplankton standing crop in relation to waterfowl and tiger salamander abundances. Panels a-j are for 1998 and panels k-t are for 1999. A legend for the symbols and lines is located at the bottom of the second page of each year.


1998 macroinvertebrates
a)
b)
c)
d)
e)
f)
Abundance
0
10
20
30
40
50
Mean length (mm)
4
6
8
10
12
Biomass (g)
0.0
0.5
1.0
1.5
2.0
0
10
20
30
40
Birds/ha/survey
0
2
4
6
8
10
12
Tiger salamanders/
pothole

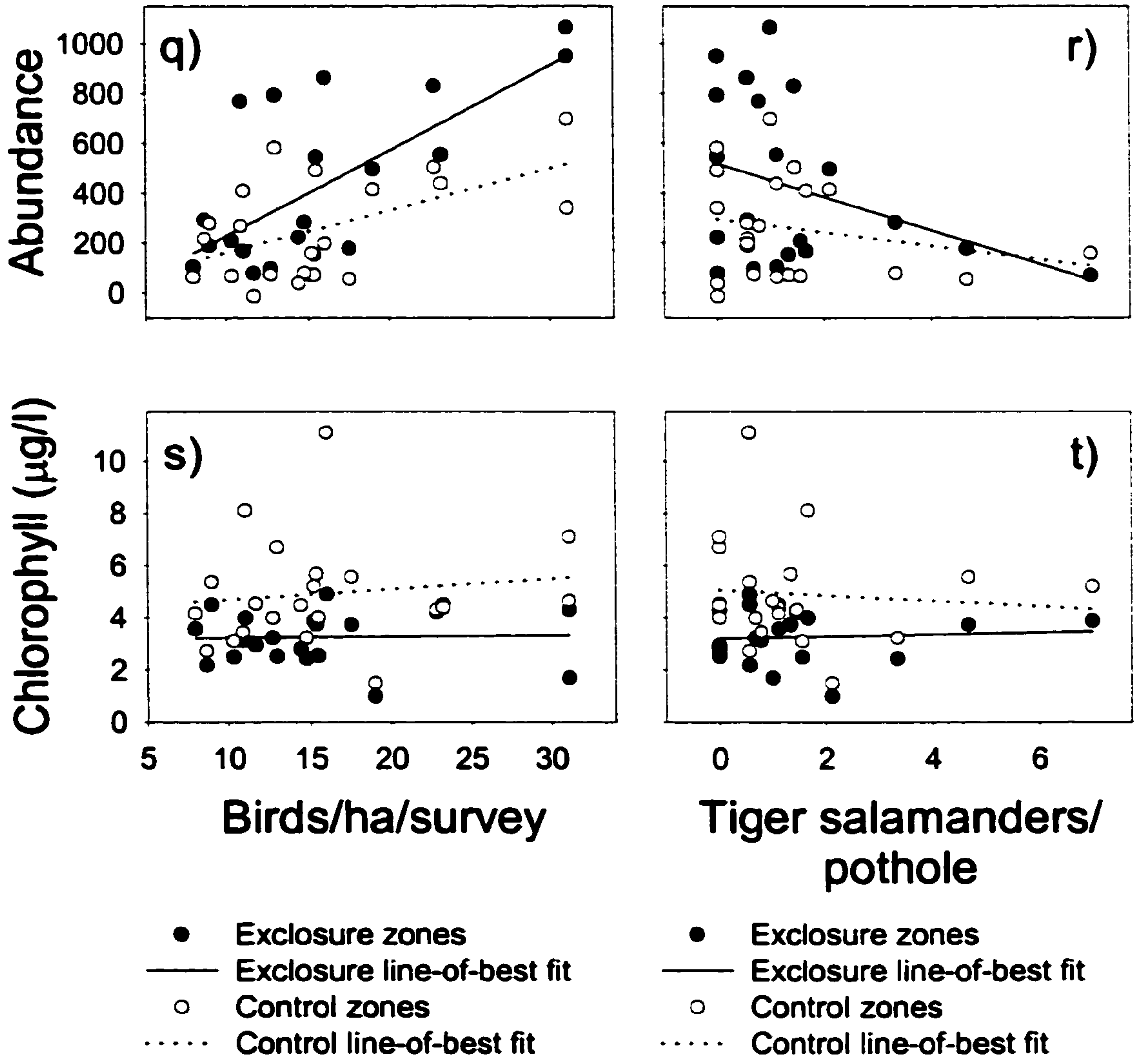
1998 microcrustaceans and algal standing crop



1999 macroinvertebrates



1999 microcrustaceans and algal standing crop



indicated lines-of-best fit yielded a very consistent pattern (Fig. 3.6a-t). For the macroinvertebrate and microcrustacean variables, as waterfowl abundance increased, effect size increased (i.e. the slopes diverged) and as tiger salamander abundance increased, effect size decreased (i.e. the slopes converged). The opposite trends occurred for comparisons involving phytoplankton standing crop (Fig. 3.6i, j, s, t).

Discussion

Effects of predation by waterfowl

The purpose of this study was to gauge the influence of waterfowl predation on pothole trophic structure and to assess whether there was evidence consistent with the hypothesis that waterfowl are resource limited during the breeding season. Across both years, waterfowl had pronounced effects on a variety of quantitative and compositional invertebrate variables, indicating that effects were diverse and comprehensive. Although the strength of the influence of waterfowl on invertebrates was greater in 1998 than in 1999, this cannot be attributed to the presence of a control zone in 1999, as it did not differ from the open water zones. Invertebrate patterns for 1999 were uniformly more synchronous during the course of the study period for all response variables. Nonetheless, within this synchrony, significant effect sizes were detected for just as many response variables as in 1998.

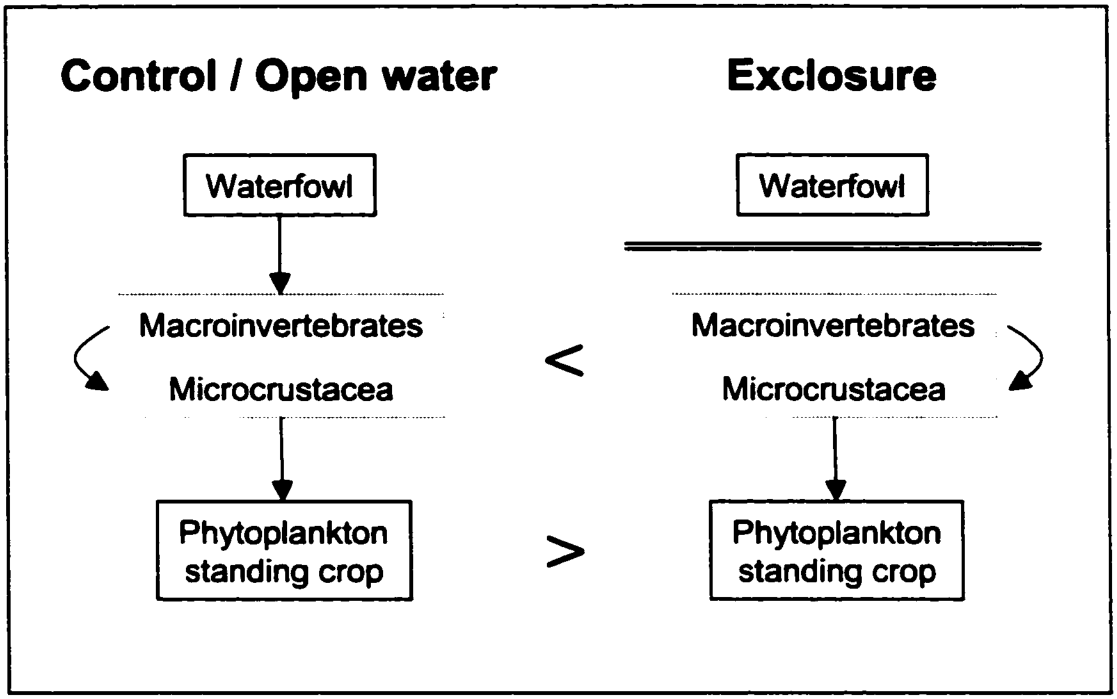
Perturbation experiments, such as the waterfowl exclosures employed in this study, are an effective way to measure the direct and indirect effects of a consumer or a group of consumers on a system (Carpenter and Kitchell 1993). Implicit to the exclosure design used for this study, mammalian and avian predators of waterfowl and, to a lesser extent, predators of other groups of organisms were also excluded from portions of potholes. Despite this, invertebrate populations increased and phytoplankton standing crop decreased in the absence of waterfowl. To corroborate experimental results, potholes were surveyed for waterfowl use as often as they were sampled to estimate the resource demand each pothole endured. It is this combination of experiment and observation that most strongly supports the assertion that waterfowl are responsible for the patterns obtained between the exclosures and the controls or open water zones.

Trophodynamic theory predicts that non-adjacent trophic levels should be positively correlated (Oksanen et al. 1981) and that the addition or removal of a resource-limited top-predator should result in a trophic cascade (Carpenter and Kitchell 1993). In this study, increases in many of the quantitative and diversity variables describing the macroinvertebrates did not translate into a decrease in microcrustacean abundance in either 1998 or 1999. This was likely because the invertebrate groups assembled for this study were based on taxonomy rather than trophic function so they do not necessarily concur with linear trophic interactions. For instance, the group Diptera includes various carnivorous, herbivorous and omnivorous taxa from both planktonic and benthic portions of pothole food webs. The microcrustaceans, and in particular, Cladocera, were actually elevated in the absence of waterfowl. The exclusion of waterfowl also resulted in decreased phytoplankton standing crop in 1998 and possibly in 1999 (see *Discussion: Phytoplankton standing crop*). Although benthic herbivores were sampled (i.e. Amphipoda and Gastropoda), epiphyton was not, so it is unclear whether waterfowl exclusion affected epiphytic standing crop. This pattern is topologically consistent with the trophic cascade hypothesis if the macroinvertebrate and microcrustacean assemblages are lumped together into one broad group of invertebrates (Chapter 1, Fig. 3.7) or if waterfowl primarily feed on herbivorous invertebrates and the invertebrate trophic level chiefly comprised of herbivores. Admittedly, this crude aggregation masks important differences in feeding behaviour, diet and ontogenetic changes among invertebrates. The entire invertebrate assemblage along with its consumers and resources would certainly be more accurately represented by a food web rather than as separate trophic levels. Such a detailed mapping of food web interactions though was not necessary to address the hypothesis that waterfowl exert trophic control on prairie potholes. In one interpretation of the hypothesis, within the context of food web complexity, trophic cascades are strong interactions that influence the properties of the system (Pace et al. 1999).

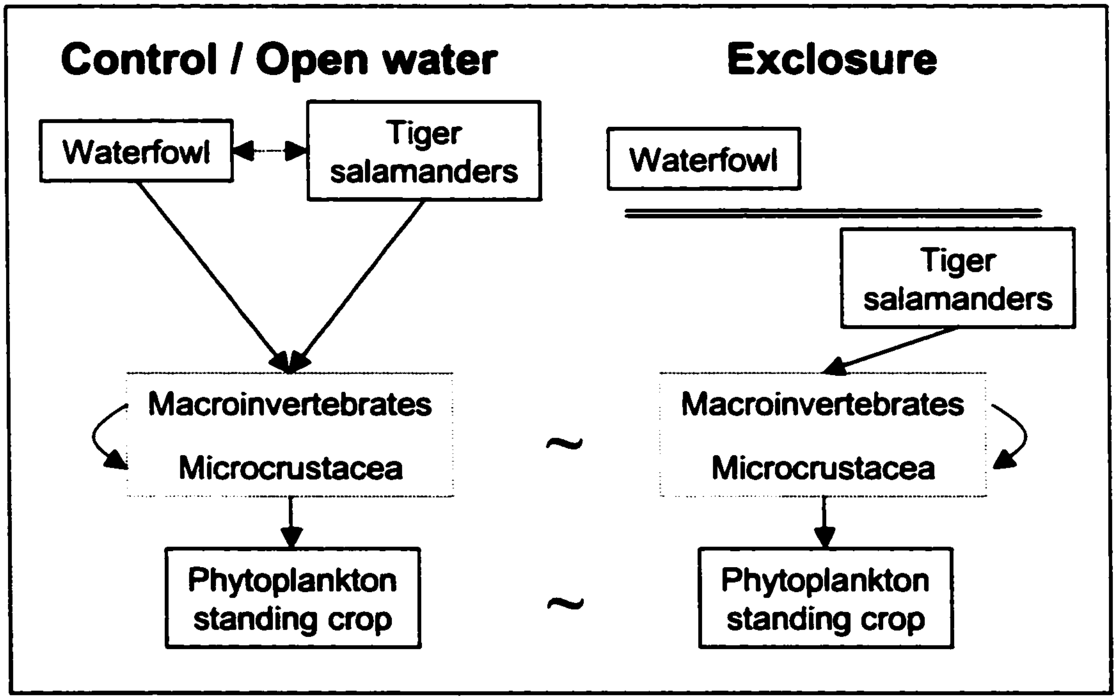
Compared to the wintering season, nearly all waterfowl species (Subfamily Anatinae) augment their variously omnivorous diets with higher proportions of proteinaceous macroinvertebrates during the breeding season. Krapu and Reinecke (1992) reviewed 18 published studies of esophageal contents for 14 species of duck and found that the percentage of macroinvertebrates (esophageal contents only, quantified by aggregate percent by volume or weight, Swanson et al. 1974) in the diets of females rose from a mean of 62.5% during the prelaying stage to a mean of 80.7% during the laying stage and dropped to 67.5% during the postlaying stage. Males also skew their diets towards animal prey during these stages, but not to the same extent as females (Krapu and Reinecke 1992). Although the remaining proportions of duck diets are comprised of vegetation, the specific plant foods consumed by ducks are mostly the seeds, tubers and turions of emergent and submergent macrophytes and floating duckweed (Lemnaceae), rather than any of the various forms of algae (Krapu and Reinecke 1992).

Figure 3.7. Path diagrams showing trophic interactions in prairie potholes as a result of waterfowl exclusion according to the presence (or low abundance) of tiger salamanders (A) and high tiger salamander abundance (B). Symbols in between diagrams indicate the overall responses of macroinvertebrate abundance, mean length, biomass, richness and diversity, microcrustacean abundance and phytoplankton standing crop between control or open water zones and exclosure zones.

a) Potholes absent (or with low abundances) of tiger salamanders



b) Potholes with high abundances of tiger salamanders



The dominant waterfowl species observed during this study were Blue-winged teal, Gadwall, Mallard and Northern shoveler dabbling ducks, Redhead and Ruddy diving ducks, and American coots. As archived in published gut contents data, this assemblage of avian consumers exploits nearly all of the invertebrates identified in this study (Chapter 2, Driver 1988, Krapu and Reinecke 1992). Thus, the presence of particular invertebrate species and the relative increase in abundance, length and biomass of invertebrates in exclosures was probably due to the absence of waterfowl predation. Direct consumption by waterfowl likely accounted for most of the differences observed between the exclosures and the control or open water zones. Alternatively, the interaction between waterfowl and some of the larger macroinvertebrates may also have been behaviourally mediated (Turner and Mittelbach 1990, Schmitz et al. 1997). This may be a more plausible hypothesis for the apparent appearance and disappearance of larger macroinvertebrates (e.g. Odonata: Anisoptera, Coleoptera: Dytiscidae) that accounted for the differences in macroinvertebrate richness and diversity. It is therefore possible that, in addition to direct consumptive effects of ducks on macroinvertebrates, the mere presence of waterfowl is sufficient to affect the distribution and movement of macroinvertebrates between exposed and protected areas.

Few other studies exist that have experimentally examined the potential influence of waterfowl on pothole communities during the breeding season, perhaps because it was traditionally assumed that prairie wetlands had "superabundant" resources (Owen and Black 1990, Krapu and Reinecke 1992). There is, however, an emerging view that birds generally, and ducks in particular, exert trophic control and affect community structure more than previously thought (e.g. rocky intertidal zones, Wootton 1992, Hamilton

2000). However, research in the prairies on this topic has been conspicuously absent, which is surprising given the proportion of North American breeding waterfowl that make use of the PPR (50-75%; Batt et al. 1989). In one of the few studies that have dealt with this topic, Wrubleski (1989) showed that foraging by diving ducks reduced chironomid densities. The mechanism linking ducks and invertebrates, in this case, was indirect as the reduction in chironomids was a consequence of herbivory for macrophyte tubers and turions.

There are a multitude of direct and indirect effects that link consumers and resources. To avoid the possibility of missing an effect of waterfowl on pothole macroinvertebrates, and to capture the particular types of interactions between waterfowl and their prey, several response variables were measured. General agreement among most of the macroinvertebrate and microcrustacean variables indicates that waterfowl have broad effects on pothole communities. The exclosures had elevated macroinvertebrate abundances and biomasses and, marginally, longer body lengths. Size-selective predation by ducks as a result of lamellar filter-feeding was not apparent in this study probably because the scale at which bill lamellae function is generally below that of the mesh size used to fractionate invertebrates (1 mm). Dabbling ducks, for which filter-feeding is a primary foraging mode, range in lamellar spacing from 0.3 mm for Northern shoveler, the most dense, to 1.0 mm for Mallard, the least dense (Nudds and Bowlby 1984, Tolkamp 1993). Size-selective predation may have occurred for these smaller invertebrates, but length measurements were not recorded for this subset of the invertebrates.

Ducks, grebes and coots not only had an effect on the number and biomass of invertebrates, but they also selectively affected the largest invertebrates. Similarly, species richness and diversity were elevated in exclosures, but evenness results were unclear. In the absence of waterfowl foraging, one species, on average, was added to the list of invertebrates and this translated into an increase in the overall diversity but not the relative diversity (Zar 1996). Taken together, these results point to two major differences between pothole macroinvertebrate populations according to the presence or absence of waterfowl. First, the overall numbers and sizes of macroinvertebrates were reduced in the presence of waterfowl. Specifically, while most species were reduced in number in the presence of waterfowl, the difference in mean lengths was attributable to reductions in larger macroinvertebrates including Chironomidae, Dytiscidae, Coenagrionidae and Lestidae and Trichoptera. Second, the reduction in richness and diversity in the presence of waterfowl points to the absence of relatively fewer, larger, macroinvertebrates or the tail of the size-frequency distribution of the invertebrate assemblage.

To suggest that, in the absence of waterfowl predation, "new" species appeared is somewhat misleading. The exclosure experiment actually relaxed "normal" waterfowl predation pressure on pothole invertebrates. Therefore, it is in the absence of predation that inferences can be made of how involved waterfowl are in shaping prairie pothole communities. In a series of experimental pond ecosystems, the simple threat of predation was sufficient to alter trophic structure (Turner and Mittlebach 1990). For prairie potholes, a similar argument can be made whereby the exclusion of waterfowl reduced the predation risk to larger macroinvertebrates, enabling them to emerge from protected littoral, vegetated habitats into the more planktonic open water areas. Larger macroinvertebrates with highly developed chemical and behavioural sensory systems can react to the threat of predation (Peckarsky 1984) and they may have altered their distribution within the exclosures.

Potential artifacts

Results for 1998 and 1999 were qualitatively similar. This was important, because ambient pothole conditions differed between years (Chapter 1); waterfowl and tiger salamander abundances and phytoplankton standing crop tended to higher in 1998, whereas most of the invertebrate abundances, mean lengths and biomasses tended to be higher in 1999. Because the control and open water zones in 1999 did not significantly differ, the comparisons between the exclosures and open water zones in 1998 were justified. In 1999, none of the contrasts between control and open water zones were significantly different ($P < 0.05$), though macroinvertebrate biomass and diversity approached significance. So, although 1998 and 1999 results were not formally combined in any statistical analyses, they were equally appropriate for addressing the research hypothesis that waterfowl are more influential as consumers than influenced by predators.

Exclosure (or enclosure) experiments are liable to spurious outcomes unless precautions are taken. Fence effects, a specific type of cage effects, result from the physical presence of experimental infrastructure that may, for example, function as substrate for algae thereby attracting invertebrates towards the edges of the exclosure (Kaushik et al. 1986). The implications of fence effects for interpreting outcomes based on solid-walled plastic exclosures is that the assemblage of invertebrates is relatively depauperate in the middle of the exclosure compared to the edges, thereby increasing the risk that effects might not be detected in the middle of the exclosure. The exclosures constructed for this study were sufficiently large enough that the potential complications associated with fence effects were avoided, providing all samples were collected within the central portions of the exclosure (and control) zones (Stephenson et al. 1984).

Cage effects refer to changes that may occur within an exclosure beyond those of the ambient study area and accounting for these effects tends to more tricky. Generally, the most common problems resulting from cage effects are the alteration of physical factors such as temperature and water column mixing that may affect biotic processes (Bloesch et al. 1988) and the potential that extraneous organisms may get trapped inside exclosures, thereby complicating interpretations of that particular replicate. In this study, exclosures were designed to be large enough to mimic ambient pothole environmental conditions. To test this assumption, in 1999, paired controls were constructed adjacent to the exclosures to assess how well the exclosures approximated the rest of the pothole. The agreement obtained between control and open water (ambient) areas, especially when compared to the exclosure zones, enabled common inferences to be made from both years. Among exclosure experiments conducted on birds in other aquatic ecosystems, there is considerable debate over whether or not paired controls are any more interpretable than comparisons between exclosures and ambient areas (Hamilton 2000). One of the more substantive concerns, with respect to the hypothesis that waterfowl are responsible for observed differences between exclosures and control or open water areas, is that birds may avoid partial cage structures (Marsh 1986). In a pilot study designed to test this assumption, it was found that waterfowl made use of control areas in proportion to the total area of the pothole (Appendix 4). Also, tiger salamanders, previously identified as potentially influential members of prairie pothole food webs (Zaret 1980, Deutschman and Peterka 1988), were permitted to enter and exit the exclosures (and controls) throughout the experiment. Rather than create another manipulation level (presence or absence of tiger salamanders), tiger salamanders were incorporated into the study as potential covariates of observed patterns (see *Discussion: Indirect interactions between waterfowl and tiger salamanders*).

Seasonal effects

Significant seasonal variation was detected for all but one of the response variables in one of the years. Prairie potholes exist in an environment that is characterized by extreme temporal variation in climate and hydrology. Near dormant biological activity during the winter is followed by rapid warming, ice and snow melting, and intense biological production. Sharp increases and decreases on particular dates for particular variables were the result of heavy rains that either prevented sampling and surveying, or temporarily flooded potholes, disturbing the abiotic environment, essentially "swamping" the pothole (e.g. late June 1998, early July 1999). In addition to the significant relationships described between the experimental zones, significant interactions were also found for approximately half of the variables between the exclosures and date. Waterfowl effects on pothole community structure may, therefore, be partially dependent on the interaction between timing of breeding and brood rearing and underlying successional changes associated with seasonal pothole chronology.

Invertebrate resource supply, relative to waterfowl demand, likely increases for adult birds and decreases for broods during the course of the breeding season. The emergence of aquatic insects follows a predictable chronology during the first few months following ice-out. Similarly, microcrustaceans recovering from diapause also exhibit high rates of production during the initial phase of the breeding season associated with initially high concentrations of nitrogen and phosphorus in the water column. After these initial "booms" though, primary and secondary production tends to decrease as nutrients become trapped in the sediments, and seasonally sequestered in emergent and submergent macrophytes and temporarily sequestered in metaphytic blooms, thereby depleting the amount cycled in the water column. Most primary production that comprises the basis for invertebrate food webs in prairie potholes comes from epiphytic, benthic and planktonic algal sources (Wrubleski and Detenbeck in Euliss 1999, Neill and Cornwell 1992), so the amount of edible algae available to potential prey for waterfowl is reduced. Thus, although most adult waterfowl become increasingly herbivorous following breeding, coincident with decreased availability of invertebrates, broods have high nutritional demands longer into the summer. This divergence in supply relative to demand is also likely to be exacerbated in the presence of tiger salamanders that exhibit their own seasonal chronology involving very high rates of production of larval cohorts (Deutschman and Peterka 1988 – See *Discussion – Indirect interactions between waterfowl and tiger salamanders*).

Phytoplankton standing crop

In both years, phytoplankton standing crop was higher in the presence of waterfowl. Differences between exclosure and control zones in 1999, but not between control and open water zones, indicates that the observed changes in phytoplankton standing crop were due to trophic or food web interactions rather than an artifact of cage effects associated with the experimental infrastructure.

Phytoplankton standing crop was inversely correlated with all of the invertebrate response variables, except evenness in 1998, suggesting that the removal of waterfowl predation resulted in increased invertebrate populations and decreased phytoplankton standing crop, the logical hypothesis being that of herbivory (Carpenter and Kitchell 1993). Although small herbivorous invertebrates, less than 1 mm, such as Bosminidae and Rotifera, were excluded from this study, the numerically dominant invertebrate taxa sampled across most potholes in this study were large-bodied Daphnia species, 1-2 mm in length with some individuals ~4 mm in length. These are the herbivores that exert considerable grazing pressure on phytoplankton and they are commonly inversely related to primary production and phytoplankton biomass (Brett and Goldman 1996). The scale of herbivory by zooplankton and other planktonic invertebrates (e.g. Chironomidae: Diptera) in prairie potholes is thought to be underestimated because algae exhibit high turnover rates and because relatively little is known regarding invertebrate feeding ecology in prairie wetlands (Euliss et al. 1999, Murkin 1989). Therefore, it is reasonable that removal of waterfowl predation on the entire assemblage of planktonic invertebrates contributed to increases in phytoplankton standing crop. Waterfowl exclusion also had an affect on benthic and littoral herbivores (e.g. Hyallelidae, Gastropoda) though any potential effects on benthic or epiphytic algae is unknown, as these sources of primary production were not sampled.

An alternative explanation for elevated phytoplankton standing crop observed in the presence of waterfowl is that algae are responding to nutrient recycling and transfer by waterfowl and that the exclusion of waterfowl reduces the amount of limiting nutrients to planktonic primary producers. In this scenario, the link between waterfowl and phytoplankton standing crop is indirect as it essentially decouples the relationship between herbivores and primary producers. This reasoning was offered as an explanation for positive correlations observed between tiger salamanders and phytoplankton standing crop among potholes (Chapter 1) and it has been invoked in several studies as a realistic indirect pathway by which top consumers and primary producers are linked (Vanni 1996, Zimmer et al. 2001b). Further, the effects of tiger salamanders on pothole invertebrates and phytoplankton standing crop were assumed to be non-linear, with effects revealed disproportionately at relatively higher tiger salamander abundances (Chapter 1). Thus, in potholes with low or absent tiger salamander populations, the effects of waterfowl on trophic structure should be more pronounced. Like tiger salamander waste, waterfowl feces are highly concentrated in nitrogen and phosphorus (Pettigrew et al. 1998), so even moderate inputs of these potentially limiting nutrients may significantly increase total algal production (Manny et al. 1994). Estimates of nutrient transfer within aquatic systems (Schindler et al. 1996, Zimmer et al. 2001b) and, potentially, subsidization from uplands, suggests that the removal of such inputs due to the presence of experimental exclosures, as in this study, may have significant effects on food web structure.

The latter hypothesis is further buttressed by patterns of invertebrate foraging. Many pothole macroinvertebrates, including Diptera, Amphipoda and Gastropoda, are to varying degrees herbivorous and they make use of epiphytic or benthic algae rather than phytoplankton as a nutritive source (Merritt and Cummins 1989). Therefore, a relaxation of predation on these organisms is less likely to result in increases in phytoplankton standing crop than a relaxation of predation pressure on zooplankton, the numerically dominant taxa included in the microcrustacean group. To resolve this question as to which of the two hypothetical pathways are more plausible, or the degree to which each is important in relating vertebrate consumers to primary production in prairie potholes, subsequent fertilization experiments involving tiger salamanders and/or waterfowl are necessary.

Indirect interactions between waterfowl and tiger salamanders

The potential effect size due to the exclusion of waterfowl appears to have been mitigated by the presence of coexisting tiger salamanders that indirectly interact with waterfowl by exploiting common prey resources (Chapter 2, Fig. 3.5). This appears to be an example of asymmetric exploitation competition (Levins 1979, Reichman 1979, Menge 1995, Hamilton 2000), such that the presence of tiger salamanders influences waterfowl interactions with pothole invertebrates, but the reverse influence does not occur, whereby waterfowl impinge on the foraging success of tiger salamanders. In terms of the exclosures and the effect sizes, this interaction was expressed as compensatory predation. Compensatory predation is generally considered to be a stabilizing force in community structure (Strong 1992) and the results of this study are consistent with this contention.

Intraguild predation (*sensu* Polis and Holt 1992) between tiger salamanders and waterfowl is not suspected to be an influential confounding factor in the interpretation of these results. Although the two grebe species (Horned and Pied-billed) included in this study are known to consume minnows and tiger salamanders, this group of consumers comprised a very small proportion of the total numbers of waterfowl and thus unlikely had a major effect on the effect sizes. Similarly, there is anecdotal evidence that American coot consume tiger salamanders (W. Reed, North Dakota State University, Fargo, North Dakota, pers. comm.), however there was no evidence of this in the one published diet paper on American coot diets for the region (Driver 1988). Thus, it was considered appropriate to place tiger salamanders in the same trophic level as waterfowl.

For macroinvertebrate abundance, biomass and, to a lesser degree, mean length, waterfowl abundance per pothole was positively related to exclosure effect size. However, tiger salamanders abundance was negatively related to exclosure effect size. Non-significant correlations were found between waterfowl and tiger salamanders for 1998 ($r = 0.246$, $P = 0.246$) and 1999 ($r = 0.011$, $P = 0.96$), suggesting at least one of two things: 1) that the interaction between the two consumers was non-linear or 2) that while the all-inclusive group "waterfowl" affected invertebrates, the various subgroups were separately related to tiger salamander abundance, but in different ways (Chapter 2).

Zimmer et al. (2000) found that the simple presence or absence of fathead minnow was a more important distinction than numerical differences in density of fathead minnow for explaining variation in invertebrate community structure because the simple presence of the planktivorous fish species conferred it as a long-term resident of the wetland. In contrast, the presence of tiger salamanders in a prairie pothole reveals little of the longer-term occupancy of that pothole by tiger salamanders as metamorphic individuals can vacate and occupy potholes within and between years. Potholes that do contain tiger salamanders tend to have lower invertebrate abundance and higher phytoplankton standing crop (Chapter 1). Thus, effects of tiger salamanders on prairie potholes may also be non-linear but skewed towards higher abundances of tiger salamanders rather than simple presence or absence. Comparisons between the presence or absence of tiger salamanders were less significant than contrasts between high and low abundances, suggesting that the mere presence of tiger salamanders was not sufficient to alter pothole trophic structure; a critical abundance of tiger salamanders was necessary (Chapter 1).

Different subgroups within waterfowl presumably vary in the type and strength of their interaction with tiger salamanders. For example, diet overlap was found to be higher between tiger salamanders and dabbling ducks than diving ducks and overlap among potholes was higher for diving ducks and tiger salamander than dabbling ducks (Chapter 2). The consequences of increased tiger salamanders occupancy rates across potholes should therefore have a greater impact on diving ducks than dabbling ducks and increased abundances of tiger salamanders within potholes should have a greater impact on dabbling ducks than diving ducks. Anecdotal accounts of predation by piscivorous birds, including Great-blue Heron, American Bittern and Horned and Pied-billed grebe (Wiedenheft 1983, personal observations) on tiger salamander larvae further suggest that occupancy rates of potholes by tiger salamanders should be inversely related to the presence of breeding grebes.

Occupancy rates and abundances of tiger salamanders across potholes in the study area are generally correlated with interannual climatic variation (the so-called "wet-dry" cycle) but it is difficult to predict specific occurrences of tiger salamanders in particular potholes. It is also unclear to what extent tiger salamanders exhibit facultative paedogenesis in this area of the Prairie Pothole Region (Deutschman and Peterka 1988). Certainly, the climatic and hydrologic conditions in the area are such that they may (Sprules 1974, Zaret 1980, Whiteman 1994). Although metamorphic and paedogenetic adults have different morphological designs and foraging strategies, they are both generalist predators (Shaffer and Lauder 1988). Larval tiger salamanders are also generalists but their diets are constrained by morphologic features such as gape-limitation (Leff and Bachman 1986). Perhaps, however, the most important aspect of tiger salamander biology, in relation to waterfowl distribution and abundance is that they exhibit commonly observed amphibian demographic patterns. Post-breeding, larval tiger salamanders can reach densities in the thousands per hectare (Deutschman and Peterka 1998), dramatically increasing the demand for invertebrate prey. This demand is temporary though as larval tiger salamanders experience very high rates of mortality and larval densities drop roughly ten-fold before the remaining individuals sexually mature into paedomorphs or metamorphs (Wiedenheft 1983, Hairston 1987, Deutschman and Peterka 1988).

Tiger salamanders probably outcompete waterfowl for shared prey within potholes. First, they are likely more numerous. Second, for much of the breeding season they are obligately aquatic. Third, they exhibit many ecological and morphological characteristics similar to planktivorous fishes (Zaret 1980, Chapter 1). Waterfowl predation is not, however, insignificant; waterfowl are larger organisms than tiger salamanders and they are endothermic rather than ectothermic so per unit body mass their nutritional demand is much higher. The biggest advantage that waterfowl, especially dabbling ducks, have over tiger salamanders in terms of the acquisition of prey is the ability to frequent multiple potholes. Decreased diet overlap between tiger salamanders and some diving ducks (Chapter 2) is consistent with this hypothesis, as they are the species thought to have relatively high pothole tenacity, along with coots and grebes. Thus, the time when competition for shared invertebrate resources might be greatest is when larval tiger salamander abundances are at their apex (and when intraspecific competition is likely greatest) especially if this time overlaps with brood rearing, when waterfowl families are least vagile and offspring demands for protein-rich macroinvertebrate prey is greatest (Krapu and Reinecke 1992). Several field studies involving food supply manipulations indicate that the brood-rearing stage may be the most sensitive to food limitation (Cox et al. 1998, Sjöberg et al. 2000, Chapter 4, but see Bataille and Baldassarre 1993 for an alternate view). This period of time is also roughly coincident with seasonal decreases in macroinvertebrate abundance and length (Mittelbach 1981, Armstrong and Nudds 1985, Barnes and Nudds in Nudds 1992).

Trophodynamic theory and prairie potholes

Trophic interactions in prairie potholes, as revealed by exclosure manipulations, were mitigated by the presence of tiger salamanders. In the absence of tiger salamanders, or at very low tiger salamander abundances, the removal of waterfowl clearly resulted in increases in measures of invertebrates and a decrease in the phytoplankton standing crop. It was only through the experimental exclusion of waterfowl that the consequences of coexisting tiger salamanders on interactions between waterfowl and invertebrates were revealed. This pattern is qualitatively consistent with predictions of the trophic cascade hypothesis (Carpenter and Kitchell 1993, Pace et al. 1999) if waterfowl primarily consume herbivores and the invertebrate trophic level is dominated by herbivores.

Strong (1992) suggested that "true" trophic cascades are more common in simple systems (but see Hairston and Hairston 1997, Pace et al. 1999 for an alternate view). The corollary to the characterization that invertebrate generalists and a high diversity of waterfowl dominate prairie potholes is that prairie pothole food webs are "webby".

Evidence from this study suggests that the condition of "simplicity" is not necessary significant trophic interactions to exist. Using comparable waterfowl exclusion manipulations in the marine intertidal, Hamilton (2000) did not find evidence of strong top-down interactions despite that fact that the community was relatively simple and dominated by specialists. However, both studies are consistent with Strong's (1992) suggestion that buffering by compensatory predators can obscure trophic cascades. Hamilton (2000) found that dogwhelks (*Nucella lapillus*) reduced blue mussel (*Mytilus edulis*) biomass to levels observed as a result of Common eider (*Somateria mollissima*) predation. Similarly, in this study, the coexistence of tiger salamanders mitigated any predicted increases in macroinvertebrates as a result of waterfowl exclusion.

This debate over "linearity" versus "webbiness" in food webs may be an artifact of deriving tractable (albeit sometimes artificial) trophic models from food webs for experimentation. Although prairie potholes are more speciose than the rocky intertidal, for example, the aggregation of functionally equivalent species into trophic levels precludes a consideration of food web complexity under manipulative conditions. Patterns of divergent trophic interactions thus represent layers of complexity added to a null model. An alternative approach to assessing the importance of waterfowl in prairie pothole communities would be to model food web interactions explicitly (e.g. Yodzis 1988, 1996). However, the suitability of such an approach is predicated on the quality of the food web data. While much is known regarding waterfowl diets and foraging strategies (Driver 1988, Krapu and Reinecke 1992) comparatively much less is known about invertebrates in prairie potholes and the algal assemblages that support them (Murkin, 1989, Goldsborough and Robinson 1994, Euliss et al. 1999).

Depending on the nature of the specific research hypothesis at hand, it is not apparent that finer taxonomic resolution necessarily improves interpretability or modifies outcomes of community patterns than coarser taxonomic resolution. This question of "taxonomic sufficiency" was addressed by Bowman and Bailey (1997), who found that, in a re-analysis of ten freshwater benthic macroinvertebrate datasets, genus-level identification did not yield a strikingly different description of assemblage patterns than family-level or order-level identification. In all likelihood, the taxonomic hierarchy for invertebrates in prairie potholes should also follow this convention, as should most other food webs that exhibit lognormal distributions in species-abundance relationships. In this study, each invertebrate group was characterized by a dominant taxa (i.e. the Amphipoda was dominated by Hyallelidae, Diptera was dominated by Chironomidae, zooplankton was dominated by Cladocera; Appendix 1) suggesting that qualitatively, the outcomes would not have differed had greater taxonomic detail been incorporated into the statistical models. This reasoning does not, however, extend beyond questions of taxonomic structure because within many insect, annelid and crustacean families, a wide variety of trophic functions may exist.

Conclusions – The hypothesis of resource limitation in migratory waterfowl during the breeding season

The question as to how waterfowl populations are regulated has been a dominant theme of waterfowl research for several decades, traditionally approached through modeling exercises of nutrient reserves (reviewed by Alisauskas and Ankney 1992) or population dynamics (reviewed by Johnson et al. 1992). Similarly, resource limitation in migratory waterfowl has been evaluated primarily via comparative studies of habitat partitioning and ecomorphological adaptations (reviewed by Nudds 1992). To more directly test hypotheses of specific factors that may be responsible for the regulation of waterfowl populations, manipulative experiments gained popularity during the 1990s. Among the most popular were predator-control experiments. A series of such exclusion experiments in the PPR revealed that in the absence or reduction of predators (i.e. mammalian consumers such as skunk, raccoon and coyote), nest success consistently increased (Garrettson and Rohwer 2001). However, in a re-analysis of historical nest success data, Beauchamp et al. (1996b) found that long-term declines in nest success were unrelated to nest loss due mammalian predators.

The trophodynamic model though, implicitly assumed in the predator management experiments, represented a novel approach to understanding community interactions that shape prairie pothole communities. Evidence of alternating competition and predation or a trophic cascade alone is insufficient to demonstrate whether a trophic level (i.e. waterfowl) is resource limited or not (Osenberg and Mittelbach 1996). However, the combination of results from this experimental study and other observational studies that have dealt with relationships between waterfowl and prairie pothole food webs (reviewed in Nudds 1992) indicate that waterfowl are engaged in competitive processes that affect pothole food web structure. A logical continuation of this research within a trophodynamic framework would involve constructing waterfowl exclosures in areas managed for predators of waterfowl (i.e. mammalian nest predators), such as those maintained in North Dakota and Saskatchewan. If predators of waterfowl are more important in controlling waterfowl populations than prey resources, then the effect sizes of invertebrate response variables between waterfowl exclusion and paired controls should be greater where predators are managed compared to my findings.

Power (1992) made the point that all communities are resource limited to a degree; prairie pothole communities are ultimately affected by the wet-dry cycle and pothole community structure is basically determined by the intraannual seasonal chronology of nutrient availability and sequestration. Osenberg and Mittelbach (1996) converted this trivially obvious statement into a testable hypothesis and found that in Lawrence Lake, a lake with three trophic levels, resource limitation was more severe than predator limitation at every trophic level and that the importance of resource limitation was greatest at the highest trophic levels. Excluding mammalian and avian predators of waterfowl, prairie potholes essentially have three broad trophic levels and the exclusion of waterfowl resulted in patterns that were consistent with trophodynamic theory. Further, while compensatory predation by tiger salamanders did obscure the occurrence of trophic interactions, it did not refute the hypothesis that the tertiary trophic level comprised of vertebrate consumers structured the secondary and primary trophic levels.

Since the mid-1980s, much of the Prairie Pothole Region was experiencing a prolonged deficit of annual precipitation. In contrast, during 1998 and 1999, southwestern Manitoba recorded some of the highest annual precipitation totals in 50 years (National Climate Data Center 2002). Potholes, therefore, were at or near their maximum water depths and, compared to most other years, a greater proportion of the land was covered by surface waters. This implies that the relationships obtained in this study are conservative, as there was likely a "surplus" of breeding habitat. The consequences of waterfowl exclusion for pothole invertebrates and algae and, by extension, estimates of resource limitation should be greater in relatively drier years. However, this prediction is predicated on the assumption that waterfowl demand for prey resources exceeds supply, a scenario that is more likely in the years immediately following peak wet years when there is a "surplus" of breeding birds relative to habitat, and one that deserves further scrutiny.

CHAPTER 4

Effects of variation in tiger salamander abundance on waterfowl foraging time, survivorship and growth rate: results from whole pothole experiments

Introduction

Asymmetric exploitation competition (*sensu* Levins 1979) is hypothesized to often occur between coexisting but distantly related taxa, particularly in variable environments (Reichman 1979). Prairie potholes are seasonally productive environments ("aestival" – Daborn 1974, Daborn and Clifford 1974) that support migratory waterfowl (i.e. ducks, coots and grebes) and, depending on hydrologic conditions, tiger salamanders (*Ambystoma tigrinum diaboli*). These consumers exhibit significant dietary overlap (Chapter 2) and tiger salamanders affect trophic interactions between waterfowl, invertebrates and phytoplankton standing crop through compensatory predation (Chapter 3). Within potholes, tiger salamanders, like fathead minnow (*Pimephales promelas*), are generally thought to outcompete waterfowl, especially dabbling and diving ducks and coots (Bouffard and Hanson 1997), for common prey suggesting that potholes containing tiger salamander populations may be marginal for breeding waterfowl.

During the breeding season, most migratory waterfowl, especially females, augment their diets during the laying stage with high proportions of aquatic invertebrates (~80%, Krapu and Reinecke 1992, Alisauskas and Arnold 1994). Similarly, for the first few weeks post-hatch, duckling, coot chick and grebe chick diets are almost entirely comprised of aquatic invertebrates (Driver, 1988, Sedinger 1992, Alisauskas and Arnold

1994). The brood-rearing stage is increasingly cited as the critical phase during the annual cycle of migratory waterfowl when mortality may be greatest (Johnson et al. 1992, Sjöberg et al. 2000). Concurrent with waterfowl nesting activities and brood rearing, tiger salamander eggs hatch into larvae that can reach densities in the thousands per hectare (Deutschman and Peterka 1988). Thus, the potential for indirect interactions between waterfowl and tiger salamanders may be greatest at this time.

Food limitation in birds, however, is challenging to detect and estimate under natural conditions. A variety of approaches have been used to address this question, including comparative studies (e.g. Pehrsson 1984, DuBowy 1988, Dzus and Clark 1997) and food supplementation experiments (see reviews in Krapu and Reinecke 1992, Sedinger 1992); these have been variously successful in testing for food limitation. Two recent studies have directly confronted the problem. Cox et al. (1998) reared mallard ducklings in experimental mesocosm wetlands that differed in aquatic invertebrate availability due to the presence or absence fathead minnow. Sjöberg et al. (2000) assessed the impact of habitat quality, a surrogate of food availability, on imprinted mallard ducklings that foraged in "poor" and "rich" lakes. Both of these studies found decreased survivorship and growth rates in ducklings associated with relatively less food availability. Still outstanding, however, is an experimental approach that tests for food limitation under natural conditions.

I manipulated invertebrate availability across a series of prairie potholes through the systematic reduction or addition of tiger salamanders. In the first experiment (hereafter referred to as the "foraging experiment"), I recorded waterfowl activities according to high or low tiger salamander abundances, and in the second experiment (hereafter referred to as the "coot chick experiment"), I measured survivorship and growth rates of American coot (*Fulica americana*) chicks according to a similar contrast in tiger salamander abundance. Coots exhibit a high degree of "pothole tenacity" relative to dabbling and diving ducks (T. W. Arnold, University of Minnesota, Minneapolis, MN, pers. comm.; W. L. Reed, North Dakota State Univeristy, Fargo, ND, pers. comm.), thereby increasing the likelihood that they can endure a greater degree of experimental intervention.

My approach to this question of food limitation in migratory waterfowl differs in this chapter compared to Chapters 2 and 3 in that I have switched the focus of the study. Rather than use measures of pothole community structure as dependent variables, I have chosen to directly test for consequences of food web variation by measuring activity budgets in adult waterfowl and survivorship and growth rates in coot chicks. First, I predicted that the proportion of time spent foraging by adult waterfowl within a pothole would be greater where tiger salamander abundances were lower. As a corollary, the species that differ most in their time spent foraging should be those identified in Chapter 2 that have the greatest diet overlap with tiger salamanders, such as dabbling ducks. Second, I predicted that coot chick survivorship and growth rate would also be greater where tiger salamander abundances were lower. Third, for both experiments I predicted that the degree of observed effects would vary with the differential in tiger salamander abundance between manipulations.

Methods

Study area

Experiments were carried out southwest of Minnedosa, Manitoba, Canada (50°16′ N, 99°50′ W) near the northeastern edge of the Prairie Pothole Region during the spring and summer of 2000. Basic geomorphological and biogeochemical features of this landscape and the biotic communities that are supported by it are described in detail in Chapters 1 and 3.

Potholes for the foraging experiment were randomly selected from a pool of potholes that were constrained by the morphometric criteria that they be no deeper than 125 cm and no larger than 0.6 ha. For the coot chick experiment, only potholes less than 0.3 ha were considered.

Foraging experiment

In early May 2000, 16 potholes were bisected by floating barriers of 5 cm × 10 cm boards that reached from shore to shore. Polyethylene plastic sheeting was attached to the boards and draped to the sediment-water interface. The sheeting was anchored with lead line, excised from freshwater gill nets, that was duct-taped to the bottom. An extra 20 to 30 cm of sheeting was allowed to hang from the boards in case water levels fluctuated (i.e. increased) or in case the barriers shifted position and the sheeting billowed. The ends of the barrier reached into the emergent vegetation and continued to the edge of the water.

Once the barriers were established, two types of trap were used to test for the presence of tiger salamanders, 1) unbaited standard-sized aluminum minnow traps and 2) salamander traps that resemble drift nets (Mushet et al. 1997). Although minnow traps are easier to use than salamander traps, the latter type of trap is tall enough to include the entire water column meaning that any trapped individuals can acquire atmospheric oxygen, if necessary, thereby reducing mortality. Both traps have approximately 2.5 cm openings. On average, five minnow traps and one salamander trap were set for each sampling effort and both traps sample passively over 24-hour periods. Upon trapping tiger salamanders in a particular pothole, the collection effort was concentrated on one side of the barrier, randomly selected. From this point on, any live tiger salamanders that were collected on one side of the barrier were simply transferred to the other side. One side was designated "LSA" (low salamander abundance) and the other "HSA" (high salamander abundance). Dead tiger salamanders were discarded. If no tiger salamanders were trapped in a particular pothole, then individuals were imported from potholes, not included in either of the experiments, that were known to have high abundances of tiger salamanders and added to one side of the barrier. Thus, paired contrasts of tiger salamander abundances were achieved within each pothole between high and low (or no) numbers of tiger salamanders.

After two to three weeks of augmenting tiger salamander abundances within potholes, observations of waterfowl activity budgets were initiated using spotting scopes. Each observation period lasted for 2 hours and they generally occurred either in the early morning or early evening to coincide with times of the day when waterfowl feeding was most intense (G. Benoy, pers. obs.). At 10-minute intervals, I recorded the number of birds on either side of the barrier, the composition of the birds and the specific behavioural activity in which each bird was engaged. Of the several activities identified, I considered only the occurrences of foraging (i.e. diving, tipping, dabbling, etc.), relative to all other activities, relevant to this study. Each pothole was observed on either three or four occasions, approximately once a week.

At the end of the observations period, tiger salamander "inventories" were initiated. Each pothole was trapped intensively with minnow traps and salamander traps on both sides of the barrier and repeatedly sampled for several days in an attempt to estimate final abundances of tiger salamander on either side of the barrier. Any tiger salamanders trapped were exported from that pothole to another pothole not included in the study to avoid the possibility of resampling.

Coot chick experiment

American coots usually initiate nesting within two weeks of arriving on the breeding grounds and peak nest initiation occurs from late-April through May (Alisauskas and Arnold 1994). During this time, I searched about 50 small potholes that contained only a single pair of coots for evidence of nest building. This experiment made use of small potholes for two reasons: 1) coots are territorial and it is unclear whether interactions between multiple breeding pairs within a pothole impinge on reproductive success (Ryan and Dinsmore 1979, Reed 1999), and 2) the abundances of tiger salamanders needed to augment food availability is likely proportional to the size of the pothole. Upon finding a coot nest, I marked it with flagging tape and monitored it every other day to determine the date of first laying. If nests were encountered already with less than a full clutch of eggs, clutch initiation date was determined by back counting (Alisauskas and Arnold 1994). Nests with an apparent full clutch of eggs (8 to 9 eggs) were simply monitored.

A cross-fostering design was employed to control for genetic variation and maternal effects among coot breeding pairs (Roff 1998, Reed 1999). Once a full clutch was laid (i.e. no eggs laid for at least 2 days) a portion of the eggs were taken to the field station and incubated until hatch (Roll-X Flowing Air Incubator, Lyon Electric Co., Inc., Chula Vista, California). Other coot eggs from nests not included in the study were used to replace eggs reared in captivity. Coot eggs hatch asynchronously (Alisauskas and Arnold 1994). Once pipping was detected, I replaced all of the eggs with a random assortment of pipping eggs and newly hatched (<1 day) coot chicks from the incubator for a total of eight fostered individuals (mean clutch size in this area of the PPR is between eight and nine; Reed 1999). Unlike previous studies on coot chick survivorship (Reed 1999, Reed and Benoy, unpublished data), I did not mark or tag the chicks as there was only one brood per pothole and coot chick broods are not known to move among potholes prior to fledging (T. W. Arnold, University of Minnesota, Minneapolis, MN, pers. comm.). The first and last coot nests were fostered in early June and late June, respectively. Chicks were successfully fostered with adults on 20 of the potholes initially scouted. Two-thirds of the reduction in the number of study potholes was due to either pothole and nest abandonment and the remaining one-third was due to depredation.

During the time when nests were monitored, minnow traps were set to determine the presence or absence of tiger salamanders. Occupancy rates of potholes by tiger salamanders were 75-80% in 1998 and 1999, but most of these potholes were between 0.5 and 1.0 ha (Chapter 1, Chapter 3). The occurrence of tiger salamanders in smaller potholes is much lower and likely more erratic because smaller potholes tend to be more ephemeral with highly variable dissolved oxygen concentrations. It was therefore unnecessary to eradicate a portion of the potholes of tiger salamanders since fifteen of them were initially free of tiger salamanders. The five potholes with tiger salamanders were simply added to and four of the remaining potholes were randomly assigned to tiger salamander additions. Potholes supplied with tiger salamanders were designated "Added" and potholes without tiger salamanders "Absent". Source potholes, not included in either of the two experiments, were used to supply tiger salamanders.

Once a coot nest was fostered, tiger salamander additions ceased and the only field activity involving that pothole for the following three weeks were observations to estimate chick survivorship. Observations were conducted using a spotting scope and lasted until the number of chicks fostered was observed or until the number of coot chicks observed was assumed to comprise the total number remaining. For the first two to three weeks after hatch, coot chicks derive nearly all their food from their parents (Ryan and Dinsmore 1979, Desroches and Ankney 1986, Driver 1988) so it was assumed that when parents were foraging with a brood, the brood included all the surviving chicks. Survivorship was expressed as the number of chicks observed at the end of three weeks divided by eight (the maximum number possible). Between 21 and 25 days post-hatch, as many chicks as possible were collected from a pothole and each was weighed to the nearest 0.1 g. The fostering design precluded the need to correct final weights with initial weights; coot chick weights at 24 hours post-hatch range between 18 and 23 g with a mean of 20.75 g. At three to four weeks coot chicks begin to become independent of their parents and their diets become increasingly herbivorous (Driver 1988). Further, chick growth rate curves are steepest during this early development phase so the possibility of detecting a difference in survivorship or mass change is likely greatest.

Collections of coot chicks were conducted in a variety of ways but far and away the most effective way was by dog retrieval (80% of the total number caught) followed by human searches (20%).

After coot chicks were collected, tiger salamanders were "inventoried" as before to estimate final abundances. Minnow traps were also set in the potholes considered to contain no tiger salamanders to check that assumption. The final set of minnow traps for this experiment was retrieved at the end of July.

Statistical analyses

For the foraging experiment I used mixed-model ANCOVA with two treatments (fixed) factors. Independent variables included side (the first fixed factor; high salamander abundance (HSA) and low salamander abundance (LSA)), guild (the second fixed factor; dabbling ducks (dabblers), diving ducks (divers), grebes and coots) and pothole (a random variable). Statistical significance was set at $\alpha = 0.05$. Interactions between fixed factor variables were noted when P   0.15; when statistical power is low, main effects are not always apparent unless interactions are considered (Winer et al. 1991). When an interaction was detected (i.e. between side and guild), reduced models were analyzed separately for each level of the interacting variable (i.e. guild) to facilitate interpretation of main effects (Keppel 1982). The dependent variable for this experiment was total foraging time. Each pothole was observed for 120 minutes and the amount of time spent foraging by all birds on both sides of the barrier was recorded. To account for the fact that a bird was rarely observed on a pothole for the full 120 minutes, the total time each bird spent on a particular side of the barrier was included in the statistical model as a covariate. The specific statistical model used for this analysis was:

$$X_{ijk} = \mu + C_{ijk} + S_i + G_j + SG_{ij} + \varepsilon_{ijk} \tag{4.1}$$

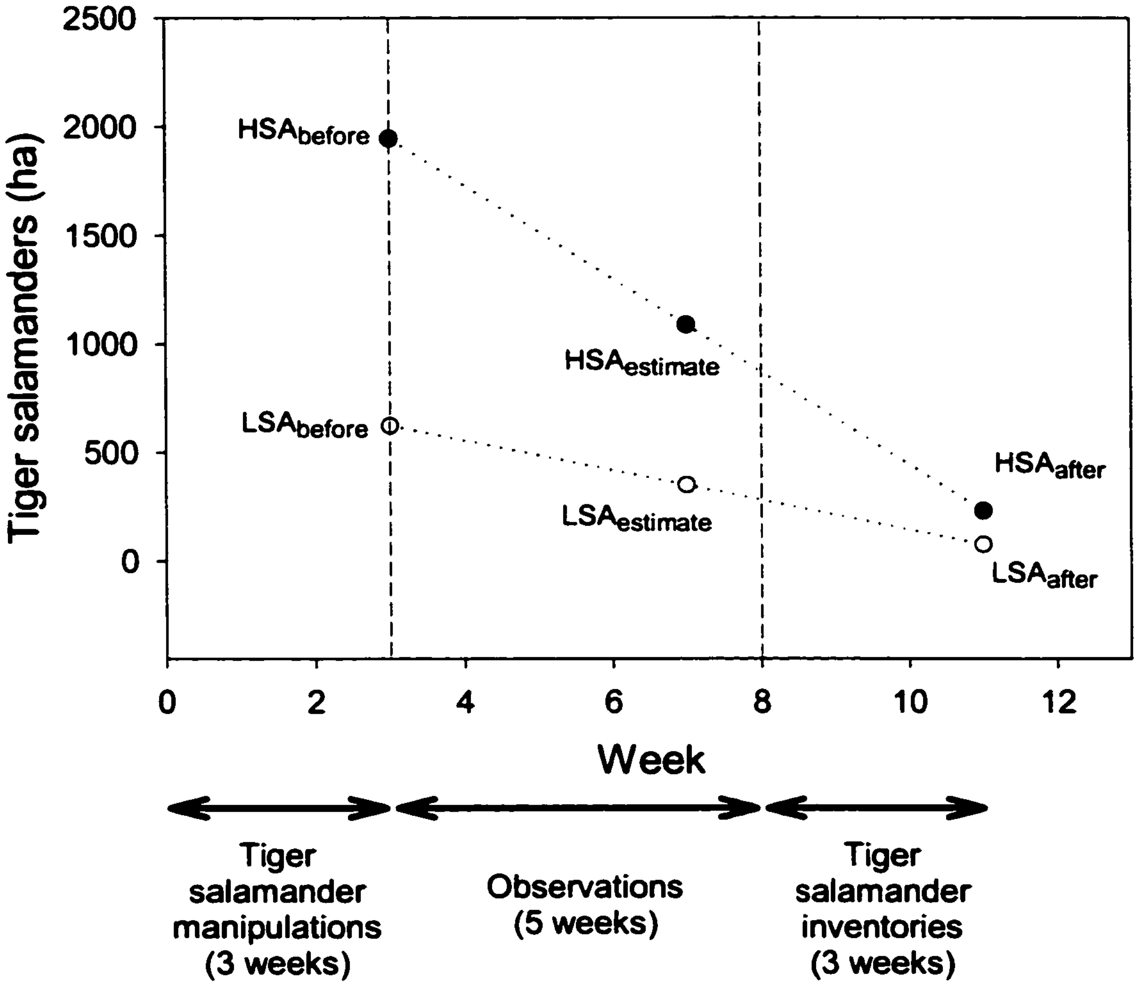
where X_{ijk} represents the foraging time response variables of the *k*th pothole on the *i*th side of the *j*th guild. μ is the overall mean for each response variable. *C* refers to the covariate (total time on each side of the barrier), *S* refers to side (LSA or HSA), *G* refers to guild (dabblers, divers, grebes or coots), *SG* is the interaction between side and guild, and ε_{ijk} is the error term. The alternative approach, including actual percentages of time spent foraging, is problematic for several reasons: 1) ratios lack normality, 2) there is an assumption that the numerator and denominator are collinear with an intercept of zero, and 3) there is an increased risk of spurious correlations (Packard and Boardman 1988, Jackson et al. 1990).

Although known quantities of tiger salamanders were removed and added on either side of the barrier in the foraging experiment, the underlying ambient tiger salamander abundances for most potholes were unknown; the exception being LSA sides of potholes where tiger salamanders were never found during trapping. For this reason, tiger salamander abundances were not formally included in any of the statistical analyses. Instead, an assessment of the tiger salamander abundances between sides of each pothole was created and used as a ranked order variable to enable graphical representation of the trends in foraging duration according to variation in differential tiger salamander abundance. Ranked order differences among potholes were calculated by linear interpolation: the difference between LSA and HSA sides of a pothole from before and after observations were summed and then divided by two, yielding a "mean" tiger salamander abundance (Fig. 4.1). The resulting values were then ranked from highest to lowest (greatest to least differences between sides over the course of the experiment; Table 4.1).

For the coot chick experiment, t-tests were used to compare estimates of survivorship and mean weights among potholes. Because nearly all of the potholes used in this experiment were devoid of tiger salamanders and known quantities were added, Pearson correlation coefficients were used to compare abundances of tiger salamanders with survivorship estimates and weights of coot chicks per pothole.

Tiger salamander and American coot manipulations for this study were approved by the Animal Care Committee (University of Guelph), on behalf of the Canadian Council on Animal Care. Permits for this research included WSP00010 (Wildlife Branch, Manitoba Conservation) and CWS00-M015 (Canadian Wildlife Service, Environmental Conservation Branch).

Figure 4.1. Schematic representation for the calculation of ranked order differences in tiger salamander abundance among potholes. P15 is used as an example. "Mean" difference in tiger salamanders = $HSA_{estimate} - LSA_{estimate}$.



Tiger salamanders (ha)
2500
2000
1500
1000
500
0
$\mathrm{HSA}_{\mathrm{before}}$
$\mathrm{HSA}_{\mathrm{estimate}}$
$\mathrm{HSA}_{\mathrm{after}}$
$\mathrm{LSA}_{\mathrm{before}}$
$\mathrm{LSA}_{\mathrm{estimate}}$
$\mathrm{LSA}_{\mathrm{after}}$
0
2
4
6
8
10
12
Week
Tiger salamander manipulations (3 weeks)
Observations (5 weeks)
Tiger salamander inventories (3 weeks)

Table 4.1. Quantities of tiger salamanders removed and added during the foraging experiment. Sides of the barrier are referred to as HSA (high salamander abundance) or LSA (low salamander abundance). Area refers to total pothole area; LSA and HSA values refer to abundances per half pothole. # added to HSA = # live trapped in LSA + total # trapped in LSA + external sources. Ranked order of differences calculated by linear interpolation at the conclusion of the experiment (see text for details).

Pothole	Area (ha)	Before observations # trapped in LSA (ha)	# added to HSA (ha)	After observations # trapped in LSA (ha)	# trapped in HSA (ha)	Ranked order of differences
C7	0.30	140.0	406.7	10.0	36.7	1
C12	0.34	0	541.2	0	65.5	2
N5	0.38	57.9	684.2	23.8	84.2	3
C1	0.22	27.3	745.5	98.2	114.6	4
P12	0.52	0	676.9	14	95.3	5
P5	0.56	60.7	707.1	44.6	191.6	6
P2	0.60	0	710.0	0	140.8	7
P4	0.23	34.8	965.2	69.6	104.3	8
P15	0.41	624.4	1946.3	76.6	232.4	9
C13	0.25	0	1152.0	0	464.0	10
P1	0.13	261.5	1984.6	61.5	81.7	11
P3	0.24	58.3	1916.7	58.3	225.0	12
P20	0.33	127.3	1963.6	106.2	312.2	13
P6	0.18	766.7	3600.0	183.6	169.2	14
P13	0.31	2458.1	5038.7	219.0	516.7	15
N14	0.20	2180.0	5240.0	330.0	910.0	16

Results

Foraging experiment

During the course of the observations, 445 birds were observed over a total of 116 hours (mean = 7.25 hours per pothole). 25.8% of the birds were found "loafing" on the barrier. The remaining birds were evenly distributed on either side of the barrier (HSA – 37.8%; LSA – 36.4%). Most individual species were also relatively evenly distributed, with the exception of Green-winged teal and Redhead (Table 4.2). Males did not exhibit a preference for either side of the barrier though almost twice as many females were observed on the LSA side. For all species except Lesser scaup, more time was spent foraging on the LSA side than the HSA side. After accounting for total time spent foraging, the next most significant factor in explaining foraging time was side, followed by guild (Table 4.3). There was no interaction between side of the pothole and guild. Dabbling ducks as a group responded most to contrasting tiger salamander abundances followed by diving ducks and coots (Table 4.4, Fig. 4.2a-c). Time spent foraging by grebes was not significantly related to the abundance of tiger salamanders although the direction of the relationship was consistent with the other birds. Finally, of the bird species that had greater than 10 individuals observed, Gadwall and Northern shoveler most skewed foraging to the LSA side of the barrier, followed by Blue-winged teal and Mallard. Redhead and Ruddy duck were the only diving ducks observed with more than 10 individuals and they were also affected by the tiger salamander treatment.

Table 4.2. Comparison of total occupancy and mean foraging times (%) by sex, guild and species across all potholes.

	Barrier	HSA occupancy	LSA occupancy	HSA foraging (%)	LSA foraging (%)
All birds	115	168	162	45.2	67.6
Male ducks	70	69	66	36.4	64.8
Female ducks	30	26	40	37.8	70.0
Dabbling ducks	86	69	80	34.4	63.6
Blue-winged teal	35	34	36	35.2	56.1
Gadwall	8	8	12	25.8	74.2
Green-winged teal	5	1	7	50.0	45.2
Mallard	14	13	12	28.2	69.3
Northern pintail	2	0	2	0	50
Northern shoveler	22	13	11	44.8	84.8
Diving ducks	14	27	23	43.7	60.3
Canvasback	2	1	1	0	0
Lesser scaup	0	2	0	100	0
Redhead	11	9	10	34.6	68.5
Ruddy	1	15	12	44.5	58.4
Grebes	0	14	11	47.8	97.0
Horned	0	7	5	44.5	93.3
Pied-billed	0	7	6	51.0	100
American coot	15	54	52	55.4	69.7

Notes: Feeding percentages need not add up to 100 as time spent foraging did not differentiate between birds that moved within a pothole or birds that arrived or departed during the course of an observation.

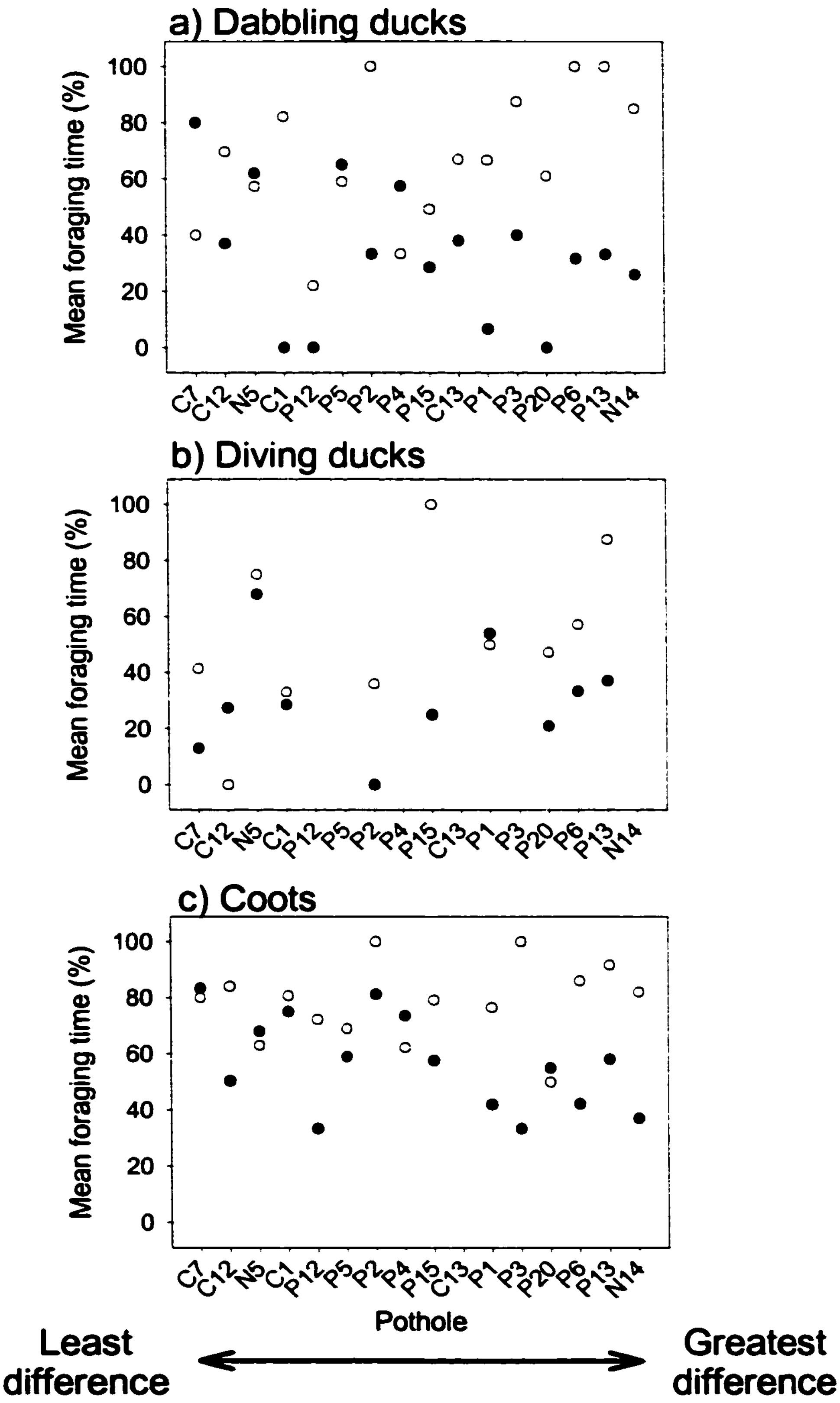
Table 4.3. ANCOVA of foraging times across potholes by Side (HSA or LSA side of the barrier) and by Guild (dabblers, divers, grebes or coots). Time (total time spent on a particular side of the barrier) is the covariate. Standard residuals were used as the error term for all analyses.

	df	F	P
Full model	8, 85	38.39	<0.0001
Time (covariate)	1, 85	182.60	<0.0001
Side	1, 85	26.41	<0.0001
Guild	3, 85	3.73	0.015
Side × Guild	3, 85	(0.56)	(0.65)

Table 4.4. ANCOVA of foraging times by Side (HSA or LSA side of the barrier), broken down according to guild and, by species, where the number of observed individuals was 10.

	df	F	P
Dabblers	1, 28	21.68	0.0001
Blue-winged teal	1, 22	6.98	0.017
Gadwall	1, 10	26.56	0.0036
Mallard	1, 14	2.71	0.13
Northern shoveler	1, 15	18.39	0.0016
Divers	1, 18	7.83	0.029
Redhead	1, 9	8.81	0.022
Ruddy	1, 11	5.66	0.068
Grebes	1, 11	3.04	0.13
Coots	1, 26	4.88	0.031

Figure 4.2. Patterns of foraging time allocations for the foraging experiment plotted against the ranked order of tiger salamander differences (i.e. N14 had the greatest difference between sides and C7 has the least difference). Filled circles represent sides of the potholes that had tiger salamanders added and open circles represent sides of potholes that were either absent of tiger salamanders or had tiger salamanders removed.



a) Dabbling ducks

b) Diving ducks

c) Coots

Coot chick experiment

Of the 20 potholes used in this experiment three had to be omitted because the chicks were never seen after the day they were fostered (Table 4.5). For two of these potholes, the parents continued to occupy the pothole, suggesting that none of the chicks survived. A total of 43 coot chicks were recaptured; 16 from the potholes with tiger salamanders and 27 from potholes without tiger salamanders. Mean chick weights among potholes were higher in the absence of tiger salamanders (Fig. 4.3a; t-test, 15 df, t = -2.145, P = 0.024, one-tailed). Even when C76 was removed from the comparison (the pothole with only one chick recaptured that weighed 303 g) the difference was still significant (t-test, 14 df, t = -2.26, P = 0.020, one-tailed). Chick survivorship was also marginally higher in the potholes without tiger salamanders though the difference was not significant (Fig. 4.3b; t-test, 18 df, t = -0.56, P = 0.29, one-tailed). Further, reduction in chick weight was greatest in potholes with the highest number of tiger salamanders added (Fig. 4.4).

Pairwise correlations among potholes between chick mean weight at 21 to 25 days and population estimates of the tiger salamanders yielded similar though statistically insignificant results; all were negatively related (Table 4.6). In contrast, no consistent pattern was observed between chick survivorship and any of the tiger salamander population estimates. However, the coefficients were slightly larger (i.e. more negative) for the larval tiger salamanders than the adults.

Table 4.5. Summary of tiger salamander and coot chick data for the coot chick study. "~" refers to potholes that were empty of tiger salamanders; none were added (i.e. "Absent"). Estimated survivorship refers to the proportion of chicks that were estimated to have survived until the time of chick retrieval. # captured refers the number of chicks and weighed to estimate growth rate.

Pothole	Area (ha)	Total # tiger salamanders added (ha)	Coot chicks			
			Estimated survivorship	# captured	Mean weight (g)	S.E.
C42	0.23	247.8	0.625	2	195.3	35.0
C31	0.09	377.8	0.75	3	192.1	39.5
C79	0.29	396.6	0			
C41	0.11	509.1	0.625	4	157.5	19.5
C70	0.22	540.9	0.375	2	198.5	26.5
C64	0.19	952.6	0.375	2	181.0	29.9
C83	0.18	1522.2	0.5	2	138.5	17.6
C52	0.11	2536.4	0			
C88	0.14	2671.4	0.375	1	134.5	
C40	0.1	~	0.375	2	190.5	15.5
C44	0.04	~	0			
C47	0.05	~	0.5	3	198.3	35.6
C49	0.13	~	0.875	5	188.4	30.3
C53	0.2	~	0.625	3	230.0	32.7
C56	0.16	~	0.5	3	172.3	21.2
C65	0.25	~	0.375	2	187.0	21.0
C67	0.24	~	0.75	3	172.3	26.8
C76	0.13	~	0.25	1	303.0	
C77	0.15	~	0.375	2	213.0	26.0
C90	0.3	~	0.5	3	195.7	17.3

Figure 4.3. Mean survivorship a) and weight b) for coot chicks (± 1 S.E.) in potholes with and without tiger salamanders. P-values indicate results of t-tests.

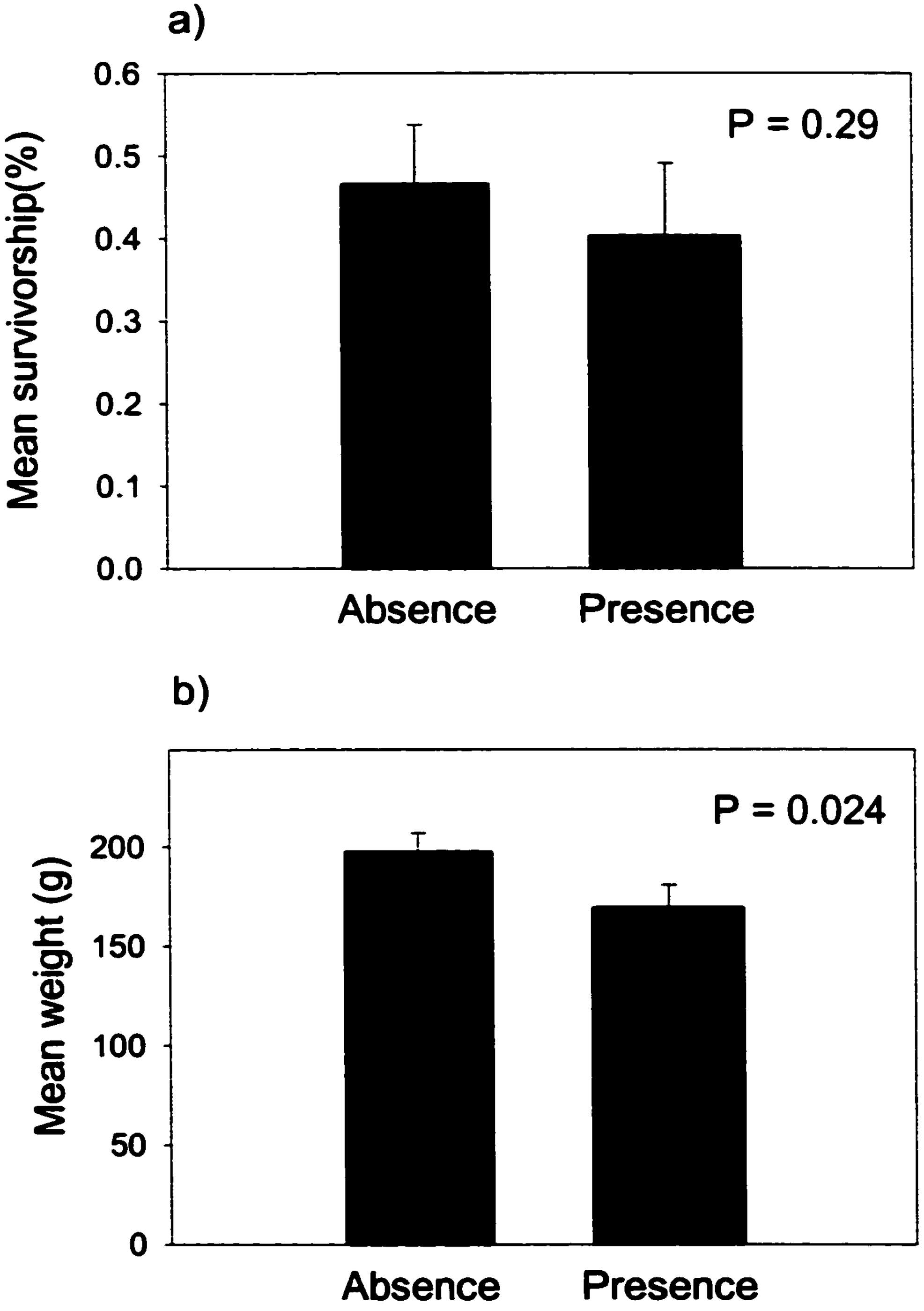

a)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mean survivorship(%)
P = 0.29
Absence
Presence
b)
200
150
100
50
0
Mean weight (g)
P = 0.024
Absence
Presence

Figure 4.4. Coot chick mean weights per pothole in relation to the number of tiger salamanders added to the high-abundance potholes. A boxplot of mean weights for potholes without salamanders is included in the figure as a reference. The lower horizontal line in the boxplot is the median and the upper line is the mean.

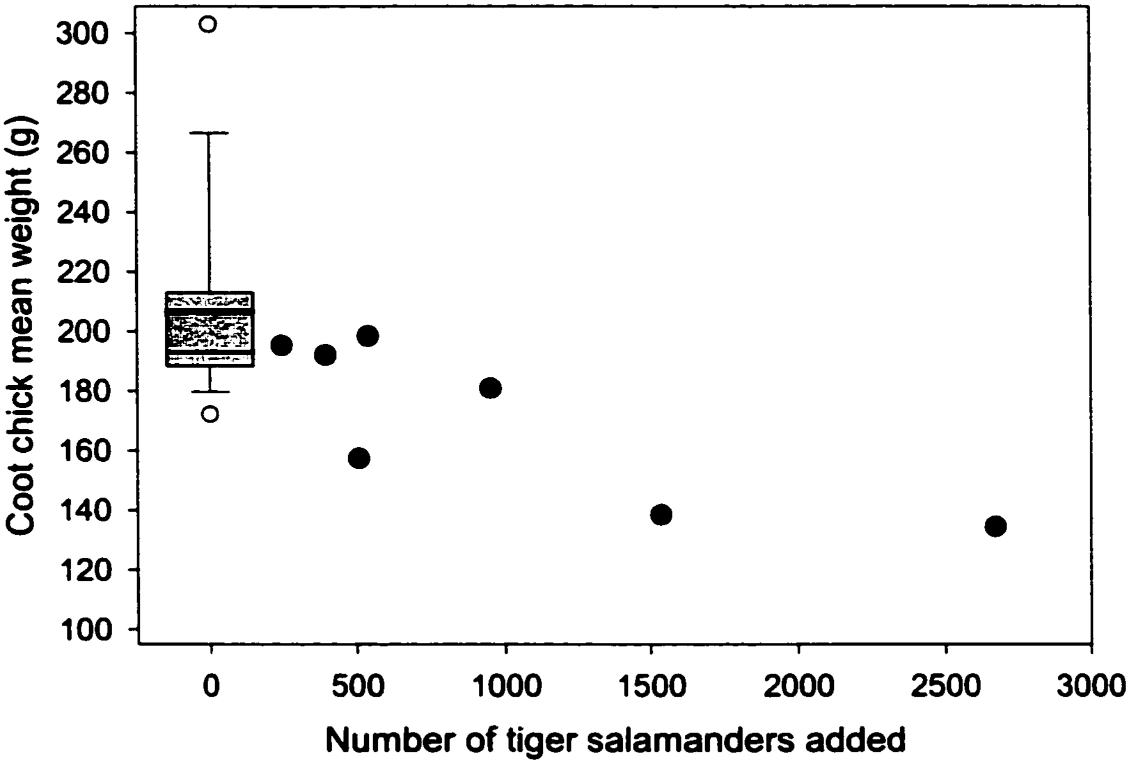

Coot chick mean weight (g)
300
280
260
240
220
200
180
160
140
120
100
0
500
1000
1500
2000
2500
3000
Number of tiger salamanders added

Table 4.6. Pearson correlation coefficients between measures of coot chick reproductive success (i.e. survivorship and weight) and tiger salamander life stages for the 9 potholes containing tiger salamanders. Analyses are based on mean survivorship and mean weight per pothole.

	N	r	P
Chick survivorship			
Total	9	-0.17	0.68
Larvae	9	-0.26	0.41
Adults	9	0.14	0.72
Mean chick weight			
Total	7	-0.47	0.20
Larvae	7	-0.51	0.16
Adults	7	-0.36	0.34

Discussion

Ecologists have postulated the importance of indirect effects in the structuring of communities for several decades (e.g. May 1973, Bender et al. 1984, Wootton 1994). Exploitation competition, whereby two species interact through a common resource, is perhaps the most familiar indirect effect (Schoener 1993). For these two experiments, I took advantage of the indirect effect of tiger salamanders on breeding waterfowl through invertebrate resources that I observed in earlier studies (Chapters 1, 3). Within potholes, waterfowl skewed their foraging time budgets towards low tiger salamander abundance areas. Similarly, among potholes, American coot chick growth rates were higher where tiger salamander abundances were lower.

In lieu of formal mark-recapture approaches to estimating tiger salamander population abundances, interpolations based on simple abundances were used to rank potholes according to tiger salamander burden. The number added to the HSA side in the foraging experiment, and the number added to the HSA potholes in the coot chick experiment, ranged from 541.2 ha to 5240 per ha. Tiger salamander abundances in the thousands per hectare were almost entirely comprised of larvae and they are comparable to the range reported for wetlands in North Dakota (Wiedenheft 1983, Deutschman and Peterka 1988). High densities of larvae tend to experience high rates of mortality and by the time the remaining larvae reach a sexually mature state, as metamorphs or paedomorphs, densities drop to hundreds per hectare (Deutschman and Peterka 1988). My estimates of tiger salamander abundance were very close to those reported in the literature.

When tiger salamanders and waterfowl do coexist, the likelihood of significant indirect interaction is high. General diet overlap exists between tiger salamanders and ducks (Chapter 2). Further, dabbling ducks have higher diet overlap with tiger salamanders than diving ducks. Results of this study indicate that dabbling ducks altered their activity budgets to spend relatively more time foraging on the LSA side of the barrier than did diving ducks. Interestingly, the two species that skewed their foraging locations most towards the LSA side of the barrier, Gadwall and Northern shoveler, also had the highest prey type overlap with tiger salamanders and were among the four species that had the highest prey size overlap with tiger salamanders, as identified in Chapter 2. These behavioural patterns are consistent with Kaminski and Prince (1981), who found that the percentage occurrence of foraging by dabbling ducks was positively correlated with mean invertebrate abundance. While male ducks showed no preference for occupying LSA or HSA sides of the barrier, females spent 50% more time on the LSA side. Similarly, females spent proportionately slightly more time foraging on the LSA side of the barrier than males did. Prelaying and laying female ducks exhibit higher demands for invertebrate prey than males (Krapu and Reinecke 1992) and other studies involving activity budgets of ducks have also found that females preferentially forage where invertebrate abundances are relatively higher and for longer periods of time (Kaminski and Prince 1981, Krapu and Reinecke 1992).

Grebes, in contrast, did not appreciably alter activity budgets in relation to tiger salamander abundances. This may be due to low statistical power to detect an effect, although there are two ecological reasons as well why grebes might not respond to tiger salamander-induced differences to the prey resource base. First, grebe diets, especially

Pied-billed, include amphibian larvae (Ehrlich et al. 1988) so their relationship with tiger salamanders may more properly be described as intraguild predation (Polis and Holt 1992). Second, tiger salamanders are gape-limited, constraining access to larger invertebrates that are otherwise potentially available to grebes (Zaret 1980). The strength of the coot response to contrasting tiger salamander abundances was intermediate to those of ducks and grebes. Adult coots are primarily herbivorous, relative to the other birds observed in this study, except during the breeding season when aquatic insects and molluscs are incorporated into the diet (Alisauskas and Arnold 1994). Therefore, although increased tiger salamander abundances may have reduced invertebrate availability, the consequences of this were, proportionally, less for coots than that for most dabbling and diving ducks.

Partial brood loss in coots is estimated to be just over 50% by the time of fledging at 60 to 70 days (Alisauskas and Arnold 1994), although the rate of attrition likely diminishes over the course of brood rearing. Newly hatched chicks are not immediately vulnerable to starvation because they have lipid stores in their yolk sac that can last for a couple of days (Hill 1988). My survivorship results are consistent with this estimate (1 – mean survivorship for all broods = 56.2%, or 4.5 chicks lost, on average) except that the proportion of brood loss in my experiment occurred in only three to four weeks. Although not statistically significant, survivorship was slightly higher in potholes without tiger salamanders (mean difference = 0.5 chicks).

Compared to adult coots, chicks rapidly change diets. Driver (1988) found that invertebrates comprised 84% (dry weight) of chick diets and that by the time the chicks were getting ready to fledge invertebrates comprised only 21%. The coot chick gut contents reported in Driver (1988) came from northeast of Saskatoon, Saskatchewan, and they included, in rank order by percent dry weight, Coleoptera, Trichoptera, Diptera, Physidae (Gastropoda), insect eggs and Odonata. This dietary profile resembles that of tiger salamanders (Chapter 1), consistent with the hypothesis that the mechanism linking tiger salamander abundances to coot chick growth rates was exploitation competition. Chick mean weights were on average 14.3% higher in the low tiger salamander abundance potholes than the high-abundance potholes after three to four weeks. It is unclear if this reduction in weight had any consequence on overall brood survivorship. If partial brood loss is a function of food limitation then the reduction in mean weight within a brood is likely to increase the vulnerability of the lightest chicks. This vulnerability is also likely exacerbated as result of sharply decreased parental involvement in feeding invertebrate prey to chicks (Driver 1988).

Mean chick weights in the potholes containing tiger salamanders were partly a function of the number of tiger salamanders added. The shape of the curve suggests that the greatest decrease in mean weights occurred in potholes with the highest number of tiger salamanders. This is consistent with Chapters 1 and 3 suggesting that the effects of tiger salamanders on pothole invertebrate community structure are apparent once a critical mass of tiger salamanders is exceeded. The relationship between invertebrate community structure and fathead minnow density also appears to be non-linear but it suggests that effects by fathead minnow are relatively even, regardless of density (Zimmer et al. 2000). Presumably, therefore, even at low fathead minnow densities, growth rates of coexisting coot chicks could also be suppressed.

In addition to food limitation, other factors have been hypothesized to account for variation in survivorship and growth rate, such as genetic differences and maternal effects (Horsfall 1984, Hill 1988, Reed 1999). These alternative hypotheses can be tentatively rejected as explanations for the results obtained for the following two reasons. First, the fostering design controlled for the effects of parentage by randomly assorting eggs and chicks among nests. Second, Hill (1988) found that when food abundance was relatively high coots increased the size of their young. The fact that most of my potholes (~75%) were devoid of tiger salamanders meant that variation in food abundance among potholes was partially controlled for by the random allocation of tiger salamanders. However, considering that only a quarter of the potholes without tiger salamanders were assigned to tiger salamander additions, there is still the possibility that other factors may contribute to explain the variation in coot chick survivorship and growth rate other than indirect interactions with tiger salamanders for common invertebrate prey resources.

Manipulative field experiments represent a powerful tool for testing hypotheses of community structure, providing appropriate controls and adequate replications are in place (Raffaelli and Moller 2000). The cumulative results of such experiments on food limitation in migratory waterfowl suggests that 1) waterfowl activity budgets and growth rates are sensitive to variation in food supply, 2) the brood stage may be the most important stage for population regulation during the breeding season, 3) coexisting tiger salamanders, especially at relatively high abundances, strongly indirectly interact with waterfowl through exploitation of common prey, and 4) hydrologic conditions favourable to the distribution and establishment of tiger salamanders have greater consequences for dabbling ducks than diving ducks.

GENERAL DISCUSSION & CONCLUSIONS

Breeding waterfowl depend on invertebrates in prairie potholes for reproduction and brood rearing and they also have pronounced effects on pothole community structure. The influence of predators on waterfowl nest success and the primal importance of vegetation in determining primary and secondary production are not disputed as a consequence of this research. Rather, the finding that waterfowl exert trophic control on invertebrate populations and phytoplankton standing crop indicates that waterfowl populations are vulnerable to the effects of food limitation. Thus, the impacts of waterfowl on prairie pothole food webs can be added to a growing list of communities that exhibit structure as a result of avian predation (Hurlbert and Chang 1983, Quammen 1984, Wootton 1992, Hamilton 2000). Further, the results obtained in this research are likely conservative as most of my study potholes were at or near their maximum depths and areas. During years with poor water conditions, resource limitation may be more severe when greater numbers of waterfowl are nesting around and foraging in fewer potholes.

Inferences based on a pothole "trophochain" are relatively straightforward. However, 1998 and 1999 were "wet" years in the long-term scheme of the wet-dry cycle and many of my semi-permanent study potholes were occupied by tiger salamanders. The presence of these consumers obscured the occurrence of waterfowl-induced trophic interactions suggesting that tiger salamanders are compensatory predators in prairie potholes with respect to invertebrate populations. More conspicuously, where tiger salamander abundances were high, waterfowl preferentially foraged elsewhere and coot chick growth rates were depressed. This remarkable and hitherto overlooked influence of tiger salamanders on prairie pothole community structure suggests that many existing studies of prairie pothole communities are incomplete.

In Chapter 1, I showed that tiger salamanders are the functional equivalents of planktivorous fish in fishless wetlands. Despite the fact that fish are the top aquatic consumers in only a portion of the Prairie Pothole Region, little else is known regarding the influence of either amphibians or macroinvertebrates that occupy the position of top aquatic consumer in potholes otherwise inhospitable to fish. Invertebrate abundance and phytoplankton standing crop varied according to tiger salamander abundance among potholes. Specifically, I found that abundances of both macroinvertebrates and herbivorous microcrustaceans were inversely related to tiger salamander abundance. I accounted for this by proposing that, for prairie potholes, many taxonomic groups of macroinvertebrates run the gamut of trophic functions (i.e. carnivorous, omnivorous and herbivorous) and the most numerous macroinvertebrate taxa were either herbivores or omnivores. Omnivory is commonly cited as one of the major reasons why trophic cascades are often attenuated at the zooplankton trophic level in lakes (McQueen et al. 1986, 1989). I also found that phytoplankton standing crop was positively related to tiger salamander abundances, which is consistent with predicted patterns of trophic structure if all of the invertebrates are grouped as a single trophic level and the majority of the invertebrates are mainly herbivorous. I invoked two mechanistic explanations for this relationship; one based on direct consumer-resource interactions and the other on processes of nutrient recycling and transfer.

In Chapter 2, I continued the functional equivalence analogy between planktivorous fish and tiger salamanders by arguing that well studied indirect interactions between fish and waterfowl should also apply to tiger salamanders and waterfowl. Tiger salamanders were shown to have substantial dietary overlap with ducks. This finding alone is not surprising as tiger salamander diets generally reflect ambient invertebrate compositions and abundances (Brophy 1980, Zaret 1980, Olenick and Gee 1981) and the diverse species of ducks in the region have morphological traits that minimize prey and habitat overlap and lead to exploitation of most invertebrate resources (Nudds and Bowlby 1986, Nudds 1992). However, I also found that ducks appear to coarsely partition prey and habitat resources in relation to tiger salamanders; dabbling ducks had greater dietary overlap with tiger salamanders while diving ducks had greater spatial overlap. Thus, the consequences of widespread occupancy of prairie potholes by tiger salamanders should have a greater impact on dabbling ducks than diving ducks.

These results from Chapters 1 and 2 helped to account for some of the variation commonly observed in community structure among potholes (Goldsborough and Robinson 1994, Murkin 1989, Euliss et al. 1999) and to establish the potential for indirect interactions between waterfowl and tiger salamanders. Coexistence between the two types of consumers appears to be facilitated by variation in climatic and hydrologic conditions. Although tiger salamanders may have advantages over waterfowl within a pothole in acquiring shared prey resources, the wet-dry cycle prevents the long-term establishment of permanent tiger salamander populations. Environmental conditions favourable to the establishment of tiger salamander populations though would also be favourable to fathead minnow and brook stickleback and both of these planktivorous fish species are able to displace tiger salamanders where they coexist (Wissinger 1999). Thus, the same fluctuating environmental conditions that are related to waterfowl diversity (Nudds 1983, 1992) and production (Batt et al. 1989) also regulate tiger salamander distributions and abundances. The consideration of fish in studies of wetland and waterfowl ecology is routine (Bouffard and Hanson 1997) and I recommend that tiger salamanders be given comparable attention in fishless wetlands.

In Chapter 3, I tested for the effects of ducks, grebes and coots on pothole trophic structure. Through the use of large exclosures in a well-replicated experiment, I showed that the removal of waterfowl foraging was responsible for significant increases in invertebrate abundance, biomass, richness and diversity. I also found that phytoplankton standing crop was decreased in the absence of waterfowl. These results are similar to those obtained in Chapter 1 on variation in trophic structure among potholes as a function of tiger salamander abundance, suggesting that the actual composition of top-consumers of aquatic prey resources in prairie potholes is less important to the determination of abundance at lower trophic levels than the overall consumer demand. This is consistent with the hypothesis that competitive interactions among breeding waterfowl are important determinants of community structure (Nudds and Wickett 1994), contrary to the conclusions of Pöysä (1983, 1984) and DuBowy (1988, but see Bethke 1991).

Subsequent analyses of the effect sizes of invertebrates and algae obtained as a result of the exclosure manipulations revealed two additional findings. First, the abundance of waterfowl at each pothole was positively related to the magnitude of the difference in effect size due to the exclosures and, second, tiger salamander abundance was negatively related. The greatest effects of waterfowl on trophic structure occurred in potholes without tiger salamanders and with high bird abundances. However, the simple presence of tiger salamanders in a particular pothole did not necessarily alter trophic structure. Only at relatively high abundances did tiger salamanders obscure waterfowl effects on invertebrates and phytoplankton standing crop. These results highlight the importance of compensatory predation by tiger salamanders in determining trophic structure in prairie potholes. This is the first study to consider the importance of compensatory predation between consumers in prairie potholes, though similar indirect effects have been observed in the marine intertidal zone involving birds (Marsh 1986, Hamilton 2000).

Strong (1992) argued that the net effect of compensatory predation, along with omnivory and substitutability of species, is to stabilize trophic structure. My results, like Hamilton's (2000), are consistent with this hypothesis. However, Strong (1992) also asserted that evidence of cascading trophic interactions should be more suppressed in "reticulate" systems. Results from my experiments and those of Hamilton's (2000) conflict with this claim. Hamilton (2000) found little evidence for trophic cascades in a relatively simple rocky intertidal system, whereas I did find evidence consistent with the trophic cascade hypothesis in the absence of tiger salamanders in the relatively more speciose prairie pothole system. I suggest that simplicity *per se* is less relevant than the composition of the consumer trophic level and the scale of the study. In my exclosure experiments, a diverse assemblage of waterfowl was excluded from portions of potholes whereas in Hamilton (2000), 95% of the avian predators were common eiders and their diets are largely comprised of one species, blue mussels.

The last major finding of Chapter 3 was that exclosure outcomes varied with time. Prairie potholes are essentially seasonal environments and many biotic communities follow predictable chronologies from ice-out to freeze-up. Competitive interactions among consumers may be greatest mid-way through the breeding season, during the brood rearing period, for several reasons, 1) broods exhibit high demands for invertebrate prey, 2) invertebrate abundance and mean length decreases (Armstrong and Nudds 1981) and 3) newly hatched tiger salamander larvae, when present, are also scrambling for prey. This variation in effect size depending on timing during the breeding season laid part of the groundwork for Chapter 4.

Others have found evidence supporting the hypothesis that food limitation in migratory waterfowl is most intense during the brood rearing phase (e.g. Cox et al. 1998, Sjöberg et al. 2000), but they did so under pseudo-natural conditions. In Chapter 4, I switched focus to measuring the effects of variation in community structure on waterfowl. I manipulated pothole prey resources by exploiting the effects of tiger salamanders on trophic structure observed in Chapter 3. I found that the proportion of time spent foraging by ducks and coots was reduced in the presence of tiger salamanders and that, consistent with diet overlap findings from Chapter 2, dabbling ducks altered their foraging time budgets more than diving ducks. I also found that American coot chick growth rates were reduced in the presence of tiger salamanders. Abundances of tiger salamanders in both experiments were within the range of observed abundances for similar prairie wetlands in North Dakota (Deutschman and Peterka 1988), so I concluded that the results obtained approximated variation under natural conditions.

The questions of competition and resource limitation in migratory waterfowl continue to be problematic for ecologists and mangers. Nudds (1992) listed three types of evidence that has traditionally been used to support arguments in defense of competition in waterfowl. The first consists of simply documenting ecological differences among species (e.g. Nudds and Bowlby 1984, Chapter 2). The second consists of measuring changes in behavioural and ecomorphological differences among species that are believed to be sensitive to competitive pressures (e.g. Nudds 1983, DuBowy 1988). Because both of these types of evidence are tautological (Peters, 1991, Nudds 1992) they are prone to be accepted as evidence for competition when other processes may actually underlie observed patterns. The third type of evidence for competition includes either manipulative or "natural" experiments. Waterfowl exclosures have been used to assay the presence of competition (or resource limitation) in both the breeding and wintering grounds but they have yielded mixed results, possibly because the exclosures were too small (Smith et al. 1986, Peterson et al. 1989, Wrubleski 1989, Barnes and Nudds in Nudds 1992). My results in Chapter 3 also qualify as the third type of evidence for competition but they are based on experimental manipulations of sufficient size that adequately mimicked ambient limnological conditions.

Whether or not evidence of competition confers evidence of resource limitation is debatable. Osenberg and Mittelbach (1996) argued that the occurrence of cascading trophic interactions is insufficient evidence because the cascade pattern can result from other processes that dynamically link adjacent trophic levels. They state that the only way to test for resource limitation is to isolate a putative limiting factor and quantify resulting per capita growth rates. However, they also state that, under manipulative field conditions, measures of change in biomass over time can be used instead (Osenberg and Mittelbach 1996, p. 138). My findings in Chapter 3, that invertebrate biomass increased in the absence of waterfowl, provides evidence towards the determination of resource limitation according to Osenberg and Mittelbach (1996) because I employed a manipulative field experiment that isolated one putative source of limitation (i.e. indirect interactions between waterfowl) and measured the response over time. For similar reasons, my result in Chapter 4, showing decreased coot chick growth rates in the presence of high tiger salamander abundances, also provides evidence consistent with resource limitation. The most complete picture of waterfowl population regulation would employ both consumer exclusions and fertility treatments in both the breeding and wintering grounds.

Conclusions

In this thesis, I tackled the vexing problems of food limitation in migratory waterfowl and interactions with other consumers during the breeding season. To do so, I employed several methodological techniques including literature-based comparative studies, observational studies and manipulative field experiments. This multi-pronged approach resulted in a comprehensive study of the relationships between ducks, grebes and coots and prairie pothole food webs. Results of Chapters 1 and 2 addressed a conspicuous inconsistency in prairie pothole ecology – the routine inclusion of planktivorous fish but the omission of tiger salamanders and their potential for indirect interactions with breeding waterfowl. Not only do tiger salamanders affect the trophic structure of prairie potholes, but they also exhibit considerable diet overlap with dabbling and diving ducks. Chapter 3 broadened our understanding of wetland ecology by showing that waterfowl are influential members of prairie pothole communities and by highlighting a previously undocumented interaction between waterfowl and tiger salamanders. Chapter 4 built on the previous chapters by demonstrating the consequences of variation in food web structure on waterfowl behaviour and American coot offspring success. The combined results of all four chapters demonstrate that waterfowl and tiger salamanders indirectly interact for prey resources indicating that waterfowl affect prairie pothole community structure and that they are sensitive to variation in food availability.

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APPENDIX 1

Species lists

The following tables are lists of species that I encountered in my study potholes during 1998 and 1999. Number refers to the number of potholes in which each species was found (maximum = 24 for 1998 and maximum = 21 for 1999). For the waterfowl (a), abundance refers to the total number of individuals observed. For the amphibians (b), the macroinvertebrates (c) and the microcrustaceans, abundance refers to the total number of individuals sampled.

a) Waterfowl

Species	1998		1999	
	Number	Abundance	Number	Abundance
family Anatidae				
subfamily Anatinae				
tribe Anatini				
Anas americana	2	4	0	0
Anas strepera	22	141	14	88
Anas crecca	12	36	5	36
Anas platyrhynchus	23	167	19	62
Anas acuta	5	14	3	10
Anas discors	24	318	15	156
Anas clypeata	19	137	12	69
tribe Aythyini				
Aythya valisneria	10	51	15	63
Aythya americana	17	100	13	43
Aythya collaris	7	40	8	26
Aythya affinis	7	19	2	12

tribe Oxyurini				
Oxyura jamaicensis	15	87	17	156
subfamily Anserinae				
tribe Anserini				
Branta canadensis	4	14	0	0
family Rallidae				
Fulica americana	24	390	20	557
family Podicipedidae				
Podiceps auritus	7	64	2	16
Podilymbus podiceps	8	47	13	71

b) Amphibians and fish

Species	1998		1999	
	Number	Abundance	Number	Abundance
order Caudata				
family Ambystomatidae				
Ambystoma tigrinum	20	527	16	375
order Salienta				
family Hylidae				
Hyla crucifer	2	6	1	3
Pseudacris maculata	20	161	15	62
family Ranidae				
Rana sylvatica	5	19	4	13
Rana pipiens	10	82	8	26
order Cypriniformes				
family Cyprinidae				
Pimephales promelas	0	0	1	5

c) Macroinvertebrates

	1998		1999	
Species	Number	Abundance	Number	Abundance
class Insecta				
order Ephemeroptera	17	99	16	91
order Odonata				
family Lestidae	24	295	21	549
family Coenagrionidae	16	89	18	133
family Aeshnidae	8	22	11	35
family Libellulidae	19	92	15	57
order Trichoptera				
family Limnephilidae	13	71	20	406
order Heteroptera				
family Corixidae	24	1000	21	1677
family Notonectidae	12	53	21	118
family Belastomatidae	1	2	3	3
order Coleoptera				
family Dytiscidae	24	1335	21	2024
family Haliplidae	24	329	20	261
family Hydrophilidae	15	202	13	106
family Gyrinidae	4	9	3	6
family Curculionidae	3	3	3	3
order Diptera				
family Chaoboridae	24	362	21	647
family Ceratopogonidae	21	64	8	17
family Chironomidae	24	2171	21	4024
family Culicidae	1	9	1	1
class Entognatha				
order Collembola	1	2	1	1

class Gastropoda				
subclass Pulmonata				
family Lymnaeidae	24	646	21	287
family Planorbidae	24	412	21	261
family Physidae	22	239	21	145
phylum Annelida				
superfamily Hirudinoidea				
family Erpobdellidae				
genus Erpobdella	18	97	21	178
family Glossiphoniidae				
genus Helobdella	24	387	21	525
genus Placobdella	12	32	8	16
subphylum Crustacea				
order Amphipoda				
family Hyallelidae	21	1704	20	5294
family Gammaridae	1	2	2	7
order Anostraca				
genus Eubranchipus	1	7	0	0

d) Microcrustaceans

	1998		1999	
Species	Number	Abundance	Number	Abundance
class Arachnida				
subclass Acari	24	675	21	652
subphylum Crustacea				
order Conchostraca	13	3072	3	111
order Anomopoda (Cladocera)	24	55255	21	120341
class Ostracoda	24	45932	21	3389
class Copepoda	24	3626	21	13203

APPENDIX 2

Zaret's characteristics that qualify *Ambystoma* as "a fish in amphibian's garments"

The set of six characteristics that Zaret (1980, p. 44) listed to use as criteria by which to estimate the similarity of tiger salamanders and planktivorous fish on aquatic food webs.

1. They exhibit a gape-limited electivity curve for zooplankton, with the upper limit set by mouth diameter.
2. They are visually dependent predators.
3. Adults grow to a relatively large size, up 8 cm snout to vent, or about 25 cm total length, considerably larger than their prey.
4. The larger adults take snails, amphipods, and insect larvae; the smaller larvae seem to rely more on zooplankton.
5. They select *Chaoborus* over crustaceans and cladocerans over copepods of comparable or larger size.
6. They are predatory on salamanders and tadpoles.

APPENDIX 3

Invertebrates eaten by tiger salamanders in the Minnedosa, Manitoba, area of the Prairie Pothole Region

Below is a list of invertebrate prey consumed by the tiger salamanders dissected for Chapter 2. Number refers to the number of tiger salamanders that consumed each invertebrate species (maximum = 98).

Species	Number
Chironomidae	87
Chaoboridae	12
Ceratopogonidae	8
Corixidae	74
Dytiscidae	48
Haliplidae	14
Hydrophilidae	3
Unknown Coleoptera	3
Lestidae	21
Libellulidae	7
Coenagrionidae	14
Unknown Zygoptera	6
Ephemeroptera	20
Trichoptera	10
Lymnaeidae	16
Physidae	20
Planorbidae	22
Unknown Gastropoda	2
Hyallelidae	39
Eubranchipus	1

Acari	4
Cladocera	53
Copepoda	11
Ostracoda	59
Conchostraca	31

APPENDIX 4

Distribution of waterfowl in relation to exclosure infrastructure

In Chapter 3, in 1999, paired controls were constructed adjacent to waterfowl exclosures to test for "cage effects" that may bias outcomes towards an increase in Type I error. However, it is not always clear that paired controls are appropriate when perturbation experiments involving birds are run because there is a concern that birds may modify behaviour and avoid the partial exclosure structure (e.g. Marsh 1986). Inferences regarding the influence of waterfowl on prairie pothole trophic structure beyond the experimental infrastructure are, therefore, predicated on the assumption that waterfowl are proportionately distributed between controls and the open water. I tested this assumption by observing waterfowl in three potholes on three to five occasions over one month in 1998. These three potholes were members of the study set in 1998 until repeated "swamping" due to heavy rains invalidated the effects of waterfowl exclusion. After repairs and removal of the netting, observations were initiated. Three-hour observation periods included recording the composition and location of all waterfowl at 10-minute intervals across the entire pothole.

The number of waterfowl occupying the open water was much greater than the controls, which was not surprising given the relatively small size of the control relative to the whole pothole (Table A.3.1). 32.4% of all the birds observed were "loafing" on the experimental infrastructure and most of these were dabbling ducks following by diving ducks and American coots. A chi-square goodness of fit test between "Area ratio" and

"Waterfowl ratio" revealed that the two distributions did not significantly differ ($\chi^2_{0.05,2}$ = 5.991 > 4.946). Although 81 more birds were observed in the open water than the controls, the usage rate between areas was directly proportional to area. Thus, inferences based on comparisons between controls and exclosures in 1999 can be extrapolated to the whole pothole.

Table A.3.1. Mean number of waterfowl observed according to specific location by pothole. "Loafing" refers to birds that were observed directly on the infrastructure (preening, sleeping, etc.). "Area ratio" refers to the pothole area divided by the control area (60 m^2) and "waterfowl ratio" refers to the bird counts in open water divided by controls.

Pothole	Area (ha)	Area ratio	Waterfowl locations			Waterfowl ratio
			Loafing	Controls	Open water	
P5	0.521	86.83	0.10	0.045	4.30	96.27
P6	0.560	93.33	1.25	0.051	3.81	74.63
P25	0.413	68.83	0.31	0.11	8.06	72.13