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Invertebrate Community Structure in Relation to the Foraging Ecology of Mallard and Bufflehead Ducklings in Western Canada

Spine Title: Duckling Diets and Aquatic Invertebrates

by

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Hope and the future for me
are not in lawns and cultivated fields,
not in towns and cities,
but in the impervious and quaking swamps.

-Henry David Thoreau

Dedication

For Richard and Sharon, for their unwavering belief in my abilities;
and Christine, for her support and encouragement.

Abstract

Aquatic invertebrates are an integral part of wetland function and are essential for duckling growth and development. The western boreal forest (WBF) is the primary breeding ground for Bufflehead ducks (*Bucephala albeola*) and supports more than one quarter of the Canadian breeding Mallard (*Anas platyrhynchos*) population. Understanding invertebrate community ecology and how ducklings use this food source within the WBF are important as this area faces ongoing anthropogenic alteration. Furthermore, there are continental population implications as boreal wetlands can act as alternate breeding habitat for waterfowl during drought years in southern locales.

Aquatic vegetation complexity and prevalence, and fish presence were used to predict the distribution of invertebrate biomass in 24 wetlands within the southern portion of the WBF. Brook Stickleback (*Culaea inconstans*) significantly reduced overall invertebrate biomass and the biomass of most functional feeding groups of invertebrates, suggesting a competitive relationship with ducklings. The biomass/L of most invertebrate feeding groups was negatively correlated with dissected-leaf plant dominance, such as Northern Watermilfoil (*Myriophyllum exalbescens)*; presence of this plant has been associated with anthropogenic influence.

Comparative dietary and stable isotope analysis showed that Bufflehead ducklings from the WBF significantly preferred predaceous aquatic invertebrates as prey, specifically the larval form of the predaceous diving beetle (Coleoptera: Dytiscidae). Mallard duckling stable isotope signatures and dietary constituents were compared to the stable isotope signatures and availability of invertebrate prey over three ecozones: boreal plain, aspen parkland, and prairie. Overall, Mallard ducklings also preferred predaceous invertebrates (specifically Coleoptera) and maintained a more constricted foraging niche in boreal habitats, suggesting that the WBF

provides more available resources for foraging ducklings than the other two ecoregions. Boreal wetlands also had the highest invertebrate biomass/L. Food limitation can structure waterfowl populations; therefore the food preferences outlined here may help managers understand wetland characteristics important for the sustainability of ducks in the WBF and in other regions.

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Chapter 1

Ducklings and Aquatic Invertebrates of the Western Boreal Forest

The sound management of waterfowl populations requires an understanding of their feeding ecology and food preferences, especially during early life stages when mortality is high. Aquatic invertebrates are the primary protein source for duckling growth and development. Efficient foraging on aquatic invertebrates results in increased duckling survival (Cox et al. 1998), one of the three key determinants of waterfowl population dynamics (Hoekman et al. 2002). Hence, understanding the distribution and abundance of duckling food resources is needed for the management and sustainability of waterfowl. After the Prairie Pothole Region (PPR; Figure 1.1: Mixed-grass Prairie), the Western Boreal Forest (WBF; Figure 1.1: Boreal Plain) provides breeding habitat for the greatest number of North American waterfowl. This area has been assessed as the third most important waterfowl area in North America by Ducks Unlimited Canada (2000), because of its role in sustaining continental waterfowl populations, the lack of ecological information from the area, and rate of landscape alteration. This study is conducted over three ecoregions; the WBF, PPR and the Aspen Parkland (Figure 1.1).

The Functional Ecology of Western Boreal Forest Wetlands

The WBF in Alberta is undergoing rapid anthropogenic alteration (Schindler 1998). This area provides excellent habitat for waterfowl and other waterbirds, mammals, and invertebrates with its relatively contiguous habitat and numerous wetland complexes (Thomas 1998, Afton and Anderson 2001). Northern wetlands are hypothesized to support continental Mallard (*Anas platyrhynchos*) populations by providing breeding habitat when wetland conditions in the PPR are not favourable (Johnson and Grier 1988, Niemuth and Solberg 2003). Over the past 40 years, Canadian Wildlife Service waterfowl surveys have found that a decrease in breeding Mallard numbers in the Canadian Prairies has been offset by stable or increasing numbers in the WBF (Figure 1.2). Conversely, when breeding waterfowl numbers have periodically decreased in the WBF an increase was found in the PPR, with researchers attributing the PPR increases to improved prairie wetland condition and density (Canadian Wildlife Service Waterfowl Committee 2003).

More Bufflehead (*Brucephala abeola*) ducklings are reared in the WBF than in any other region on earth (Erskine 1972, Gauthier 1993) highlighting this area's role for the species. Unfortunately, the amount of research initiated on boreal wetlands, especially with regard to invertebrates, has left the aquatic trophic dynamics of the pre-disturbance state poorly understood and has increased the potential for the mismanagement of boreal natural resources (Kellomaki 2000). It is important that the wetlands of the boreal forest be studied in light of the ongoing alterations to which they are being subjected.

While little is known about the aquatic invertebrates of the WBF, it is certain that this area has low overall species diversity because of its northern latitude and recent glacial history (Schindler 1998). Low diversity leads to a lack of functional redundancy that can make aquatic invertebrate communities there relatively susceptible to drastic alteration (MacArthur 1955, Rosenzweig 1995, Jacobsen et al. 1997). This sensitivity may result in drastic changes in invertebrate composition from seemingly innocuous landscape alterations, and may have ramifications for waterbirds that depend on invertebrates. Winters are long in the WBF, with ice forming early and persisting into the spring. This increases the likelihood of a fish winterkill thereby altering wetland aquatic community composition and changing the relationship migratory birds have with wetlands (Bouffard and Hanson 1997).

Waterfowl studies initiated within the Fennoscandian boreal region are not easily compared when considering wetlands in the WBF. Nutrient states differ drastically; Fennoscandian wetlands are considered 'rich' waterfowl ponds at phosphorus concentrations of 19 – 30 μg/L (Sjöberg et al. 2000), while in the WBF phosphorous concentrations average 120 μg/L (Bayley and Prather 2003). Less than 7% of 148 southern boreal plain wetlands surveyed by Bayley and Prather (2003) were below a phosphorus threshold at which wetland invertebrate productivity results in Mallard duckling food limitation (Sjöberg et al. 2000). The unique and understudied status of WBF wetlands warrants rigorous investigation to facilitate sound management practices thereby ensuring the sustainability of the waterfowl that depend on them.

The Community Ecology of Aquatic Invertebrates

Fish and other invertebrate predators

Aquatic invertebrates provide essential trophic links between wetland primary consumers (Zimmer et al. 2001), macrophytes (Pieczynska et al. 1999), and insectivores like fish and waterfowl (Diehl 1992, Sedinger 1992, Cox et al. 1998). Macroinvertebrates communities have been shown to vary predictably with depth (Murkin 1984), agricultural chemicals (Dieter et al. 1996, Beeson et al. 1998), nutrient regimes (Pieczynska et al. 1999), winter hypoxia (Nelson and Kaldec 1984), and fish presence (Mallory et al. 1994, Zimmer et al. 2001).

Insectivorous fish are purported to alter the aquatic invertebrate community of a wetland substantially, suggesting that fish and waterfowl compete for the same invertebrate resource (Bouffard and Hanson 1997). Alternatively, some researchers have found no effect of fish presence on aquatic invertebrates (see review in Wooster 1994) or that invertebrate prey communities are well adapted for, or can quickly respond to, fish predation (Wellborn and Robinson 1991, Osenberg and Mittelbach 1996). In these latter scenarios predaceous macroinvertebrates may dominate higher trophic levels of the aquatic food web (Diehl 1992). Furthermore, predaceous invertebrates like dytiscids (Hicks and Larsson 1995, Dolmen and Solem 2002) and odonates (Johansson and Nilsson 1991) are well equipped to survive a winterkill-mediated extirpation from a wetland, a major determinant of fish distribution in the WBF (Tonn et al. 2004). Therefore, the influence of predaceous macroinvertebrates on invertebrate community ecology within the WBF may be wider-reaching than other top level predators, such as fish. In Chapter 2, I investigate the relationship between fish, predaceous macroinvertebrates, and the aquatic invertebrate community after classifying invertebrates into feeding guilds.

Vegetation

The abundance of aquatic invertebrates is roughly proportional to the biomass and complexity (greater incidence of stem and leaf bifurcation per volume occupied) of macrophytes (Krecker 1939). Studies of aquatic invertebrate communities have corroborated this simple model (Dvorak and Best 1982, Humphries 1996, Harrison 2000, Marklund et al. 2001). More specifically researchers have found significant relationships between macrophytes and epiphytic invertebrate biomass (Cyr and Downing 1988, Jeffries 1992, Lillie and Budd 1992), benthic invertebrate biomass (Kornijow et al. 1990), and combined epiphytic and benthic invertebrate biomass (Diehl and Kornijow 1998). Invertebrates may respond strongly to particular plant species (van den Berg et al. 1997, Cheruvelil et al. 2002). The factors of plant complexity (degree of bifurcation), plant species, and the proportion of water volume not occupied by plants (open water), and their effect on the aquatic invertebrate community, are also investigated Chapter 2.

Waterfowl Duckling Foraging Ecology

Waterfowl need protein for growth and development of new tissues. The percent composition of dry weight protein in plant matter is low, usually less than 15%, making it an inadequate protein source for ducklings (Baldassarre and Bolen 1994). Street (1977) showed that the rate of weight gain for ducklings decreased as the dry weight of dietary protein fell below 50%. Vegetative foods also lack required essential amino acids that cannot be synthesized by birds and are therefore only available via ingestion. Molting birds, hens, and ducklings cannot obtain the necessary protein and essential amino acids for growth and development from plants alone (Moyle 1961, Baldassarre and Bolen 1994).

To meet protein needs, both dabbling duckling (tribe Anatini; Mallard) and diving duckling (Aythyini; Bufflehead) diets almost exclusively include invertebrates during their first weeks of life. As they mature, dabbling ducklings begin to incorporate more plant material into their diets, until their diet consists mostly of plants (Chura 1961). Diving ducklings incorporate more seeds and vegetative material later in life, although aquatic invertebrates comprise the majority of food items selected throughout their life (Erskine 1972). Tables 1.1 and 1.2 display the results of dietary analyses for Mallard and Bufflehead ducklings found in the literature.

The determination of duckling preference

Few studies of waterfowl diets apply rigorous statistical procedures to detect and measure selection or avoidance of foods. Most of the studies listed in Table 1.1 were either pseudoreplicated (Chura 1961, Perret 1962, Street 1977) by incorrectly treating ducklings taken from the same wetland, or even the same brood, as independent samples (Hurlbert 1984). The remaining studies (Bartonek 1972, Bengston 1975) did not adequately specify methods to the contrary. Furthermore, all Mallard diet studies (Table 1.1) bias their results toward numerous small invertebrates by comparing percent abundance instead of the more energetically meaningful measure of biomass (addressed in Chapter 4). None of the dietary studies listed in Tables 1.1 and 1.2 compared the food items ingested to items available. Because resource use is assumed to change as availability changes, to reach valid conclusions with regard to resource selection one must compare consumed items to that which is available (Manly et al. 1993). All of the research

I found investigating the diets of ducklings merely listed dietary items with accompanying data on the frequency of occurrence, percent abundance (Table 1.1), or percent volume (Table 1.2) in the diet. This work uses peer-reviewed techniques to determinate food preference for Bufflehead ducklings (Chapter 3; using Savage 1931 reviewed in Stevenson 2004) and Mallard ducklings (Chapter 4; using Manly et al. 1993).

Summary of Knowledge Gaps

There is a lack of information on the aquatic invertebrate community ecology of the WBF wetlands. These wetlands are unique (physical structure, hydrologic flows, temperature, and pH) making the application of results found in southern locations (PPR) or rock dominated boreal wetlands (Boreal Shield, Fennoscandian) spurious. Fish are presumed to have a substantial influence on WBF wetland invertebrate abundance and composition; this relationship is investigated here with the same detail it has been afforded on other landscapes (Zimmer 2001, Bouffard and Hanson 1997). Understanding the relationship between vegetation and aquatic invertebrates will also aid wetland resource management by highlighting the important processes and functions of the invertebrate community. **(Addressed in Chapter 2)**

The WBF is the second most important breeding habitat for waterfowl in North America. This landscape will undergo industry-mediated forest clearing, channelization of hydrologic flow resulting from road building and soil compaction, increased human access, and susceptibility to hydrocarbon contamination in the coming decades (Thomas 1998). Waterfowl managers will have to make conservation decisions that rank wetlands according to their value to waterfowl; knowing which invertebrates are important in duckling diets will help make those decisions. **(Addressed in Chapters 3 and 4)**

Often only inferential conclusions are reached concerning the relationship between ducklings and invertebrate utilization, using invertebrate surveys with ducklings weights (see Cooper and Anderson 1996, Cox et al. 1998, Sjöberg et al. 2000), or duckling stomach contents alone (see Chura 1961, Pehrsson 1984). An investigation of ducking dietary preference, using rigorous techniques to calculate resource selection is undertaken here. **(Addressed in Chapters 3 and 4)**

I found no study that compared waterfowl diets between landscapes. Mallards are ubiquitous, with the largest worldwide distribution of any dabbling duck, yet the paradigm that implicates chironomidae as a preferred food source has been employed over a wide geographical region, from the Northwest Territories (Bartoneck 1972) to Fennoscandia (Sjöberg et al. 2000). Virtually all paradigms of brood ecology for North American waterfowl have originated on the prairies under the hydrologic and food base conditions found there. Resource use commonly changes with availability (Manly et al. 1993), and I investigated the preferences of Mallards over changing resource levels and ecozones. **(Addressed in Chapter 4)**

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Table 1.1* - The percent abundance of foods of the Mallard duckling. Only counts of individuals included in the diet were available, therefore data represent the percent of total abundance. Invertebrate groups are arranged from highest to lowest weighted average.

Location	Manitoba Canada [1]	Iowa USA [2]	N.W.T. Canada [3]	Iceland [4]	England [5,†]	Average
Number	62	69	5	16	99	
Diptera[§]	39.3	44.4	65.1	49.7	13.2	**42.3**
Crustacea	2.7	27	2.1		30.8	**12.5**
Coleoptera[§]	6.6	12.5	10.1		13.2	**8.5**
Gastropoda	11.7	7.7		45.7	1.1	**13.2**
Trichoptera[§]	28.1	0.8		4.6	1.1	**6.9**
Hemiptera[§]	3.5	3.0	12.6		13.2	**6.5**
Odonata[§]	6.1	0.2			2.2	**1.7**
Ephemeroptera		3.2			12.1	**3.1**
Hirundea	1.4				1.1	**0.6**
Hymenoptera	0.5	0.5				**0.2**
Collembola		0.6				**0.1**
Arachnoidea	0.1	0.1				**trace**
Other			10.1		12.0	**4.4**

* - Invertebrate species groups are not the same as originally reported. Many invertebrate groups were reclassified to a higher taxonomic group to maintain comparable results (i.e. Simulidae, Chironomidae, Tendipedidae, and Tabanidae all become Diptera; Cladocera and Amphipoda become Crustacea). Data sources: 1 - Perret (1962); 2 - Chura (1961); 3 -Bartonek (1972); 4 - Bengston (1975); 5 - Street (1977)

† - Fish eggs were eaten by 8 of 69 1a – 1c ducklings in one of three years of study. Street (1977) makes mention of how they biased the data and therefore were not included here.

§ - Includes both adult and larval forms.

Table 1.2* - The percent volume of foods of the Bufflehead duckling. Data adapted from that reported in Erskine (1972). Invertebrate groups are arranged from highest to lowest weighted average.

Location	Alberta, Canada[1]	British Columbia, Canada[2]	California, USA[3]	Average
Number	11	20	4	
Odonata§	22.8	29.6	49.2	**33.9**
Coleoptera§	56.5	36.5		**31.0**
Corixidae	3.1	6.8	49.2	**19.7**
Amphipoda		20.3		**6.8**
Ephemeroptera§	10.7			**3.6**
Chironomidae§	1.8	4.6		**2.1**
Trichoptera§	4.2	2.3		**2.2**
Annelida			1.6	**0.5**
Porifera	0.3			**0.1**
Cladocera	0.3			**0.1**
Hydrachnidae	0.1			**trace**

* - Invertebrate species groups are not the same as originally reported. Many invertebrate groups were reclassified to a higher taxonomic group to maintain comparable results (i.e.Dysiscidae, Haliplidae, Hygrotus all become Coleoptera). Data sources: 1 - Erskine (1972); 2 - Munro (1942); 3 - Dixon (1926)

§ - Includes both adult and larval forms.

Figure 1.1 – Ecological regions of interest in Western Canada showing the approximate areas where research was conducted.

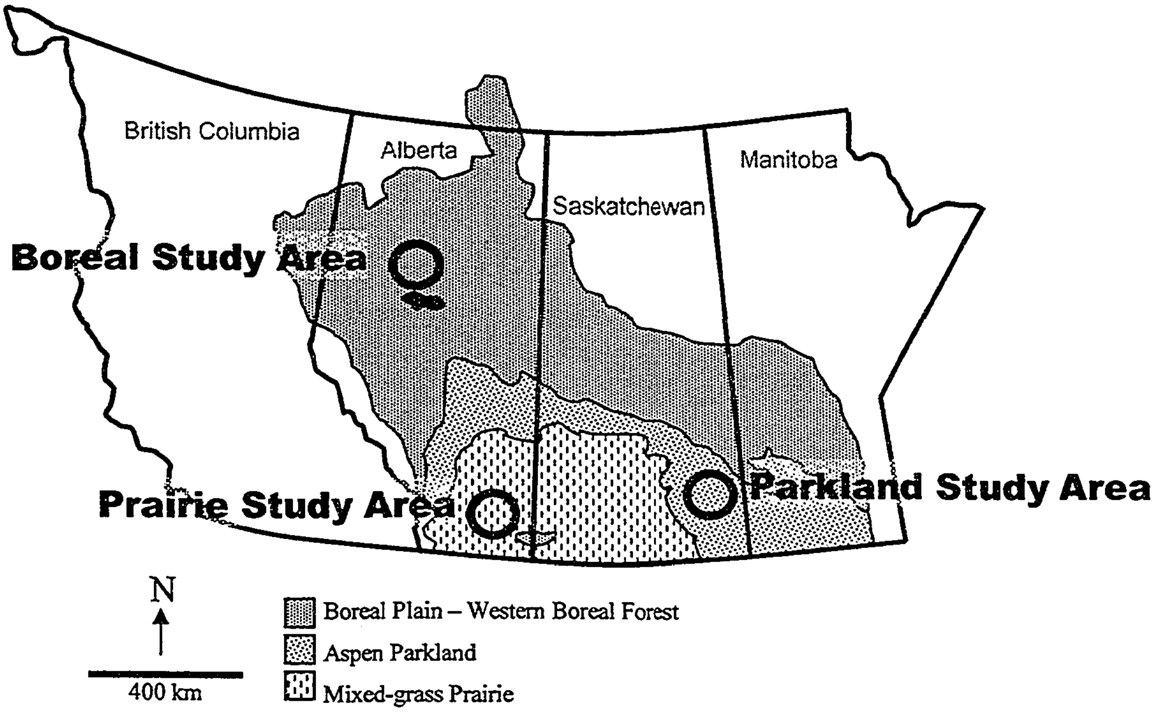
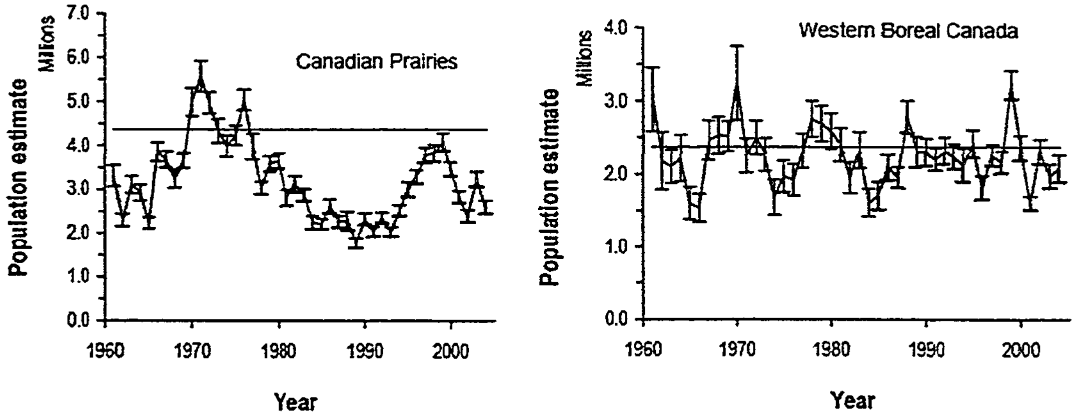


Figure 1.2 – Mallard breeding population estimates of the Canadian Prairies and the Western Boreal Forest. Figure from the Canadian Wildlife Service Waterfowl Committee (2004) migratory birds report. Bars equal ±1 SE while the horizontal line represents the North American Waterfowl Management Plan (NAWMP) population goal.



Chapter 2

Aquatic Invertebrate Responses to Fish Presence and Vegetation Complexity in Western Boreal Wetlands with Implications for Waterfowl Productivity[1]

Introduction

The trophic interactions that shape aquatic invertebrate communities vary with habitat complexity (Cheruvelil et al. 2002) and fish presence (Diehl 1992, Bouffard and Hanson 1997) and can alter wetland food webs (Batzer and Wissinger 1996, Abjornsson et al. 2002, Zrum and Hann 2002, Hall et al. 2004). Aquatic invertebrates in boreal wetlands link primary production with many larger organisms, including waterfowl (Cox et al. 1998, Murkin and Ross 2000). Highly productive eutrophic systems, like those studied here, provide essential resources for much of North America's waterfowl (Donaghey 1974, van de Wetering et al. 2000). I selected 24 wetlands in Alberta's southern boreal forest to investigate the effects of vegetation structure, abundance, and fish presence on aquatic macroinvertebrate biomass. New information can improve wetland management and protection as energy and forestry activities continue to alter Alberta's boreal forest (Schindler 1998, Thomas 1998).

Macrophyte abundance and diversity appears to affect aquatic invertebrate distribution by providing invertebrates refuge from predators (Mittlebach 1988), increasing the availability of food resources (Campeau et al. 1994), and furnishing attachment sites or building materials (Lodge 1985, Dudley 1988). De Szalay and Resh (1996) found that changing wetland vegetation influenced colonization patterns of invertebrate species, thereby impacting wetland dependent birds. Fish presence significantly alters the composition and abundance of aquatic invertebrate communities (Batzer et al. 2000, Zimmer et al. 2001), and typically reduces invertebrate availability to waterfowl (Bendell and McNicol 1995, Bouffard and Hanson 1997). Omnivorous

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[1] A version of this paper has been submitted to *Wetlands* journal. Corresponding styles and format apply to citations, figures and tables.

fishes, like the Brook Stickleback (*Culea inconstans*), interact with macroinvertebrates by predating both their early instars (predation) and prey base (competition).

Waterfowl of the western boreal forest (WBF) consume predaceous macroinvertebrates because of their high relative abundance (Elmberg et al. 2000) and large size (Driver et al. 1974). Furthermore, benthic invertebrates commonly associated with waterfowl diets, like chironomids (Dzus and Clark 1997), are less abundant in the WBF (Sjöberg and Danell 1982, compared to Nelson 1989), or are not available in their larval form as most wetlands are uniformly deep with flocculent bottoms (Mitsch and Gosselink 2000). Finally, many predaceous invertebrates (Dytiscids, Notonectids, Hemipterans) make frequent trips to the water's surface to respire, increasing their availability to 1-3 week old ducklings that feed at the surface.

My objective was to explain the distribution of aquatic invertebrate biomass as it relates to plant abundance and complexity, and fish presence. Two testable hypotheses were generated; i) percentage of the water column occupied by vegetation and the architectural complexity (incidence of bifurcation) of the vegetation will be positively related to the biomass/L of aquatic invertebrates, and, ii) the presence of Brook Stickleback reduce invertebrate biomass.

Materials and Methods

Description of Study Site

I studied 24 wetlands in a 30 km by 20 km study area approximately 110 km north of Slave Lake, Alberta, Canada (56° 00' – 56° 20' N, and 115° 20' – 115° 40' W; Figure 1.1 – Utikuma Study Site). Grey luvisols and deep organic peat deposits were the dominant substrate type underlying aspen (*Populus tremuloides*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*) forests (Alberta Environmental Protection 1998). All wetlands were associated with established floating peat beds, allowing the classification of peatlands (Vitt et al. 1998) or quaking peatlands (Mitsch and Gosselink 2000), had an average depth of less than 2 m, mean total phosphorus of 95.3 μg/L, mean total nitrogen of 2813.8 μg/L, and mean pH of 8.02. Wetlands received minimal meltwater in the spring, and were maintained with mid-summer precipitation and some groundwater inflow. Midsummer phytoplankton blooms were not uncommon, but many wetlands retained a clear water column for the entire summer. All wetlands had flocculent bottoms.

Invertebrate Sampling Protocol

A total of 6 sampling rounds, each separated by approximately 2.5 weeks, occurred between 10 May and 5 September, 2001. Each round lasted no longer than a week. All wetlands were visited four times (sampling rounds 1, 2, 3 and 5), while only 8 of the 24 wetlands were surveyed for invertebrates in rounds 4 and 6 due to logistic reasons. The data from rounds 4 and 6 are presented here solely in graphical form to maintain temporal continuity. Three sub-sampling locations were established at each wetland using a stratified random design. All sampling locations were randomly selected along a transect that ran parallel to the wetland shore and was one third the entire shoreline length. The transect at each wetland was set away from confounding factors such as roads, cut lines or oil well locations.

Upward, vertical sweeps with a standard D-shaped invertebrate dip net (640 cm^2 opening, 500 micron mesh size), beginning with the net pushed 5 cm into sediment, were made in the aquatic/terrestrial interface zone (at wetland edge), emergent vegetation zone (within 1m from edge), and the submerged vegetation zone (between 1m and 2m from edge) at each of the 3 sub-sampling locations along the shoreline transect. Two sweeps were collected from each aquatic zone for a total of 18 sweeps per wetland per visit (2 sweeps per zone X 3 zones X 3 sampling locations). Water depth (vertical sweep length) was measured at each sweep location to calculate the volume of water sampled. The large mesh size of the dip net did not allow for the adequate sampling of meiofauna (0.063 – 0.5 mm). Because of the predominance of *Sphagnum spp.* surrounding most wetlands, the aquatic/terrestrial interface zone was commonly represented by a floating bog mat that extended underwater 5 to 30 cm. If this vertical interface was missing from a site due to drawdown, the shallow water near the shore was sampled. To maintain consistency between invertebrate and vegetation sampling locations, no dip samples were taken greater than 2m from shore.

Aquatic invertebrates were kept chilled in sealed plastic bags to reduce oxygen depletion and predation. Invertebrates were sorted from vegetation within 4 hours of sampling and preserved in a 70% ethanol / 3% formalin solution. Invertebrates were then identified to the lowest possible taxonomic resolution (Clifford 1991, Merritt and Cummins 1996). This resulted in most species being identified to genus, with a small fraction to family or species (Appendix A).

After identification, each invertebrate was assigned a small/medium/large size class based on size guilds within each taxonomic grouping (usually family or genus). Estimates of biomass for each size class were obtained by calculating the mean of approximately 30 dried individuals.

Total invertebrate biomass and the total water volume strained through the dip net were then averaged over the three sub-sampling locations at a wetland to obtain the value for the experimental sampling unit: invertebrate mg/L per wetland per sampling round (hereafter biomass). Invertebrate composition and aquatic vegetation can change significantly over the summer months, therefore when invertebrate biomass was analysed in relation to aquatic vegetation, only invertebrate samples from rounds 3 and 5 were used to coincide with vegetative sampling periods taken at the same time.

Invertebrates were grouped into functional feeding groups (Merrit and Cummings 1996), detailed in Appendix A. There is difficulty assigning a resource utilization generalization to some aquatic invertebrates, especially omnivorous taxa. For example, MacNeil et al. (1997) found that freshwater *Gammarus* spp., which comprises a significant amount of the invertebrate biomass found here, feed on many different food sources. Therefore, I created an omnivore feeding group that included taxa previously described as omnivorous (Edmunds et al. 1976, Martin et al. 1981, Berte and Pritchard 1983, Mihuc and Toetz 1994, Wiggins 1996, Wiggins and Parker 1997, Barbour et al. 1999, Huryn and Gibbs 1999, Wissinger et al. 2004).

Aquatic Vegetation and Fish Sampling

Aquatic vegetation characteristics were recorded in 2 rounds from 1 - 9 July and 15 - 20 August, 2001, to coincide with peak standing crop. Two adjacent $1m^2$ quadrats were established at each sub-sampling location, extending from the shoreline towards the center of the wetland. Aquatic plants were identified to species using Moss (1983) and mean water depth measured. Measurements of submersed plant height (h; cm) and areal plant cover (A; cm^2) for each species were used to estimate plant volume within the quadrat by using the volumetric equation: A x h = plant volume (cm^3). Finally, the total plant volume was divided by the total water volume to estimate the percent volume of the quadrat occupied by plants. This value was averaged over the 2 quadrats and then averaged over the 3 sub-sampling locations at the wetland. The single value of percent water volume occupied by plants for a wetland incorporates the mean derived from both sampling rounds. To measure the relationship between invertebrate biomass and plant structural differences, each species of plant was assigned to a group: dissected leaved architecture (i.e. filamentous metaphyton, *Ceratophyllum demersum, Myriophyllum exalbescens, Calla palustris*), broad leaved architecture or emergent with submerged stems (i.e. *Sagittaria cuneata, Poa* spp., *Potomageton richardsonii, Scripus* spp., *Carex* spp., *Typha latifolia, Polygonum* *punctatum, Potamogeton friesii, Caltha palustris*), and floating plants (i.e. *Lemna minor, Lemna triscula, Nuphar variegatum*).

Fish presence/absence was determined using 4 Gee minnow traps (0.5 cm^2 wire-mesh with 2 funnel entrances) set at each wetland for 25 hours, providing over 100 trap hours per wetland per round. Fish trapping was conducted over 2 rounds, 11 – 15 May and 18 – 22 July, 2001, totaling 200 trap hours per wetland.

Statistical Analysis

I used a repeated measures ANOVA to test whether invertebrate biomass was significantly different (alpha = 0.05) over the summer (n = 4 rounds) with respect to fish presence (n = 4 wetlands) or absence (n = 20). Because overall and functional feeding group data were skewed and contained zeros, a log (x+1) transformation was used to normalize the invertebrate biomass data, then normality checked with a Lilliefors test. Mauchly's Test of Sphericity was used to monitor the spherical statistical violations unique to repeated measures analysis. Levene's Test of Equality of Error Variances was used to test homogeneity of variances between groups through time (sampling rounds) and between treatments (fish/no fish). Violations of repeated measures statistical assumptions were problematic due to the unbalanced sample size ($n_{\text{fish absent}} = 20$; $n_{\text{fish present}} = 4$), therefore analysis of some of the invertebrate feeding groups were inappropriate.

I suspected, because predatory invertebrates are visually oriented predators, that they may prefer open water environments and may forage less effectively in sites occluded with dense dissected leaved plants. I also tested for a relationship between overall invertebrate biomass and overall plant volume using a simple linear regression with proportion plant volume as the dependent variable. Plant proportion data were arcsine transformed to maintain normality (McCune and Grace 2002) before being used in regressions and ordination analysis.

Canonical Correspondence Analysis (CCA), a multivariate ordination technique, was used to investigate the relationships between the invertebrate composition (measured as biomass/L) and the aquatic plant prevalence in fishless wetlands. CCA is a direct gradient analysis ordination technique, relating the species (here invertebrates) and environmental (here aquatic macrophytes) data matrices to each other by way of regression. Hypothesis testing is straightforward with CCA using a Monte Carlo randomization test (Manly 1992), indicating whether or not the species matrix is associated with the environmental matrix once both have been randomly rearranged and the analysis run again. An invertebrate feeding group or plant species was included in the CCA only if non-zero data existed for at least 4 of the wetlands considered. Both matrices were checked for variable correlations above 0.70 (McCune and Grace 2002), biplot scaling was used, interspecies correlations were preserved, and a Monte-Carlo Permutation procedure was used to test the null hypothesis that the species matrix was not related to the chosen environmental variables.

An ordination biplot of invertebrate feeding groups and plant species reduced complex sets of ecological variables into a two dimensional representation while maintaining accurate depictions of relationships between them (McCune and Grace 2002). Pairs of CCA variable vectors for both plants and invertebrates (arrows in biplot) are positively correlated if they point in a similar direction; have no correlation on each other if they are at right angles to one another; and are negatively correlated to each other if pointing in opposite directions (Jongman et al. 1995). Longer arrows represent stronger correlations, having more of an influence in distributing the variables in ordination space.

Results

All wetlands were associated with peat-based soils, had an average depth of less than 2m, and were eutrophic based on the total phosphorus criteria described by Wetzel (1983). Four of the wetlands contained Brook Stickleback. Fish survived through the winter because most wetlands, including those without fish, did not freeze to the bottom or have lethal O_2 concentrations (confirmed during winter sampling), and were not connected to other surface waters during the 2001/2002 seasons.

The aquatic invertebrate community contained 11 taxonomic orders, incorporating a total of 105 unique species, genera or families (Appendix A). *Gammarus lacustris* (Amphipoda) was the most abundant taxa, contributing 30% to the total biomass and 81% to the omnivore feeding group. Other invertebrates that contributed greatly to overall biomass included *Hyallela azteca* (Amphipoda) at 8.2%, *Dytiscus* spp. (Coleoptera) at 5.9%, *Asynarchus* spp. (Trichoptera) at 5.3% and *Notonecta* spp. (Hemiptera) at 5.0% of total biomass. Invertebrates from the predatory functional feeding group comprised 33% of the standing invertebrate biomass, and 51% of the total after excluding *Gammarus lacustris*.

Invertebrate biomass and aquatic plant volume were positively associated ($P = 0.009$; $r^2 = 0.27$; Figure 2.1). In most sampling rounds the mean invertebrate biomass was higher in the absence of Brook Stickleback (Figure 2.2). Predator biomass was significantly negatively correlated with the volume of dissected leaved aquatic plants ($P < 0.001$; $r^2 = 0.83$) the relationship is corroborated in the CCA biplot (Figure 2.3). The predator ($P = 0.040$), gatherer / collector ($P = 0.011$), or herbivore ($P = 0.010$) functional feeding group biomass was significantly greater in the absence of fish. The effect of fish presence was also significant when considering all invertebrates together ($P < 0.001$; Figure 2.2A). The within-subjects factor (sampling rounds) and the interaction between fish presence and sampling round were found to be non-significant ($\alpha = 0.05$).

After removing fish-bearing wetlands from the analysis, I produced a biplot using CCA data reduction (Figure 2.3). The first two axes explained 93.6% of the variation and the sum of all eigenvalues was 0.720. A Monte Carlo test of all canonical axes was significant ($P = 0.015$; 9999 permutations).

Discussion

Aquatic invertebrates use macrophyte structure for predation refugia, as grazing substrate, as a food source after senescence and death, and as components for case construction (Diehl and Kornijow 1998). I found a positive relationship between invertebrate biomass and the prevalence (proportion volume) of submersed plants (Figure 2.1). Similar relationships have been found relating macrophyte biomass to epiphytic invertebrate biomass (Cyr and Downing 1988, Jeffries 1992, Lillie and Budd 1992), to benthic invertebrate biomass (Kornijow et al. 1990), and to combined epiphytic and benthic invertebrate biomass (Diehl and Kornijow 1998). The congruence between published results to those found here help validate our methods of macrophyte community measurements using percent water volume occupied (following Canfield et al. 1984 and Burks et al. 2001) as opposed to direct biomass determination via drying and weighing.

By separating invertebrates into functional feeding groups (Merritt and Cummins 1996), and plants into floating or dissected leaved or simple leaved architecture, I more closely investigated invertebrate preference for particular plant arrangements and addressed processes that explain these associations. The negative relationship between predator biomass and dissected leaved plants was evident. I advance two possible explanations; (1) visually-oriented predators flourish in habitats with enough structural complexity to provide increased prey biomass and hunting cover, but not so much as to make predation difficult, and (2) the phenolic compounds in *Myriophyllum* spp. are mobilized to combat herbivory, decreasing prey abundance and thereby decreasing predator abundance. These defensive hydrolysable tannins are present at levels in *M. exalbescens* an order of magnitude more than other aquatic plants and discourage direct herbivory and the growth of epiphytic algae important for herbivorous invertebrates (Leu et al. 2002, Gross 2003).

The CCA biplot (Figure 2.3) suggests that invertebrate predators preferred habitats lacking a high percentage of dissected leaved plants, consistent with the result from the linear regression discussed above. Furthermore, the positive association omnivores had with dissected leaved plants, as interpreted in the CCA biplot, could highlight the importance of refugia for these invertebrates (Thorp and Bergey 1981) and increased detrital material to scavenge as these plants senesce (MacNeil 1997). The effect of *M. exalbescens*'s defensive compounds, with broad biological activity against herbivorous invertebrates, algae, cyanobacteria, and heterotrophic bacteria (Gross 2003), are well illustrated in Figure 2.3. Not only are predators negatively associated with this plant, the herbivorous groups represented by gatherer / collectors, shredders, and piercers avoided them as well.

The predicted negative effect of fish on invertebrate population demonstrated here is consistent with results from other studies (Bouffard and Hanson 1997, Zimmer et al. 2001). Brook Stickleback reduce predaceous invertebrate biomass by competing directly for similar food resources and by consuming early life stages of resident invertebrates when they are smaller and more vulnerable (Tompkins and Gee 1983). Not only did their predatory and competitive interactions with aquatic invertebrates correspond with a depletion of the biomass of non-insectivorous invertebrates, they replaced predaceous macroinvertebrates at the top of the aquatic food chain. Many aquatic insects emerge synchronously from aquatic larval to terrestrial adult stages in large numbers, presumably to dilute an individual's predation risk (Corbet 1999). During these emergence events, aquatic insects move from deeper refugia to the surface or shoreline vegetation during which time waterbirds feed heavily on them (de Szalay et al. 2003). The peaks in invertebrate biomass seen in Figures 2.2B-2.2G and 2.2I, represent emergence events not found in wetlands containing Stickleback.

Waterfowl abundance has been shown to vary predictably with predaceous invertebrates in boreal systems, as these invertebrates are an important food source for waterfowl (Elmberg et al. 2000). Disregarding amphipods, which are not commonly eaten by Mallard ducklings (Chura 1961, Bengtson 1975, Street 1977), predaceous invertebrates represent 51% of the available biomass for duckling food. I assert that boreal wetlands contribute to Mallard duckling protein needs via surface and shore dwelling predaceous invertebrates, unlike the more productive, hard-bottomed prairie wetlands with accessible and abundant, emerging and benthic larval midge populations consumed in both larval and emergent forms (Nelson 1989, Dzus and Clark 1997). While extensive sampling aimed at the chironomid population did not occur here (emergence or sticky traps, aerial sampling), dip samples that partially sampled the benthic environment found mean larval chironomid density at 50 / m^2 (maximum of 1000 / m^2; # of chironomidae found/benthic area scooped into net), which is much lower than 27,000 / m^2 reported from the prairie pothole region (Nelson 1989) or 3000 / m^2 reported from other boreal systems (Sjöberg and Danell 1982). At lower chironomidae abundance predaceous macroinvertebrates could assume a larger role in duckling diets. Dissected leaved aquatic plants can decrease the availability of predaceous invertebrate duckling food. Elmberg et al. (1993) showed that boreal dabbling duck species richness in Fennoscandia was related to aquatic vegetation complexity, while de Szalay and Resh (2000) used plant removal experiments to arrive at a similar conclusion regarding the availability of invertebrates for feeding waterfowl in aquatic habitats with little cover. I found that when submersed aquatic habitats are dominated by dissected leaf aquatic plants like *M. exalbescens* there are fewer invertebrates available for duckling foraging.

Management Implications

The presence of Brook Stickleback resulted in the removal of invertebrate protein that would be otherwise available to hatchling waterfowl (Pehrsson 1984, DesGranges and Gagnon 1994, Giles 1994, Nummi et al. 2000). A duckling / fish competitive relationship could be exacerbated by anthropogenic influences (Bouffard and Hanson 1997). When access to remote lakes is increased via forestry or energy sector practices (Thomas 1998), sportfishing can introduce Brook Stickleback as baitfish (Schindler 1998), thereby decreasing available biomass as represented by invertebrate emergence events. While winterkill does control many fish populations in the boreal zone (Danylchuk and Tonn 2003), many of the wetlands studied here do not freeze to the bottom and Stickleback can tolerate extremely low oxygen levels (Joynt and Sullivan 2003). Furthermore, clear-cutting increases runoff (Evans et al. 2000), potentially providing colonization corridors for Stickleback via overland hydrological connections.

In the absence of fish, those invertebrates important for duckling diets are more available in aquatic habitats lacking an abundance of dissected leaved plants and filamentous algae. The effects of anthropogenic activities in the WBF, including forestry and access-road development, often resemble those following fire by increasing runoff, silt, and nutrient loads to wetlands (Nicolson 1975, Harr and Fredriksen 1988). This can allow dissected leaved plants, like *Myriophyllum exalbescens,* to dominate aquatic habitats through increased nutrient loads (Carpenter et al. 1998), decreasing the availability of those invertebrates important for waterfowl diets.

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Figure 2.1 - Aquatic invertebrate biomass (mg/L) versus total proportion plant water volume occupied by aquatic plants ($P = 0.009$; $r^2 = 0.27$). Open circles represent fish-bearing wetlands.

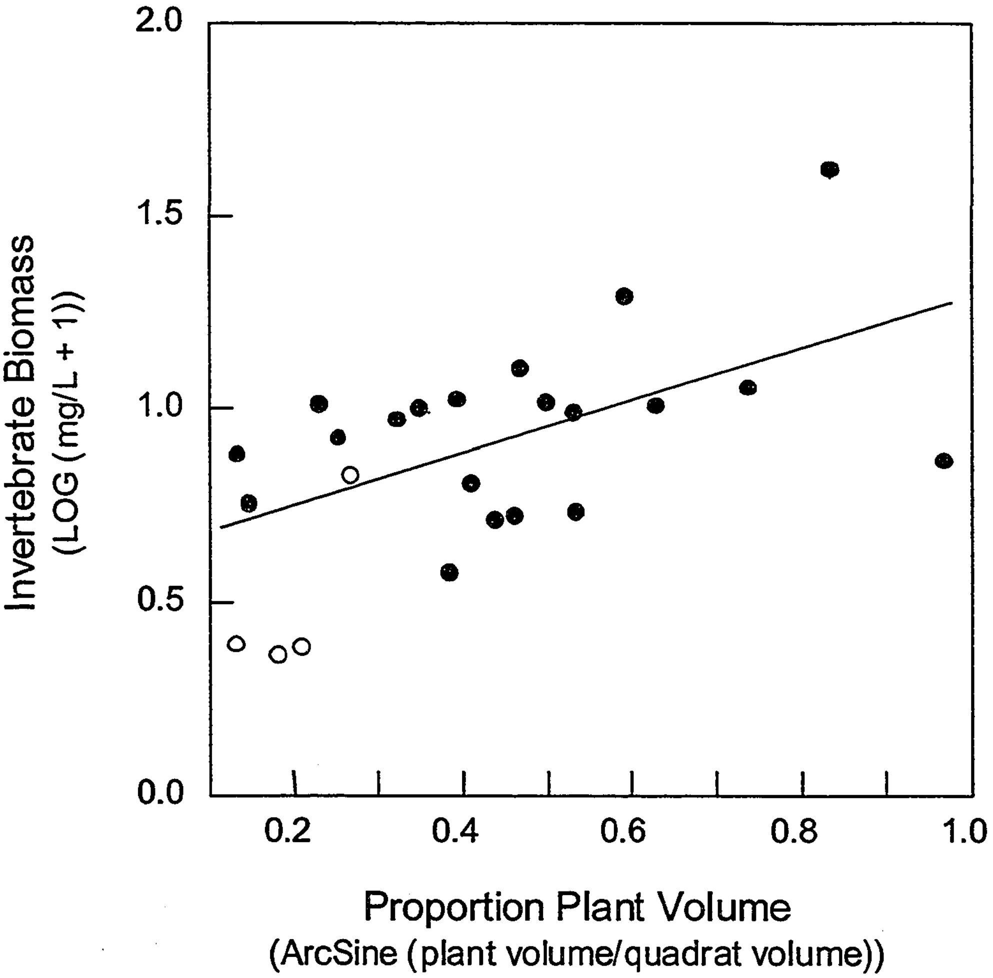


Figure 2.2 - Biomass of invertebrate functional feeding groups sampled over 6 sampling rounds in 2001 between fishless (n = 20 for rounds 1-3, 5; n = 5 for rounds 4 and 6) and Brook Stickleback (*Culaea inconstans*) inhabited wetlands (n = 4 for rounds 1-3, 5; n = 3 for rounds 4 and 6). *P*-values on graphs represent significance of the between subjects main effects factor of fish presence for repeated measures analysis. Round 1 coincides with the dates 11-15 May; round 2, 3 - 10 June; round 3, 30 June – 6 July; round 4, 18 – 22 July; round 5, 15 – 20 August; round 6, 3 – 5 September.

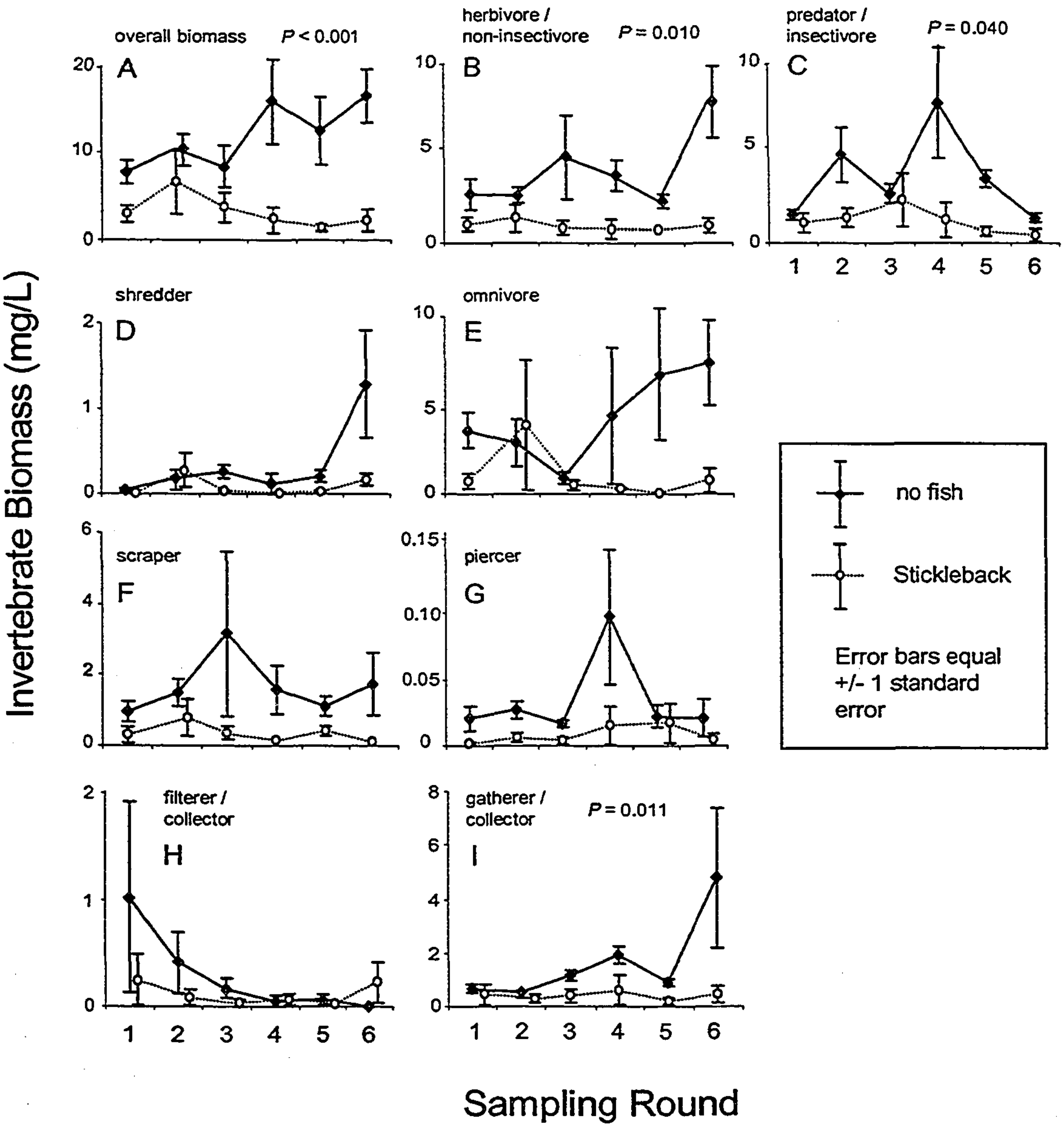
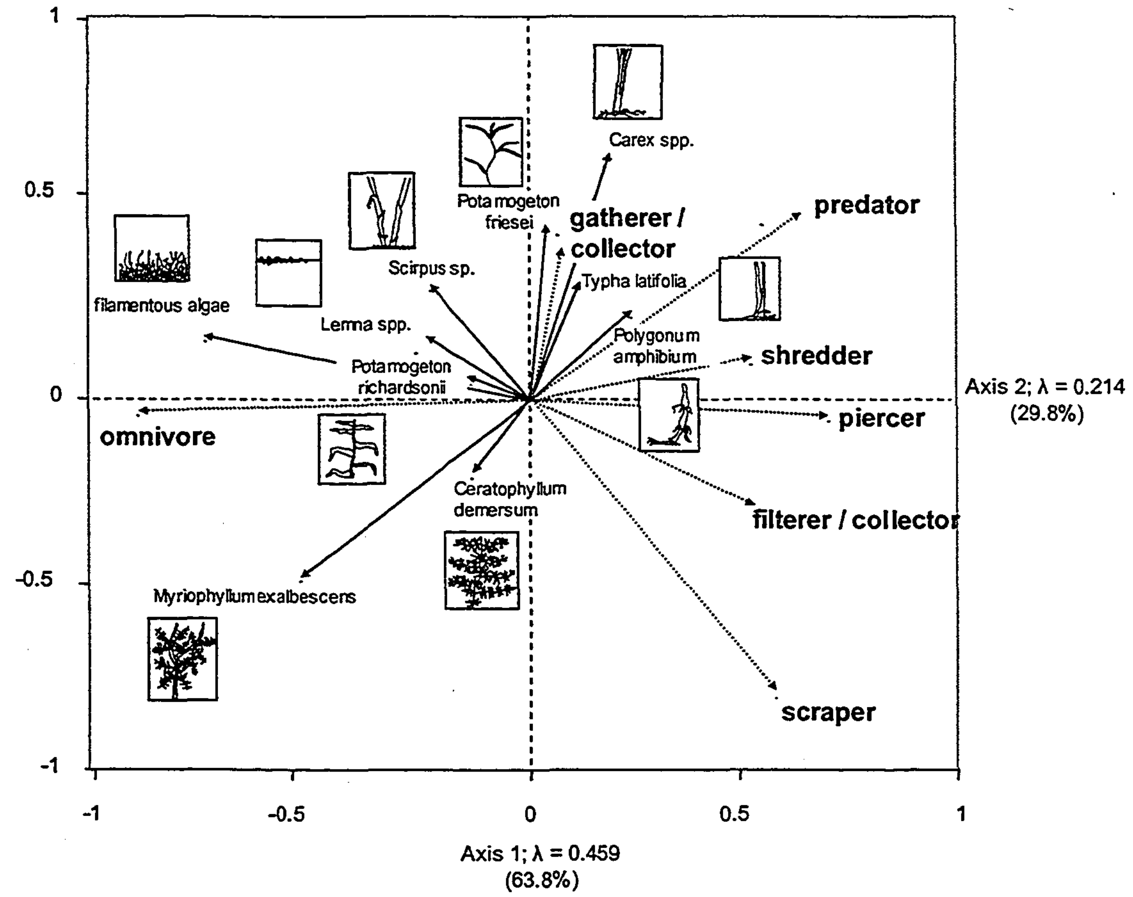


Figure 2.3 - Biplot of Canonical Correspondence Analysis representing the influence aquatic plant species have on invertebrate functional feeding group biomass. Eigenvalues associated with the first two axes are listed next to that axis and values in parentheses represent the percentage of variation explained by that axis. Line drawings in boxes demonstrate submerged plant complexity.



Appendix 2A - Aquatic invertebrate species identified from boreal wetlands in Northern Alberta, Canada with total number of individuals found (Abun.) per round and total biomass (Bio.; milligrams) in parentheses. Values are separated into rounds, corresponding to the dates 11-15 May for round 1, 3-11 June for round 2, 28 June to 6 July for round 3, 18–22 July for round 4, 15-20 August for round 5, and 5-6 September for round 6. Totals for abundance and biomass for rounds 1-3 and 5 incorporate the sampling of 24 wetlands, while in rounds 4 and 6 eight wetlands were sampled.

Feeding Group	Order	Family	Genus / Species	Ref*	Round 1 Abun.(Bio.)	Round 2 Abun.(Bio.)	Round 3 Abun.(Bio.)	Round 4 Abun.(Bio.)	Round 5 Abun.(Bio.)	Round 6 Abun.(Bio.)
filterer / collector	Diplostraca	Lynceidae	Lynceus	1			9 (3.6)			
	Diptera	Culicidae	Aedes	2		1 (1.9)				
			Anopheles	2		10 (8.9)	10 (2.4)	1 (0.2)		
	Veneroida	Pisidiidae	Pisidium	2	19 (155.8)	98 (803.6)	12 (98.4)	2 (16.4)		1 (8.2)
			Sphaerium	2	222 (2220.0)	11 (110.0)	10 (100.0)	6 (60.0)	8 (80.0)	16 (160.0)
gatherer / collector	Amphipoda	Hyalellidae	Hyalella azteca	2	1717 (1732.9)	875 (860.8)	2299 (1740.9)	1339 (1015.3)	3059 (1664.7)	1018 (1546.5)
	Diptera	Chironomidae		2, 3	137 (82.2)	419 (261.1)	990 (368.0)	232 (80.8)	165 (68.1)	34 (28.8)
		Dixidae	Dixella	2		16 (5.9)	13 (4.8)	8 (3.0)	28 (10.4)	2 (0.7)
		Chironomidae pupae		2	480 (606.9)	172 (243.5)	138 (116.6)	7 (7.7)	3 (2.1)	1 (1.4)
		Stratiomyidae		2, 3	4 (11.0)		1 (11.7)			
	Ephemoptera	Caenidae	Caenis	2	80 (20.0)	106 (38.0)	106 (26.5)	2 (0.5)	28 (7.0)	37 (9.3)
		Siphlonuridae	Siphlonurus	2, 5, 6		26 (307.1)	27 (318.9)	10 (118.1)	1 (11.8)	
		Baetidae	Callibaetis	2			69 (64.8)	21 (27.5)	46 (26.1)	33 (47.0)
			Centroptilum	3						1 (1.4)
	Gastropoda	Planorbidae	Promenetus exacuous	2						1 (4.0)
			Promenetus umbilicatellus	2	61 (93.6)	83 (122.9)	103 (149.4)	69 (100.1)	23 (33.4)	31 (45.0)
	Oligochaets	Lumbriculidae		2	47 (28.7)	51 (31.1)	137 (84.3)	22 (13.4)	11 (6.7)	12 (7.3)
		Naididae		1		4 (2.4)	36 (22.0)	13 (7.9)	13 (7.9)	

Feeding Group	Order	Family	Genus / Species	Ref*	Round 1 Abun.(Bio.)	Round 2 Abun.(Bio.)	Round 3 Abun.(Bio.)	Round 4 Abun.(Bio.)	Round 5 Abun.(Bio.)	Round 6 Abun.(Bio.)
			Stylaria lacustris	1, 2						13 (7.9)
	Ostracoda			2			16 (3.2)			
	Trichoptera	Leptoceridae	Cerclea	4				1 (0.5)		
omnivore	Amphipoda	Gammaridae	Gammarus lacustris	2	472 (4185.8)	1181 (11267.3)	305 (1659.0)	392 (1806.3)	1417 (9299.8)	535 (3296.0)
	Coleoptera	Hydrophilidae	Hydrobius	2, 3		4 (11.0)	16 (21.9)		3 (4.1)	
	Diptera	Tabanidae	Chrysops	2					1 (1.6)	
	Trichoptera	Limnephilinae	Arctopora	7, 8, 21	116 (23.2)	9 (1.8)	65 (13.6)	136 (27.2)	80 (16.0)	
			Glyphopsyche	2, 9, 10			10 (27.0)			
			Asynarchus	7, 8	197 (4091.7)	24 (498.5)	10 (187.7)	5 (103.9)	32 (664.6)	1 (20.8)
		Phryganeidae	Banksiola	9	50 (161.2)	20 (139.8)			95 (50.2)	2 (14.0)
			Phryganea	2, 3, 9, 11	1 (7.0)				7 (3.2)	13 (45.2)
			Ptilostomis	3, 9				1 (0.5)	12 (51.2)	
piercer	Coleoptera	Haliplidae	Haliplus	3, 12	24 (33.9)	44 (66.4)	26 (35.8)	32 (48.3)	41 (53.7)	6 (9.1)
	Trichoptera	Hydroptilidae	Orthotrichia	9					2 (0.9)	
predator	*Trombidiformes*	*(Hydrachnidia)*		1, 2	115 (73.0)	150 (117.6)	*84 (30.1)*	39 (12.7)	117 (50.2)	*4 (2.9)*
	Coleoptera	Dytiscidae	Acilius	3, 13	2 (34.8)					
			Agabus	3, 13		4 (99.0)	49 (378.4)	2 (64.0)	3 (33.4)	
			Anacaena	3, 13		2 (3.5)	3 (8.3)			
			Colymbetes	3, 13		7 (19.3)	60 (132.2)	5 (13.8)		
			Dytiscus	3, 13	4 (1440.3)	6 (2160.5)	16 (1497.3)	2 (660.2)	1 (360.1)	
			Graphoderus	3, 13	9 (288.1)	18 (576.2)	31 (993.4)	7 (552.1)	30 (960.4)	
			Hydaticus	3, 13	1 (32.0)		3 (9.0)			
			Hydroporus	3, 13	6 (16.6)	5 (14.0)	1 (2.8)		12 (33.8)	3 (8.3)
			Hygrotus	3, 13	23 (63.5)	29 (80.0)	85 (100.1)	20 (32.4)	41 (136.2)	7 (19.3)
			Ilybius	3, 13		4 (128.0)	3 (38.0)			
			Laccophilus	2, 13	13 (65.1)	14 (34.5)	36 (29.0)	12 (33.1)	21 (49.7)	11 (88.9)
			Laccornis	3, 13	1 (2.8)		3 (8.3)			

Feeding Group	Order	Family	Genus / Species	Ref*	Round 1 Abun.(Bio.)	Round 2 Abun.(Bio.)	Round 3 Abun.(Bio.)	Round 4 Abun.(Bio.)	Round 5 Abun.(Bio.)	Round 6 Abun.(Bio.)
			Liodessus	3, 13	5 (13.8)		6 (8.3)	3 (8.3)	1 (2.8)	
			Oreodytes	3, 13			2 (1.4)			
			Rhantus	3, 13	5 (160.1)	28 (369.8)	78 (133.0)	6 (16.6)	1 (0.7)	1 (2.8)
		Gyrinidae	Gyrinus	3	18 (22.5)	1 (1.3)	7 (10.8)	1 (1.3)	1 (1.3)	22 (27.5)
		Hydrophilidae	Laccobius	2			23 (30.4)	1 (2.8)	1 (2.8)	
			Paracymus	2, 3			2 (5.5)			
	Diptera	Ceratopogonidae		2, 14	100 (26.0)	105 (27.3)	232 (60.3)	38 (9.9)	55 (14.3)	40 (10.4)
		Chaoboridae	Chaoborus	3	303 (239.4)	30 (24.1)	35 (27.7)		97 (76.6)	6 (4.7)
		Sciomyzidae		3		2 (34.6)	4 (6.5)			
		Chironomidae	Tanypodinae	2, 3	12 (4.0)	13 (5.6)	37 (16.5)	17 (5.3)		11 (16.4)
	Hemiptera	Corixidae		2, 15	51 (171.4)	15 (21.8)	151 (129.6)	136 (127.2)	171 (312.3)	25 (49.6)
		Gerridae	Limnoporus	3	7 (9.1)	7 (18.4)	13 (16.9)	16 (20.8)	13 (16.9)	
		Mesoveliidae	Mesovelia	3		4 (5.2)	1 (1.3)	1 (1.3)		
		Veliidae	Microvelia	3	3 (0.4)	4 (0.6)	47 (6.6)	1 (0.1)	3 (0.4)	
		Notonectidae	Notonecta	3	27 (405.5)	16 (278.0)	68 (866.0)	90 (1284.7)	164 (2276.6)	3 (67.7)
	Rhynchobdellida	Glossiphoniidae	Glossiphonia complanata	2	15 (74.1)	11 (96.3)	9 (32.5)	11 (21.3)	12 (23.3)	13 (205.1)
			Helobdella stagnalis	2	8 (30.5)	20 (316.3)	12 (23.3)	5 (9.7)	19 (36.9)	
			Theromyzon	2			1 (1.9)			
			Helobdella elongata	2	1 (1.9)					
	Arhynchobdellida	Haemopidae	Haemopis grandis	2	10 (124.3)	8 (364.5)			1 (65.7)	
			Haemopis marmorata	2		5 (328.7)				
		Erpobdellidae	Dina or Mooreobdella	2		15 (186.7)	36 (238.6)	11 (85.1)	12 (38.3)	5 (9.7)
			Nephelopsis obscura	2	15 (89.1)	20 (350.1)	19 (299.4)	1 (1.9)	3 (5.8)	
			Erpobdella punctata	2	2 (33.9)	3 (133.4)	3 (35.8)	5 (9.7)	4 (22.8)	
	Odonata (Suborder: Anisoptera)		(immature)	2, 3	8 (40.6)	40 (229.1)	3 (15.2)		41 (208.3)	1 (5.1)
	Odonata	Aeshnidae	Aeshna	2, 3	8 (56.6)	6 (289.7)	41 (165.0)	44 (104.4)	32 (649.5)	1 (15.4)
		Coenagrionidae	Coenagrion	2, 3		3 (7.9)	1 (2.6)	4 (10.6)		

Feeding Group	Order	Family	Genus / Species	Ref*	Round 1 Abun.(Bio.)	Round 2 Abun.(Bio.)	Round 3 Abun.(Bio.)	Round 4 Abun.(Bio.)	Round 5 Abun.(Bio.)	Round 6 Abun.(Bio.)
			Enallagma	2, 3	175 (591.5)	119 (490.1)	86 (295.9)	29 (94.9)	178 (397.9)	43 (86.2)
		Lestidae	Lestes	2, 3		16 (37.0)	60 (294.2)	15 (93.2)		
		Libellulidae	Sympetrum	2, 3		7 (311.2)	5 (44.6)	9 (105.3)		5 (53.9)
			Leucorrhinia	2, 3	9 (382.7)	51 (2614.4)	21 (243.0)	4 (42.2)	12 (541.7)	3 (25.9)
			(Immature)	2, 3	5 (230.5)	3 (207.1)	1 (11.7)		6 (178.2)	
		Corduliidae	Cordulia shurtleffi	2, 3	7 (421.3)	20 (912.7)	1 (11.7)	2 (138.1)		1 (11.7)
			Somatochlora	2, 3	1 (7.1)	5 (102.0)	22 (245.4)	2 (23.4)	9 (330.0)	
	Trichoptera	Phryganeidae	Agrypnia	9	33 (99.0)	4 (28.0)	1 (0.5)	5 (2.3)	5 (2.3)	18 (60.5)
		Leptoceridae	Mystacides	9	8 (21.6)	66 (178.2)	4 (10.8)	3 (8.1)	21 (56.7)	20 (54.0)
			Oecetis	2, 9		13 (5.9)	11 (5.0)		1 (0.5)	
		Polycentripodidae	Polycentropus	9	21 (35.9)	9 (146.9)	2 (1.5)			
			Rhyacophila	9						1 (20.8)
scraper	Coleoptera	Haliplidae	Brychius	2				3 (4.5)		
		Helodidae		2				2 (5.5)		
	Gastropoda	Planorbidae	Mentus cooperi	2						6 (24.2)
			Gyraulus	2	33 (165.9)	52 (101.3)	23 (41.1)			
		Planorbidae	Helisoma	2	22 (633.8)	15 (1160.9)	32 (1853.7)	9 (107.8)	27 (193.4)	
		Physidae	Physa	2	380 (1098.2)	263 (1050.1)	252 (638.0)	97 (239.4)	219 (625.2)	83 (333.4)
		Valvatidae	Valvata sincera helicoidea	2	23 (33.4)	8 (14.2)	30 (66.8)	8 (11.6)	3 (4.4)	1 (1.5)
			Valvata sincera sincera	2	1 (1.5)					8 (27.1)
		Lymnaeidae	Lymnaea stagnalis	2	7 (492.2)	39 (1809.7)	10 (358.3)	8 (319.7)	25 (1177.1)	7 (407.5)
			Stagnicola	2	3 (10.1)	3 (23.0)	1 (3.4)	8 (52.6)	15 (82.6)	
shredder	Coleoptera	Curculionidae		2		17 (45.9)	15 (40.5)	1 (2.7)	4 (10.8)	3 (8.1)
		Heliophoridae	Helophorus	3	26 (71.5)	2 (5.5)	2 (5.5)		1 (2.8)	
		Chrysomelidae	Neohaemeonia	16			1 (2.7)			1 (2.7)
			Pyrrhalta	17			1 (2.7)			
	Diptera	Tipulidae	Prioncera	2, 18			12 (25.2)	3 (2.8)	35 (73.0)	

Feeding Group	Order	Family	Genus / Species	Ref*	Round 1 Abun.(Blo.)	Round 2 Abun.(Blo.)	Round 3 Abun.(Blo.)	Round 4 Abun.(Blo.)	Round 5 Abun.(Blo.)	Round 6 Abun.(Blo.)
			Tipula	2		1 (0.7)	2 (3.2)		4 (1.9)	
	Lepidoptera			2, 3		2 (14.0)			1 (7.0)	
	Trichoptera	Limnephilidae	Nemotaulius	9, 19		4 (0.8)				
			Limnephilus	2	57 (32.0)	48 (257.6)	9 (84.1)	25 (46.1)	576 (204.2)	43 (833.1)
		Leptoceridae	Nectopsyche	9			15 (6.8)			
			Triaenodes	20	1 (2.7)	168 (453.6)	106 (286.2)		14 (37.8)	4 (10.8)

* 1 - Clifford 1991; 2 - Barbour et al. 1999; 3 - Merritt and Cummins 1996; 4 - Resh 1976; 5 - Huryn and Gibbs 1999; 6 - Edmunds et al. 1976; 7 - Wissinger et al. 2004; 8 - Mihuc and Toetz 1994; 9 - Wiggins 1996; 10 - Berte and Pritchard 1983; 11 - Martin et al. 1981; 12 - Lillie 1991; 13 - Deding 1988; 14 - Shemanchuk 1972; 15 - Scudder 1987; 16 - Askevold 1987; 17 - Juliano 1988; 18 - Lantsov 1984; 19 - Pritchard and Berte 1987; 20 - Tindall 1960; 21 - Wiggins and Parker 1997.

Chapter 3

Dietary and stable isotope analysis indicates Bufflehead (*Bucephala albeola*) duckling's reliance on larval Dytiscidae within the Western Boreal Forest [2]

Introduction

Duckling survival is one of the most important factor determining waterfowl population dynamics (Dzubin & Gollop 1972, Hoekman *et al.* 2002) and foraging is a critical component of this survival (Street 1977, Reinecke & Owen 1980, Cox *et al.* 1998, Sjöberg *et al.* 2000). Duckling mortality has been shown to be the key factor that determines autumn populations (Hill 1984). Ducks rely almost exclusively on aquatic invertebrates as a protein source for growth, development, and survival during the first month of life (Driver 1981, Sedinger 1992, Pelayo & Clark 2003). Ducklings with higher nutrient reserves and efficient foraging strategies are better equipped to avoid weather-caused mortality (Talent, Krapu & Jarvis 1983, Gendron & Clark 2002) and predation (Mauser, Jarvis & Gilmer 1994, Nummi, Sjöberg & Pöysä 2000).

The western boreal forest (WBF; residing on the boreal plain) is an important area for breeding waterfowl, housing an estimated 9.7 ± 0.4 million ducks, approximately 26% of North America's waterfowl (Canadian Wildlife Service Waterfowl Committee 2001). The WBF in northern Alberta is very important habitat for Bufflehead (*Bucephala albeola* Linnaeus); wetlands there provide rearing habitat for the greatest proportion of their population (Erskine 1972). Between 1990 and 2003 Bufflehead numbers have had a significant negative trend, decreasing by 5.8% per year (Canadian Wildlife Service Waterfowl Committee 2003). With increased development on this landscape, managers will have to decide which wetlands are most important to sustain breeding waterfowl numbers. Exactly which groups of invertebrates Bufflehead ducklings prefer and utilize is important as this information can be useful in the delineation and enhancement of waterfowl habitat quality (Schroder 1973).

Bufflehead ducklings feed at the water's surface during the first few days after hatch or during periods of heavy invertebrate emergence, but in later developmental stages ducklings rely

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[2] A version of this paper has been submitted to the journal *Functional Ecology*. Corresponding styles and format apply to citations, figures and tables.

on diving to capture prey (Bellrose 1978). It stands to reason that large-bodied, conspicuous invertebrates comprise a large portion of the diet for this visually oriented predator. Erskine (1972) reported on Bufflehead diets from Alberta and neighbouring British Columbia where Coleopterans (larvae and adults) represented the highest percent volume of all food ingested. Along with Odonata and Corixidae, large-bodied, nektonic invertebrate groups represented 69 percent by volume of all food. While this and other studies of Bufflehead duckling diets (Dixon 1926, Munro 1949) have contributed to our understanding of this species and its management, I found no papers that compare dietary constituents to that which is available. Without information on the availability of invertebrate prey items the importance of abundant and readily available invertebrates may be overemphasised while those invertebrates that are available at low densities, yet present at moderate proportions in the diet, could be underemphasised or vice versa (Krapu & Reineke 1992).

The objective of this study was to compare invertebrates ingested by Buffleheads to measurements of the invertebrate community available to them on WBF ponds. I tested if Bufflehead ducklings demonstrate a preference for a particular family of aquatic invertebrates, in relation to their availability. I also used stable isotope analysis (SIA) to provide a time-integrated estimator of trophic position and, by extension, dietary selection of Bufflehead ducklings.

Materials and Methods

Study Area

This study is one aspect of the Hydrology, Ecology, and Disturbance (HEAD) research project initiated at the universities of Alberta and Waterloo. In 1999, this multi-disciplinary group chose 24 wetlands 20 kilometres north of Utikuma Lake, Alberta, Canada, (56° 00' - 56° 20' N, and 115° 20' - 115° 40' W; Figure 1.1 – Utikuma Study Site) within the Mid-Boreal Upland Ecoregion of the WBF. The WBF comprises approximately 85% of the boreal forest natural region in Alberta, Canada (greater than 293,000 km^2; Thomas 1998), and represents more than 50% of the mixedwood section of Canada's Boreal Forest Region (Rowe 1972) stretching from north western Ontario to the Yukon. All wetlands were classified as eutrophic (S. Bayley unpublished data) with total phosphorus levels >25 mg per litre (Wetzel 1983), occurred on low-relief, poorly drained sedimentary tills (Prepas *et al.* 2001), and all were associated with established peat beds, allowing the additional classification of peatland according to Vitt *et al.* (1998).

Bufflehead Samples

During the summers of 2001 and 2002, I used a shotgun to collect class II (Gollop & Marshall 1954) Bufflehead ducklings from wetlands within the WBF under Canadian Wildlife Service Permit (WSA-8-01) and under approval of the University of Alberta's Animal Care and Use Committee (Protocol #2001-36B). When more than one individual was taken from a brood their results were combined to produce one sample. Immediately after collection, each ducklings' proventriculus and oesophagus (hereafter proventriculus), and gizzard (ventriculus) was removed and their contents preserved separately in 70% ethanol/3% formalin. Wetland samples of aquatic invertebrates were taken by vertically sweeping a dip net at the duckling's feeding location, observed before shooting, and at two random locations along the wetland shore. At all three locations I sampled the open water, emergent cover, and the peat/water interface with vertical net sweeps, ensuring to submerge the dip net into the flocculent detritus approximately 5 cm before raising it vertically. Live invertebrates were chilled, sorted from plant matter within 12 hours, preserved in 70% ethanol/3% formalin solution, and later identified to the taxonomic resolution of species or genus. During identification each invertebrate was assigned a small/medium/large size class, based on size guilds within each taxonomic grouping (usually family or genus). Estimates of biomass for each size class were obtained by calculating means of approximately 30 dried individuals.

Invertebrates in wetland samples were collected for stable isotope analysis and allowed to void their gut contents before freezing. I collected representatives of both the aquatic invertebrate primary consumers (Lymanalidae, Heliosoma, Chironomidae, Ephemeroptera, Amphipoda) and secondary consumers (larval Dytiscidae, adult Dytiscidae, Anisoptera, Zygoptera) at each wetland (trophic classification via Barbour *et al.* 1999). Invertebrate stable isotope samples and duckling livers were frozen, freeze dried, pulverized, packed into tin cups and CO_2 and N_2 gases analysed with a VG Optima triple collector isotope-ratio mass-spectrometer via open split at the National Water Research Institute in Saskatoon, Saskatchewan, Canada. I expressed stable isotope ratios in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material ($\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$) where R was the ratio of ^{13}C to ^{12}C or ^{15}N to ^{14}N. Standards for carbon and nitrogen were Pee Dee belemnite and atmospheric nitrogen, respectively.

Statistical Analysis

The proportion each invertebrate group contributed to the dietary biomass of each duckling was averaged across all ducklings to produce an invertebrate group's mean dietary proportion (Table 3.1). I measured duckling foraging selectivity by calculating the proportion each invertebrate group represented of the total ingested biomass ($\%B_{duckling}$; as above) and subtracting the proportion that specific prey group represented in the corresponding wetland dip sample ($\%B_{wetland}$). This number was a positive value if the prey group was selected by the duckling more frequently than it was represented in the wetland (Figure 3.1).

Proportion data were arcsine transformed and tested for normality with a Shapiro-Wilk test. Wilcoxon - Signed Ranks test was used to test if the observed mean of the invertebrate group's relationship with duckling stomach contents ($\%B^{duckling}$ - $\%B^{wetland}$ over all duckling ponds; Figure 3.1) were significantly above or below zero. Following Reinecke & Owen, only those ducklings that contained more than four discernible invertebrates were considered in the analysis (1980). Duckling oesophagus/proventriculus contained low invertebrate species richness, probably due to rapid food passage, and few ducklings had more than four invertebrates; therefore, only the combined (oesophagus/proventriculus/gizzards; hereafter stomach) measure was used in the selectivity analysis. Indeed, Danell & Sjöberg (1980) found that ducklings, unlike adult ducks, show little difference in dietary constituents between the gizzard and the proventriculus, due to the small grit size found in the gizzard. An invertebrate group had to occur in the diets of at least three ducklings (corresponding to > 23% of total duckling diets) to be counted as the absence of a particular invertebrate from the stomach may indicate unavailability as opposed to avoidance. ANOVA was used to assess variation in mean SIA values among the duckling, primary, and secondary consumer groups, followed by a multiple comparison Tukey HSD test.

Results

A total of 13 broods were sampled (1 duckling from 11 broods, 2 ducklings from 2 broods) for dietary invertebrates. Invertebrate identification of duckling stomach contents yielded 14 groups of aquatic invertebrates (Table 3.1). Our Wilcoxon Signed Ranks test indicated a significant preference in Bufflehead ducklings for larval Dytiscidae (Order: Coleoptera), larval Zygoptera (Order: Odonata), and adult Coleoptera not including Dytiscidae (hereafter simply adult Coleopterans) (Figure 3.1).

Ducklings were more enriched in $\delta^{15}N$ than their prey ($F_{2, 55} = 32.870$; $P < 0.0001$). Secondary consumers such as dytiscids were also enriched over primary consumers as all three groups were significantly different from each other (Tukey HSD, $P < 0.001$). The $\delta^{13}C$ values between the three groups were not significantly different ($F_{2, 55} = 3.83$; $P = 0.712$). The trophic shift in nitrogen isotope ratios between primary consumers and secondary consumers ($\Delta\delta^{15}N$) was +2.4 ‰, while the shift between secondary consumers and ducklings was +1.5 ‰. The average $\Delta\delta^{15}N$ up one trophic level in aquatic environments is +2.3 ± 0.28 ‰ (McCutchan *et al.* 2003).

Discussion

Interpreting dietary preference requires measurement of both the ingested items and the availability of those items. Krapu & Reineke (1992) warned that estimating waterfowl food availability is difficult because commonly employed sampling methods inadequately describe this complex variable. When relating diet constituents to food availability with other duckling species, some authors have derived invertebrate measures by using insect traps that only capture free-swimming or emerging aquatic invertebrates (Street 1977), while others were unable to coordinate the timing of invertebrate surveys to coincide exactly with diet sampling periods (Nummi 1993), or in some cases, invertebrates were not sampled at all (Hohman 1985). I attempted to sample all common pond microhabitats, from benthic to surface, obtained by scraping vegetation with nets at observed foraging positions.

Bufflehead ducklings' foraging strategies include diving and visually searching for invertebrates from the nekton of wetlands as well as surface feeding (Erskine 1972). Larval dytiscids, preferred here (Figure 3.1), are large-bodied (2 - 6 cm) invertebrates that make frequent trips between nektonic hunting sites and the water's surface to respire. Zygoptera larvae can also be quite conspicuous, especially when they migrate to the shore to metamorphise. Non-dytiscid Coleoptera (mainly of the genus *Haliplus*) are also active in the nekton, maintaining an air bubble under the elytra that needs to be replenished with trips to the water's surface. The active, conspicuous behaviour of the above mentioned invertebrates may explain why Bufflehead ducklings selected for them (Figure 3.1). In addition, optimum foraging theory (MacArthur & Pianka 1966) corroborates our prediction that the relatively large size of larval dytiscids (high calorific content per individual) makes them a valuable prey item.

Adult dytiscids were also an important prey item for ducklings here, representing a major portion of ingested biomass (17%), yet they were neither preferred nor avoided (Table 3.1). These invertebrates are active free-swimmers, highly visible in the nekton making them likely candidates for dietary preference. They may not have been preferred because of their large size (MacArthur & Pianka 1966; *D. alaskanus* = 25mm), robust hard shell, and anti-predatory steroid defence (Scrimshaw & Kerfoot 1987), which all serve to increase the handling time required for their ingestion. I note that without data on their availability they almost certainly would have been interpreted as a highly selected food item (sensu Erskine 1972). Furthermore, this may point to other important criteria of Bufflehead-selected items; both Zygoptera and larval Dytiscidae have soft, un-sclerotized bodies potentially facilitating handling or digestion.

The analysis of duckling stomach contents in relation to available food provides only a snapshot estimate of the trophic interactions important to ducklings. Bufflehead ducklings are highly mobile feeders that search for optimum prey concentrations (Kaminski & Prince 1981) adapting their diet over their range (Dixon 1926, Munro 1949 and as they age (Erskine 1972, Stott & Olson 1973, Thompson & Ankey 2002). SIA provides a time-integrated measure of a duckling's diet (Gannes, O'Brien & Martinez del Rio 1997, Hebert & Wassenaar 2001). The recorded trophic shift in nitrogen isotope ratios establishes that these ducklings predominantly selected predatory invertebrates. Very little of their diet originates at the primary consumer trophic level, as corroborated by our dietary analysis; 83% of the invertebrate biomass Bufflehead ducklings ingest are secondary consumers. I suggest that the reason there is a $\Delta\delta^{15}N$ of 1.5‰ between the secondary consumers and ducklings, and not the average 2.3‰ in aquatic habitats (McCutchan *et al.* 2003), is because of the contribution of a limited amount of primary consumer prey and isotopically depleted plant material in the diet (Jones *et al.* 2004). Conversely, because the $\Delta\delta^{15}N$ between primary producers and ducklings is greater than 2.3 ‰, ducklings must be ingesting predatory invertebrates (secondary consumers) to elevate their average $\delta^{15}N$ values.

Future studies of duckling foraging should incorporate theoretical considerations by testing concepts like the marginal value theorem of optimal foraging theory (Charnov 1976), with much more detailed data on the availability of invertebrates. Other waterfowl studies have found that waterfowl adhere to other optimal foraging assumptions, like patch feeding times (Tome 1989) and area-restricted searches (Wood 1985). Krapu & Reinecke (1992) assert that estimates of abundance of all food items for all microhabitats or patches are essential, and the profitability of prey items ranked. While I precisely sampled invertebrates in duckling feeding areas and used biomass estimates of diet items to more closely link calorific profitability, I feel even more detailed work can be conducted in this area of research through empirical modelling of prey switching behaviour under varied prey concentrations in concert with optimal foraging theory considerations to isolate the benefits of specific wetland environmental characteristics and invertebrate compositions.

The WBF in northern Alberta is rapidly being developed by the energy and forestry sectors (Schindler 1998). This area is very important to the North American population of Bufflehead as it houses the highest density and largest proportion of breeding pairs (Canadian Wildlife Service Waterfowl Committee 2001). Ecologists are currently working with industry in the WBF to minimise the anthropogenic impacts; the results found here can be implemented where Bufflehead conservation is a consideration by equating the relative abundance of those preferred invertebrate groups with favourable Bufflehead habitat. Clear water and relatively shallow wetlands are ideal for diving beetles because they are visually oriented and obligated to respire at the surface (Lundkvist 2003). The analysis of ingested items as related to available invertebrate resources, and stable isotope analysis allowed us to extend the foraging results over time and remove some speculation on dietary items important for Bufflehead ducklings, previously emphasizing only Zygoptera and Coleoptera (Erskine 1972). Our analysis confirms that larval predaceous diving beetles are preferred, comprising almost half of the ingested biomass for these ducklings. Larval Dytiscidae play an indispensable role in the diets of Bufflehead ducklings within the WBF. Clear water wetlands with abundant Dytiscid beetles should be set aside or the upland surrounding these wetlands protected from clear-cutting if Bufflehead populations are a conservation priority.

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Table 3.1 - Invertebrates consumed by Bufflehead ducklings from the Western Boreal Forest, Alberta, Canada. Invertebrate groups are arranged in decreasing order of mean dietary proportion. The invertebrate group 'other Coleoptera' includes non-Dytiscid coleopterans. Positive Z scores indicate preference, negative indicate avoidance, and significant P-values are bolded with an asterisk appearing next to the invertebrate group.

	Invertebrate Group	Mean Dietary Proportion (±SE)	Selectivity test (Wilcoxon Signed Ranks)		Total Biomass (mg)	Mean Biomass (±SE) (mg)	Present in (n) of 13 Total Ducklings
			Z score	P-value			
*	Larval Dytiscid	0.457 (0.090)	2.82	**0.005**	1100.7	73.4 (28.8)	13
	Adult Dytiscid	0.169 (0.080)	1.19	0.236	613.7	40.9 (25.5)	6
*	Zygoptera larvae	0.142 (0.052)	2.40	**0.016**	683.7	45.6 (13.4)	11
*	Other Coleoptera	0.047 (0.017)	2.31	**0.021**	95.1	6.3 (1.8)	11
	Corixidae	0.043 (0.018)	1.41	0.158	65.3	4.4 (1.9)	10
	Acarina	0.016 (0.018)	-1.79	0.074	30.8	2.1 (2.3)	3
	Diptera larvae	0.014 (0.013)	-1.73	0.084	58.2	3.9 (4.1)	3
	Trichoptera	0.014 (0.015)	-1.72	0.086	64.8	4.3 (4.7)	4
	Anisoptera larvae	0.005 (0.004)	-1.52	0.128	17.5	1.2 (1.1)	3
	Larval Corixid	0.004 (0.003)	-0.68	0.499	6.4	0.4 (0.2)	5
	Ephemeroptera	0.001 (0.001)	-1.52	0.128	1.9	0.1 (0.1)	3
	Gastropoda	0.001 (0.001)	-	-	2.5	0.2 (0.2)	1
	Oligochaeta	trace	-	-	1.2	0.1 (0.1)	2
	Larval other Coleoptera	trace	-	-	0.7	0.1 (0.1)	1

Figure 3.1 - Dietary preference by Bufflehead ducklings. Preferred invertebrate groups are positive values, avoided groups are negative. Significant difference above (prefence) or below (avoidance) zero is indicated by * ($p < 0.05$; Wilcoxon Signed Ranks test).

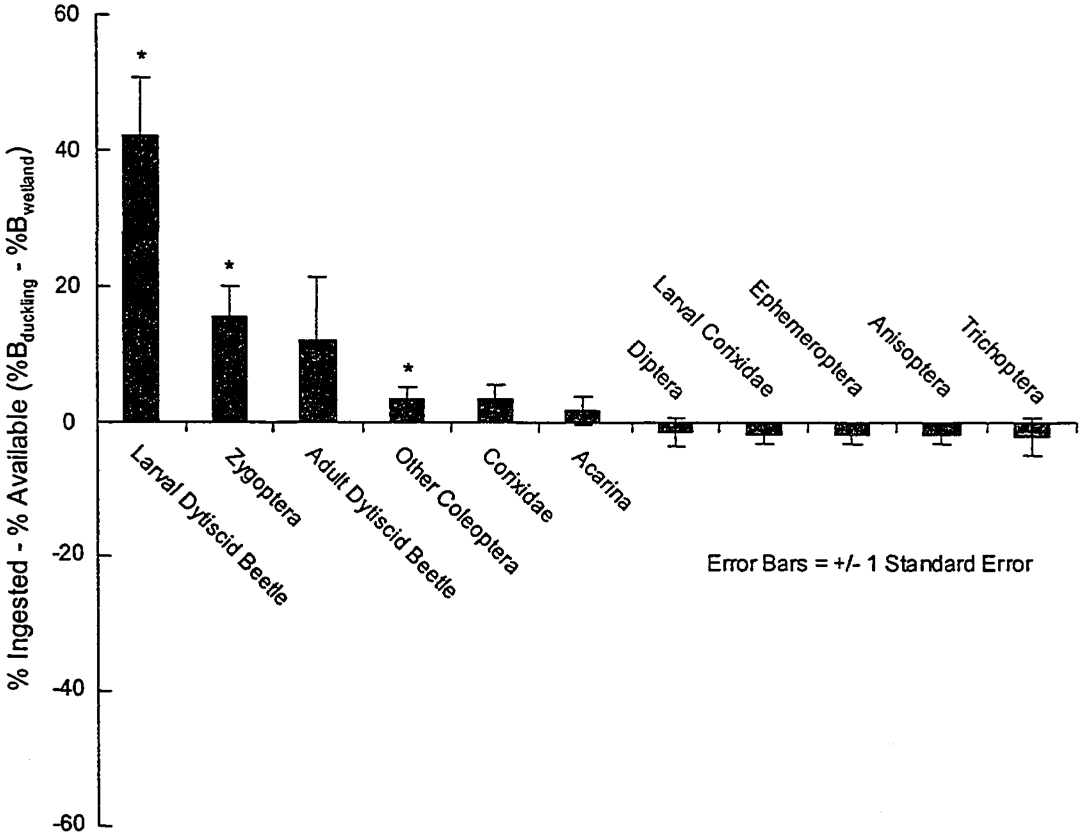
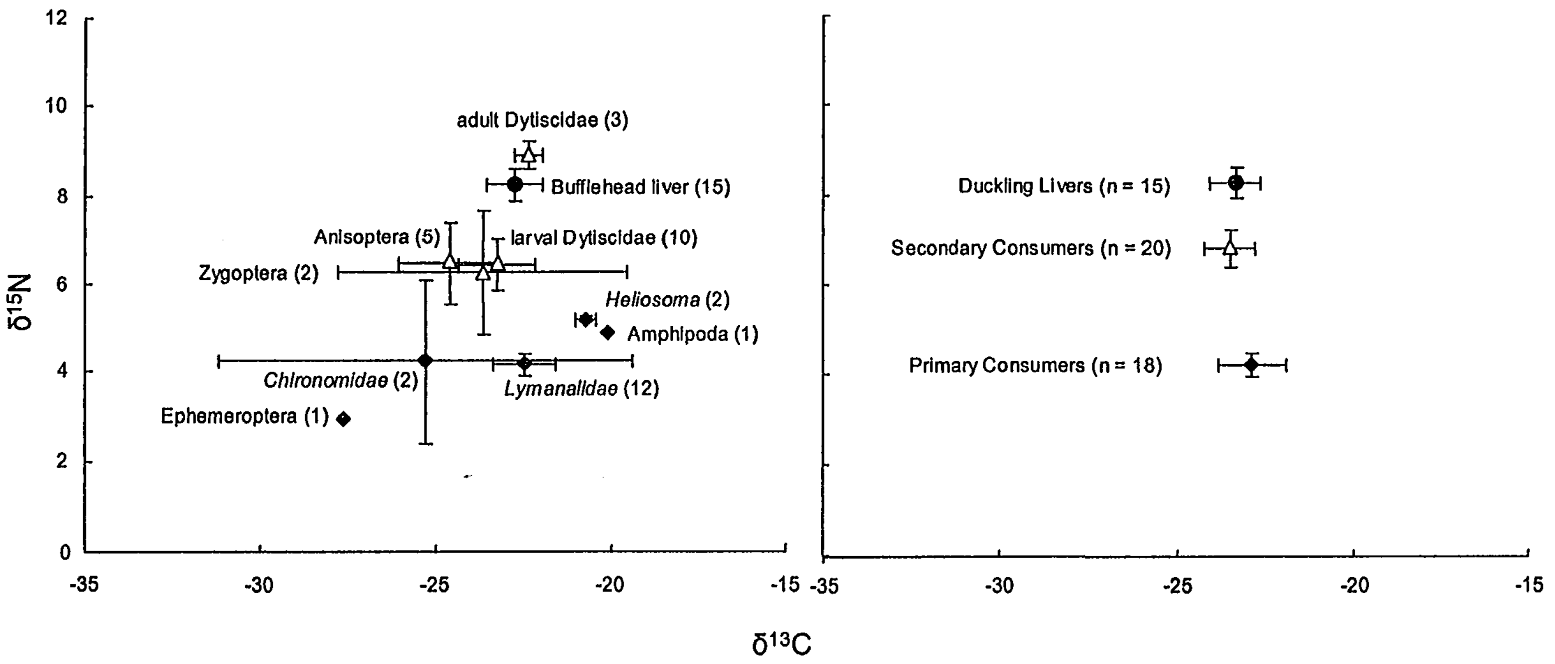


Figure 3.2 - Aquatic food web isotope values for Bufflehead ducklings and invertebrates collected from feeding wetlands. Values on the right are grouped by trophic level. Values in parenthesis indicate the number of samples for that group while error bars equal ± 1 Standard Error. Primary consumers are denoted by diamonds, secondary consumers by triangles, and ducklings by circles.



Appendix 3A – Stable isotope ratios for invertebrates and Bufflehead ducklings analyzed in Chapter 3.

Tissue Type	Date	Pond	Trophic Level	$\delta^{13}C$	$\delta^{15}N$	Code
Amphipod	2002	59	Primary Consumer	-20.1	5.0	59aph4
Chironomidae	2002	118	Primary Consumer	-31.2	2.4	118ch10
Chironomidae	2002	59	Primary Consumer	-19.4	6.1	59ch4
Ephemeroptera	2002	118	Primary Consumer	-27.6	3.0	118ep10
Heliosoma	2001	168	Primary Consumer	-20.4	5.3	168HEL21
Heliosoma	2001	168	Primary Consumer	-21.0	5.2	168HEL3
Snail	2001	121	Primary Consumer	-26.4	4.1	121LS1
Snail	2001	121	Primary Consumer	-24.2	3.3	121LS20
Snail	2001	121	Primary Consumer	-23.9	2.9	121LS21
Snail	2001	122	Primary Consumer	-20.4	3.4	122LS20
Snail	2001	122	Primary Consumer	-21.8	4.6	122LS21
Snail	2001	168	Primary Consumer	-18.7	4.3	168LS1
Snail	2001	1	Primary Consumer	-26.1	4.3	1LS21A
Snail	2001	1	Primary Consumer	-27.3	3.8	1LS21B
Snail	2001	48	Primary Consumer	-20.0	4.7	48LS11
Snail	2001	48	Primary Consumer	-19.3	5.3	48LS21A
Snail	2001	48	Primary Consumer	-20.3	5.1	48LS21B
Snail	2001	59	Primary Consumer	-19.7	5.4	59LS1
Anisopteran	2001	121	Secondary Consumer	-27.9	4.2	121AN1
Anisopteran	2001	122	Secondary Consumer	-23.3	8.5	122AN20
Anisopteran	2001	168	Secondary Consumer	-22.1	8.8	168AN3
Anisopteran	2001	1	Secondary Consumer	-28.1	5.1	1AN29
Anisopteran	2001	59	Secondary Consumer	-21.7	5.9	59AN1
Dytiscus	2001	122	Secondary Consumer	-21.8	9.2	122DA20
Dytiscus	2001	168	Secondary Consumer	-23.1	9.3	168DA3
Dytiscus	2001	48	Secondary Consumer	-22.2	8.3	48DA11
larv dytiscid	2001	121	Secondary Consumer	-24.2	6.4	121DL1
larv dytiscid	2001	121	Secondary Consumer	-21.8	6.8	121DL11
larv dytiscid	2001	168	Secondary Consumer	-19.6	7.5	168DL11
larv dytiscid	2001	168	Secondary Consumer	-19.9	6.9	168DL3
larv dytiscid	2001	1	Secondary Consumer	-27.5	2.8	1DL29
larv dytiscid	2001	48	Secondary Consumer	-25.8	8.2	48DL11
larv dytiscid	2001	59	Secondary Consumer	-23.5	8.8	59DY
larv dytiscid	2002	118	Secondary Consumer	-29.3	4.0	118dl10
larv dytiscid	2002	59	Secondary Consumer	-21.9	5.9	59dd4
larv dytiscid	2002	59	Secondary Consumer	-19.0	7.2	59dl4
zygopteran	2002	118	Secondary Consumer	-27.8	4.9	118zy10
zygopteran	2002	59	Secondary Consumer	-19.5	7.7	59zygop4
Duckling Liver	2002	118	Tertiary Consumer	-26.3	6.2	118ba
Duckling Liver	2002	118	Tertiary Consumer	-26.3	5.5	118bb

Tissue Type	Date	Pond	Trophic Level	$\delta^{13}C$	$\delta^{15}N$	Code
Duckling Liver	2002	118	Tertiary Consumer	-26.2	5.9	118bc
Duckling Liver	2002	59	Tertiary Consumer	-21.0	7.8	59ba
Duckling Liver	2002	59	Tertiary Consumer	-21.1	8.0	59bb
Duckling Liver	2001	121	Tertiary Consumer	-21.5	9.6	121BUFFA11
Duckling Liver	2001	121	Tertiary Consumer	-21.6	9.4	121BUFFB11
Duckling Liver	2001	122	Tertiary Consumer	-20.1	10.2	122BUFF20
Duckling Liver	2001	168	Tertiary Consumer	-18.7	9.1	168BUFF11
Duckling Liver	2001	168	Tertiary Consumer	-18.2	9.3	168BUFF17
Duckling Liver	2001	1	Tertiary Consumer	-26.8	8.5	1BUFFA29
Duckling Liver	2001	1	Tertiary Consumer	-26.9	7.9	1BUFFB29
Duckling Liver	2001	48	Tertiary Consumer	-23.6	8.8	48BUFFA11
Duckling Liver	2001	48	Tertiary Consumer	-23.3	8.5	48BUFFB11
Duckling Liver	2001	59	Tertiary Consumer	-19.7	9.5	59BUFF
Leech	2001	121	Tertiary Consumer	-27.0	11.0	121LE11
Leech	2001	168	Tertiary Consumer	-21.3	8.4	168LE11
Leech	2001	1	Tertiary Consumer	-29.5	6.2	1LE29
Leech	2001	48	Tertiary Consumer	-23.6	7.5	48LE11
Leech	2001	59	Tertiary Consumer	-24.1	9.0	59LE1

Chapter 4

Mallard duckling dietary analysis over three landscapes: niche breadth and the importance of Coleoptera [3]

Introduction

The sustainability of waterfowl populations depend on duckling survival and development, and therefore the management and protection of wetlands that provide broods with sufficient foraging opportunities. Duckling survival is one of the most important factors determining waterfowl population dynamics (Dzubin and Gollop 1972; Johnson et al. 1989; Nummi et al. 2000, Hoekman et al. 2002). Efficient foraging on aquatic invertebrates results in an increased chance of survival (Cox et al. 1998; Sjöberg et al. 2000; Robinson et al. 2003), resistance to weather-caused mortality (Talent et al. 1983; Gendron and Clark 2002), and predation (Mauser et al. 1994; Nummi et al. 2000). Accurate information on duckling food choices and the associated environmental characteristics can aid in the management and conservation of wetlands along the front of anthropogenic activities of the wetland rich landscapes of the western boreal forest (WBF).

It is not clear which groups of invertebrates are preferred by Mallard ducklings. In the Prairie Pothole Region (PPR), Chura (1961) found dipterans to be the most abundant aquatic invertebrate in Mallard duckling diets. Although correlative, a theory relating duckling success to dipteran abundance arose as a convenient and measurable metric of habitat quality, and was adopted in subsequent studies across a broad geographical area (Danell and Sjöberg 1980; Sjöberg and Dannell 1982; Pehrsson 1984; Dzus and Clark 1997; Ashley et al. 2000). Duckling foraging studies in boreal regions indicated that large bodied macroinvertebrates were important. In Sweden, Nummi (1993) found Mallard ducklings cued in on larger insects, and Elmberg et al. (2000) related duckling density to dytiscid water beetle distribution. Researchers of Mallard feeding habits found that ducklings forage preferentially where invertebrates tend to be the largest near the shoreline (Perret 1962). Optimal foraging theory suggests that the handling time

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[3] A version of this paper has been submitted to *The Canadian Journal of Zoology*. Corresponding styles and format apply to citations, figures and tables.

ducklings expend to include dipteran larvae in the diet requires many captures, resulting in a low caloric reward relative to the larger bodied predaceous invertebrates (MacArthur and Pianka 1966).

Approximately two million Mallards breed within the WBF yet little is known about waterfowl feeding ecology there; I feel the common practice of extrapolating results from southern locales is questionable (Bellrose 1980; Austin et al. 2000; Canadian Wildlife Service Waterfowl Committee 2003). Boreal wetlands play a vital role during the years the prairies experience drought as breeding Mallards "overfly" these unsuitable or crowded prairie wetlands to breed near more dependable, underutilized boreal habitats (Niemuth and Solberg 2003). I compared the diets of Mallard ducklings from the WBF to diets from the prairie and parkland ecoregions of the PPR to better understand Mallard food preferences and the relative importance of the WBF. Investigating dietary selection can provide insight into the availability of preferred resources, and by extension habitat quality. Optimal foraging theory states that a more productive environment permits a higher degree of specialization in the diet (MacArthur and Pianka 1966).

Our objectives were to investigate Mallard duckling diets across three ecozones, comparing resource selection and environmental characteristics to estimate habitat suitability. I investigated the hypotheses that i) Mallard ducklings prefer large-bodied nektonic invertebrates as opposed to small, benthic-dwelling chironomid larvae, ii) large-bodied nektonic invertebrates occur in Mallard duckling diets in proportion to their availability, iii) ducklings select sites within the wetland where invertebrate resources are the highest, and iv) ducklings in the more productive prairie and parkland ecoregions will show a higher degree of dietary specialization.

Study Area and Methods

Duckling collection

I examined three study areas: the Mid-Boreal Upland Ecoregion of the WBF of northern Alberta (56° 00' – 56° 20' N, and 115° 20' – 115° 40' W; Figure 1.1- Utikuma Study Site, boreal plain), the Mixed Grassland Ecoregion of southern Alberta (50° 15' – 50° 45' N, and 111° 30' – 112° 15' W; Figure 1.1 – Prairie Study Site), and the Aspen Parkland Ecoregion of south eastern Saskatchewan (50° 35' – 50° 55' N, and 102° 30' – 103° 40' W; Figure 1.1 – Parkland Study Site). Only wetlands on which Mallard ducklings were observed feeding were used in this study. Class IC to class III ducklings (Gollop and Marshall 1954) were collected using a shotgun under

Canadian Wildlife Service Permit (WSA-8-01) and under approval of the University of Alberta's Animal Care and Use Committee (2001-36B). Ducklings were shot during early morning foraging bouts (within 3 hours of sunrise) and in the late afternoon (2 hours prior to sunset). Only ducklings observed feeding were collected. When more than one individual was taken from a brood their results were combined to produce one sample. Immediately after shooting, ducklings were weighed, classified by developmental stage, the oesophagus/proventriculus and gizzard (ventriculus) removed and their separate contents preserved in a 70% ethanol / 3% formalin solution. I identified all invertebrates to the lowest possible taxonomic grouping and measured either invertebrate length or head capsule size to ascertain biomass estimates for each individual using power relationships from Smock (1980) and Benke et al. (1999). I ignored seeds and other plant material.

Wetland Invertebrate and Vegetation Surveys

Invertebrate surveys of the sample wetlands consisted of two vertical sweeps of a standard D-shaped aquatic dip net, starting with the net submerged 5 cm into the benthic material. Water depth was recorded at each sweep site to calculate invertebrate occurrence on a per water-volume basis. A benthic sample was taken by dragging the dip net along the pond bottom for 30 cm. A surface sample was conducted by sweeping the water's surface in two 1 meter sweeps with the net opening ¾ submerged. Vertical, benthic and surface samples were taken at the duckling feeding location, immediately after shooting (except in two cases in 2001), and at two additional locations located 20 meters in either direction along the shoreline. Bottom slope was also measured at each collection site. Two 1 m^2 quadrats at each sampling location were established to estimate the volumetric proportion inhabited by aquatic plants and emergent cover for ducklings. Water depth (cm), submersed plant height (h; cm), and areal plant cover (A; proportion of 1m^2 quadrat) were used to estimate plant volume within the quadrat by using the volumetric equation: A x h = plant volume (cm^3). Finally, the total plant volume was divided by the total water volume of each quadrat (10000 cm^2 x quadrat water depth), to estimate the percent volume of the quadrat occupied by plants. Terrestrial plant cover was determined by areal cover alone, tabulating only the plants that exceeded 10 cm in height.

I used paired t-tests to test for differences in available prey biomass/L between feeding sites and non-feeding sites at all wetlands. Sampling invertebrates with benthic, vertical, and surface sweeps can result in varied invertebrate sample compositions; these were treated separately in the analysis. Only those invertebrate groups identified as duckling food were included so not to overemphasize the importance of invertebrate groups that were selected. I tested for differences in the invertebrate prey biomass/L between landscapes using an analysis of variance. I then repeated the above test after weighting each invertebrate group's biomass/L in the wetland sample by its proportional biomass in duckling diets so that an invertebrate group that was high in biomass but relatively unimportant or unavailable to Mallard ducklings, such as Amphipoda, did not bias the results. To compare slope, depth, cover, aquatic plant proportion, and invertebrate biomass between feeding and non-feeding sampling locations I used paired t-tests. When contrasting these environmental variables between landscapes I averaged values from feeding and non-feeding sites and used Tukey's HSD to compare individual differences; reported P-values correspond to the nearest neighbour differences. All statistical methods follow that which is outlined in Zar (1999).

Stable Isotope Analysis

To provide a secondary estimator of food habits, I analysed the stable isotopes of nitrogen and carbon in duckling livers, invertebrate predators (Anisoptera, Corixidae, Dytiscidae, Notonectidae, Tanypodinae, Zygoptera) and invertebrate grazers (Gammaridae, Chironomidae, Cladocera, Ephemeroptera, *Lymnaea stagnalis*). Live invertebrates were allowed to void their gut contents for 24 hours in distilled water then stored frozen to be freeze dried, crushed with a mortar and pestle, and packed in tin capsules for isotopic analysis in the laboratory. CO_2 and N_2 gases were analysed with a VG Optima triple collector isotope-ratio mass-spectrometer via open split. I expressed stable isotope ratios in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material ($\delta^{13}C$ or $\delta^{15}N = [(R_{sample} / R_{standard}) - 1] \times 1000$) where R was the ratio of ^{13}C to ^{12}C or ^{15}N to ^{14}N. Standards for carbon and nitrogen were Pee Dee belemnite and atmospheric nitrogen, respectively. I tested for significant differences in $\delta^{15}N$ and $\delta^{13}C$ between the invertebrate trophic groups and ducklings on each landscape with Tukeys HSD.

Bearhop et al. (2004) suggest using the variance in $\delta^{13}C$ or $\delta^{15}N$ as an indicator of dietary niche breadth; a group of individuals that consume a broad spectrum of prey species will show more isotopic variance than those which feed on a limited few prey species. I used Levene's Test to compare the variation in duckling liver $\delta^{13}C$ and $\delta^{15}N$ over the three landscapes, followed by a Tukey's HSD to delineate differences between the groups.

Dietary Analysis

Ducklings were included in the analysis if their diet contained over four discernible invertebrates (Reinecke and Owen 1980), and invertebrate groups were included only if their biomass comprised at least 5% of the (pooled across landscapes) duckling's diet. Duckling oesophagus/proventriculus contained low invertebrate species richness resulting in only few ducklings meeting the above criteria, probably due to rapid food passage, therefore only the combined (oesophagus/proventriculus/gizzards, hereafter stomach) measure was used in the selectivity analysis. Danell and Sjöberg (1980) found that unlike adult ducks the mastication of food items is not significant in the gizzard of ducklings due to the small grit size found there, and most items could still be identified.

Data on consumption and availability of invertebrates were analyzed using Manley's selection ratios ($\hat{w}_i$ - sampling protocol A, type III; Manly et al. 2002). Generally, these ratios are proportional to the probability of that resource group being utilized (groups in Appendix A). A log likelihood chi-square test was used to test the null hypothesis of no selection ($\hat{w}_i$ equal to 1), and Bonferroni confidence intervals were estimated to evaluate if each resource category was significantly selected ($\hat{w}_i >1$), avoided ($\hat{w}_i<1$) (Manly et al. 2002).

Principle component analysis (PCA), a multivariate ordination technique, was used to investigate dietary breadth shown by ducklings on the three landscapes. An invertebrate group was included in the ordination if it was in the diet of over 5% of the ducklings. Presence/absence data was used, the species matrix was checked for variable correlations above 0.70, intersample correlations were preserved, and 95% confidence ellipses around the centriods were plotted for sample scores (ducklings) grouped by landscape. An ordination biplot simultaneously displayed multiple invertebrate variables and duckling scores in a two-dimensional representation, while it maintained accurate depictions of relationships between them (McCune and Grace 2002). Pairs of PCA duckling scores were positively correlated if they were plotted close to each other and were dissimilar if plotted further from each other (Jongman et al. 1995). Invertebrate species vectors were arranged to provide the greatest separation in duckling scores; if a vector points in the direction of a 95% confidence ellipse that species was utilized more predominately by ducklings on the landscape indicated by the ellipse.

Results

Fifty-nine duckling / wetland relationships were investigated in this study with 36 from the boreal plain, 14 from the parkland, and 9 from the prairie. The invertebrate group that contributed most to duckling diets were larval and adult Dytiscidae, amounting to 72% in the boreal, 56% in the parkland and 26% in the prairie. When invertebrate consumption was compared to availability, I found that Amphipoda and Gastropoda were avoided on all landscapes (Table 1). Coleopterans, in aggregate, comprised the highest proportion of biomass in duckling diets amounting to 80% in the boreal, 71% in the parkland, and 38% in the prairie. Surface Hemiptera had the highest selection ratio ($\hat{w}_i$) on those landscapes where it was ingested (Figure 4.1), however I questioned these results because surface Hemiptera are very good at avoiding net capture and occurred in fewer than 5% of the available resource samples and have therefore been disregarded (following Manly et al. 2002). Dipterans were avoided in parkland and prairie landscapes and not selected for or against in the boreal habitat. Mallard ducklings demonstrated significant preference for Coleoptera, Dytiscidae, Trichoptera, and larval Dytiscidae on boreal wetlands, Dytiscidae and larval Dytiscidae on parkland wetlands, and Coleoptera and Corixidae on prairie wetlands.

On all landscapes Mallard duckling livers were significantly enriched in their nitrogen isotope ratios ($\delta^{15}N$) relative to their prey. Boreal ducklings averaged an enrichment of 2.6‰ in $\delta^{15}N$ over predaceous invertebrates ($P < 0.001$) and 3.7‰ over invertebrate grazers ($P < 0.001$) while predaceous invertebrates were significantly different from grazers by 1.1‰ ($P = 0.010$). There was no difference in $\delta^{13}C$ between boreal groups. Parkland ducklings were significantly enriched over predaceous invertebrates in nitrogen isotopes by 2.1‰ ($P = 0.022$), and invertebrate grazers by 2.4‰ ($P = 0.020$), while the isotopic signatures between invertebrate predators and grazers were not significantly different. Parkland $\delta^{13}C$ was the same for ducklings and invertebrates. Prairie $\delta^{15}N$ values were significantly different between ducklings and predaceous (2.3‰; $P = 0.048$) and grazing invertebrates. Although there was a large difference in the $\delta^{13}C$ means between prairie ducklings and invertebrate predators (2.7‰) and grazers (3.3‰), I detected no significant difference.

The variability in duckling liver $\delta^{15}N$ was significantly different across landscapes ($F_{2,62} = 12.03$; $P < 0.001$; Figure 4.5) with boreal ducklings showing significantly less variation in $\delta^{15}N$ (Tukey's HSD; $P < 0.001$) than the other landscapes. The Levene's Test of $\delta^{13}C$ residuals were also significant when considering the three landscape groups ($F_{2,62} = 32.50$; $P = 0.001$). Boreal ducklings had significantly less variation in $\delta^{13}C$ than ducklings from the other two study areas ($P < 0.006$).

There was no difference in invertebrate biomass sampled at feeding and non-feeding sites when considering benthic ($P = 0.152$), vertical ($P = 0.390$), or surface ($P = 0.188$) dip netting techniques (Figure 4.2). The weighted invertebrate biomass/L was not significantly different between landscapes ($P = 0.337$) although the total invertebrate biomass/L showed a significant difference between boreal and prairie landscapes (Tukey HSD < 0.05; Figure 4.3). There was more aquatic macrophyte volume at feeding sites in boreal wetlands ($P = 0.036$), less emergent cover at feeding sites in prairie wetlands ($P = 0.029$), and a steeper bottom slope at non-feeding sites in parkland wetlands ($P = 0.046$; Figure 4.4). The boreal wetlands sampled in this study had less aquatic ($P = 0.015$; Tukey's HSD) and emergent ($P = 0.017$) macrophyte cover per volume, were deeper ($P = 0.050$), and their depth increased more rapidly away from the shoreline ($P = 0.098$).

The first two axes of the PCA ordination explained 62.6% of the variation (Figure 4.6). The 95% confidence ellipse of boreal duckling scores was contained within the prairie and parkland ellipses.

Discussion

Mallard Duckling Diets

Interpreting dietary preference requires measurement of ingested items and the availability of those items. Krapu and Reineke (1992) warned that most studies of waterfowl feeding ecology have inaccurate estimates of food availability. Other duckling foraging ecology studies have surveyed the invertebrate community using insect traps that only capture free-swimming or emerging aquatic invertebrates (Street 1977). To overcome these limitations I attempted to sample all common pond microhabitats, using three dip-netting techniques immediately after duckling collection, at observed foraging positions. Furthermore, I avoided biasing the preference results by removing those invertebrates not included in duckling diets, presumably inaccessible to ducklings, from the calculation of our foraging Manley's section ratios.

Most studies of Mallard duckling diets designate dipteran larvae as the dominant food source, suggesting a link between Mallard duckling success and chironomid abundance (Danell and Sjöberg 1980; Sjöberg and Danell 1982; Talent et al. 1982; Batzer et al. 1993; Dzus and Clark 1997; King and Wrubleski 1998; Ashley et al. 2000). Our data did not support this. I found that Mallard ducklings either consume dipterans in proportion to their availability or avoid them within the ecoregions studied here (Table 1). Chironomidae larvae can reach high densities within the benthic zone of wetlands, especially in southern prairie wetlands where Chrua (1961) first studied Mallard duckling diets (Nelson 1990). I suspected that benthic chironmids were not ingested by many ducklings because those younger than class II prefer not to submerge their nares and therefore do not employ a tip-up feeding strategy by which they can exploit the benthos. This offers only a partial explanation, as 78% of all the ducklings examined were of class IIA or older. Water depth may have prevented Chironomidae from being included in duckling diets; observed feeding sites were deeper that 20cm on all landscapes thus making tip-up feeding infeasible for ducklings that have a maximum reach of only 14cm (Sugden 1973, Pehrsson 1979). Again, this does not fully explain the incongruity between our results and those from the literature as 81% of the ingested Dipteran biomass found here were in pupae and emergent forms, suggesting that surface feeding was preferred to tip-up feeding, even in older ducklings.

A clear explanation for the emphasis prior research has placed on Chironomidae emerged from our review of Mallard duckling dietary studies (Chura 1961; Perret 1962; Bengtson 1975; Street 1977). I found that assumptions regarding preference were made by considering the numerical abundance of dietary constituents, not the more biologically and energetically meaningful measure of biomass.

Amphipoda was avoided on all landscapes. Again, I interpreted this as evidence that ducklings did not forage in the benthic zones of the wetland, where Amphipoda take refuge (Åbjörnsson et al. 2004). Mallard ducklings are described as tactile foragers (Sedinger 1992), but the large size, random distribution, and free swimming behaviour of those preferred invertebrates (Table 1) suggests a visually oriented, surface-foraging behaviour. This underscores the importance of Coleoptera, and further the family Dytiscidae, in the diets of Mallard ducklings. In boreal and parkland habitats the Dytiscidae group were significantly selected for and provided the most dietary biomass. In prairie habitats non-dytiscid Coleoptera are preferred; this group along with Dytiscidae, still comprise the bulk of the dietary biomass there. The only other invertebrate groups preferred by Mallard ducklings were Trichoptera within the boreal and Corixidae within the prairie.

I propose that measures of Coleoptera biomass (with emphasis on Dytiscidae) become the new benchmark by which to assess Mallard duckling invertebrate resource availability, as opposed to Chironomidae abundance. Similarly, Elmberg et al. (2000) have associated dabbling duck distribution with Dytiscidae abundance on boreal wetlands in northern Europe. I also acknowledge that because dytiscids are predaceous, they may have a dependence on the abundance of chironomidae. This is consistent with our isotopic findings from boreal habitats.

Stable Isotope Analysis

The analysis of gastrointestinal contents to infer duckling preference for invertebrate groups provides only a snapshot estimate of the trophic interactions important to ducklings. Stable isotope analysis (SIA) helps to corroborate these results and fill the temporal gap as it provides a time-integrated measure of a duckling's diet (Gannes et al. 1997, Hebert and Wassenaar 2001). Mallard ducklings are highly mobile feeders that search for optimial prey concentrations (Kaminski and Prince 1981) and rapidly change food preferences throughout the precocial period (Chura 1961). The trophic shift in nitrogen isotope ratios between ducklings and predaceous invertebrates on all landscapes suggest that these invertebrates comprise a large portion of their diets, although it is only with boreal samples that I can confidently separate predaceous invertebrates from grazers with $\delta^{15}N$ and therefore conclude that ducklings are relying on predaceous invertebrates. I suspect the nitrogen isotope ratios from the prairie and parkland landscapes have been elevated as a result of the application of agricultural fertilizer or manure to uplands adjacent to the study wetlands (Hebert and Wassenaar 2001). Bearhop et al. (2004) suggest that the variation in $\delta^{13}C$ and $\delta^{15}N$ within a group can indicate the breadth of the dietary niche. Ducklings from the boreal ecoregion had significantly less variation in their carbon and nitrogen isotopic signatures; if this is true I would conclude that their diet was more specialized.

Mallard Duckling Foraging Niche

I found that duckling foraging sites within the wetland could not be predicted by available invertebrate biomass (Figure 4.2). This suggests that ducklings do not search out or follow the hen to patches of high invertebrate density (Monda and Ratti 1988). Other criteria, such as predator avoidance, may have directed area use more than food availability; however I found that ducklings on prairie wetlands foraged where cover was significantly reduced (Figure 4.4). Despite the aforementioned and isolated significant result, and the significant results from other landscapes (slope in the parkland; aquatic plant prevalence in the boreal), I found no consistent trend across all landscapes that could predict where ducklings would forage within the wetland. Choices with respect to feeding location are likely made by the hen at the resolution of the entire wetland, not through consideration of microhabitats within the wetland (Monda and Ratti 1988, Fast et al. 2004).

The environmental characteristics of boreal wetlands may explain why ducklings there preferred larval Dytiscidae (65% of dietary biomass; $\hat{w}_i = 1.68$). Brood-rearing wetlands in the WBF were deeper, more steeply sloped, and had less aquatic vegetation and cover than wetlands in southern locals (Bethke and Nudds 1993). Predatory invertebrates that are visually-oriented, like Dytiscidae adults and larvae, thrive in wetlands with a deep nekton and few aquatic plants (Elmberg et al. 2000; Hornung and Foote 2005).

To compare landscape suitability I employed optimal foraging theory's most robust theorem, stating that dietary breadth contracts when food is abundant and expands when food is scarce (Pianka 1991). Ducklings from boreal landscapes demonstrated a high degree of selectivity by significantly avoiding or preferring all but one of the invertebrate groups found in their diets. The 95% confidence interval ellipses of duckling dietary scores from each landscape can be interpreted as measures of niche breadth (Figure 4.6). The boreal duckling ordination scores result in a significantly smaller dietary ellipse, contained within the ellipses from the other two landscapes, indicating a more specialized diet.

Dietary breadth has been used to infer habitat suitability between geographic regions (Pedrini and Sergio 2002), foraging areas and season (Tebbich et al. 2004), and levels of prey cover (Anderson 1984). Competitive interactions can also constrict dietary niche breadth (Roughgarden 1974); this may be the case in regards to the competitive interaction between fish and waterfowl considered here (Bouffard and Hanson 1997). As a result of winterkill or hens choosing wetlands where fish are absent (Pehrsson 1984; McNicol and Wayland 1992; Mallory et al. 1994) fish occurrence in the study wetlands over all three landscapes is reported as consistently low (Lawler et al. 1974; Benoy et al. 2002; Danylchuck and Tonn 2003). Fish were detected in few invertebrate samples during this study.

The constricted dietary niche in boreal habitats as indicated by Manly's selection ratios (Table 4.1), the relatively small boreal ellipse within the ordination biplot (Figure 4.6), and the low variability in $\delta^{15}N$, in addition to the significantly higher biomass/L of invertebrate resources in boreal wetlands (Figure 4.3), suggests that boreal wetlands provide more invertebrate resources for Mallard ducklings as compared to prairie and parkland wetlands. Why then, given adequate wetland conditions, do Mallards breed in the greatest densities in prairie and parkland habitats? This question is important to assess the potential of the northern boreal plain; I show that it is not because of a lack of invertebrate food resources. Sjöberg et al. (2000) have shown that food limitation may prevent Mallards from rearing young on many boreal wetlands in Sweden. An explanation for the incongruity found here is furnished by comparing total phosphorus concentrations. Fennoscandian wetlands are considered 'rich' waterfowl ponds at phosphorus levels of 19 – 30 µg/L (Sjöberg et al. 2000), while in the WBF phosphorous levels average 120 µg/L (Bayley and Prather 2003).

Management Implications

Shallow, chironomid-rich wetlands are important for Mallards, especially in the fall when high densities of these invertebrates can inhabit the benthic zone of wetlands and adult ducks can access them via tip-up feeding (Dykman and Hann 1996). Conversely, during the cool spring months in Canada when Mallard ducklings hatch, brooding wetlands are generally deep with spring meltwater making benthic zones unreachable, and chironomids averse to emerge. Instead ducklings rely on aquatic predaceous macroinvertebrates that dwell near the surface and can overwinter as either larvae or adults.

Our results give evidence that Mallard rearing habitat should be assessed by the abundance of coleopterans, specifically Dytiscidae, and not dipterans, specifically Chironomidae (Danell and Sjöberg 1980; Sjöberg and Danell 1982; Swanson et al. 1985; Jacobson 1991; Batzer et al. 1993). Boreal habitats provide abundant food resources and foraging opportunities for Mallard ducklings, as indicated by dietary niche breadth. Reasons why more southerly wetlands result in a wider dietary niche for Mallard ducklings, and less of a specialization on particular invertebrate groups, could be the increased competition from other broods, predator avoidance resulting in sub-optimal foraging, or anthropogenic influence resulting in decreased habitat suitability. I have further outlined how boreal wetlands play a role in Mallard ecology, and provided a new criterion (predaceous invertebrates as a food resource) for managers to use to assess habitat quality for Mallards in the understudied, and rapidly changing WBF.

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Table 4.1 - Invertebrates in Mallard duckling diets percent availability (%A), percent consumption (%C) and Manley's selectivity ratio ($\hat{w}i$) arranged in descending order of boreal %C. Letters following the selectivity ratio indicate the result of pairwise comparisons between landscapes (Bonferroni corrected alpha). The 95% confidence intervals (95% CI) were also adjusted with a Bonferroni corrected alpha and used to determine whether the selection ratio indicated the significant preference (P) or avoidance (A) Mallard ducklings have for that invertebrate group.

	BOREAL						PARKLAND						PRAIRIE					
Invertebrate Grouping	%C	%A	$\hat{w}_i$		95% CI	P/A	%C	%A	$\hat{w}_i$		95% CI	P/A	%C	%A	$\hat{w}_i$		95% CI	P/A
Larval Dytiscidae	65.1	16.1	1.68		0.24	(P)	25.8	12.9	3.81		1.7	(P)	15.5	19.6	1.15		1.12	
Diptera	11.8	3.7	1.08	A	0.62		0.7	7.9	0.05	B	0.04	(A)	2.2	5.8	0.42	A	0.44	(A)
Coleoptera	8.3	0.7	14.81		4.18	(P)	5	4.9	2.25		1.6		12.2	1.5	7.10		5.63	(P)
Dytiscidae	6.8	10.9	10.62		2.79	(P)	30.5	2.9	4.66		3.19	(P)	10.3	13.5	0.87		1	
Surface Hemiptera	2.9	0.4	163.30		82.09	(P)	2.2	0.1	4320.00		6447			tr				
Trichoptera	2.3	1.6	9.22		4.65	(P)	7.9	8.3	2.28		2.12		4.3	4.1	1.96		2.15	
Zygoptera	1.5	10.0	0.67		0.26	(A)	5	3.1	0.23		1.74		19.5	10.5	2.14		3.06	
Gastropoda	0.5	15.5	0.06	A	0.02	(A)	7.6	34.5	0.04	B	0.2	(A)	17.6	15	0.49	C	0.5	(A)
Corixidae	0.4	1.1	0.47	A	0.15	(A)	4.8	2.3	0.62	B	0.29	(A)	11	1.8	4.60	C	2.27	(P)
Larval Coleptera	0.2	0.5	0.33	A	0.09	(A)	9.7	1.4	13.58	AB	16.11			1.2				
Immature Corixidae	0.1	0.7	0.10	A	0.04	(A)	0.6	0.5	0.18	B	0.06	(A)	3.5	0.6	3.72	AB	3.25	
Hydrachnidia	tr	0.7	0.02	A	0.01	(A)	tr	0.5	0.01	B	0.04	(A)	1.2	0.9	1.24	AB	2.03	
Amphipoda	tr	8.0	<0.01	A	<0.01	(A)	tr	5.7	<0.01	B	<0.01	(A)	2.7	5.3	0.34	C	0.4	(A)
Anisoptera		3.4						6.9						3.8				
Ephemeroptera		2.6						4.1						5				
Hirudinea		10.4						0.2						5				
Immature Notonectidae		0.6						1.4						2.5				
Notonectidae		13.1						2.4						3.9				

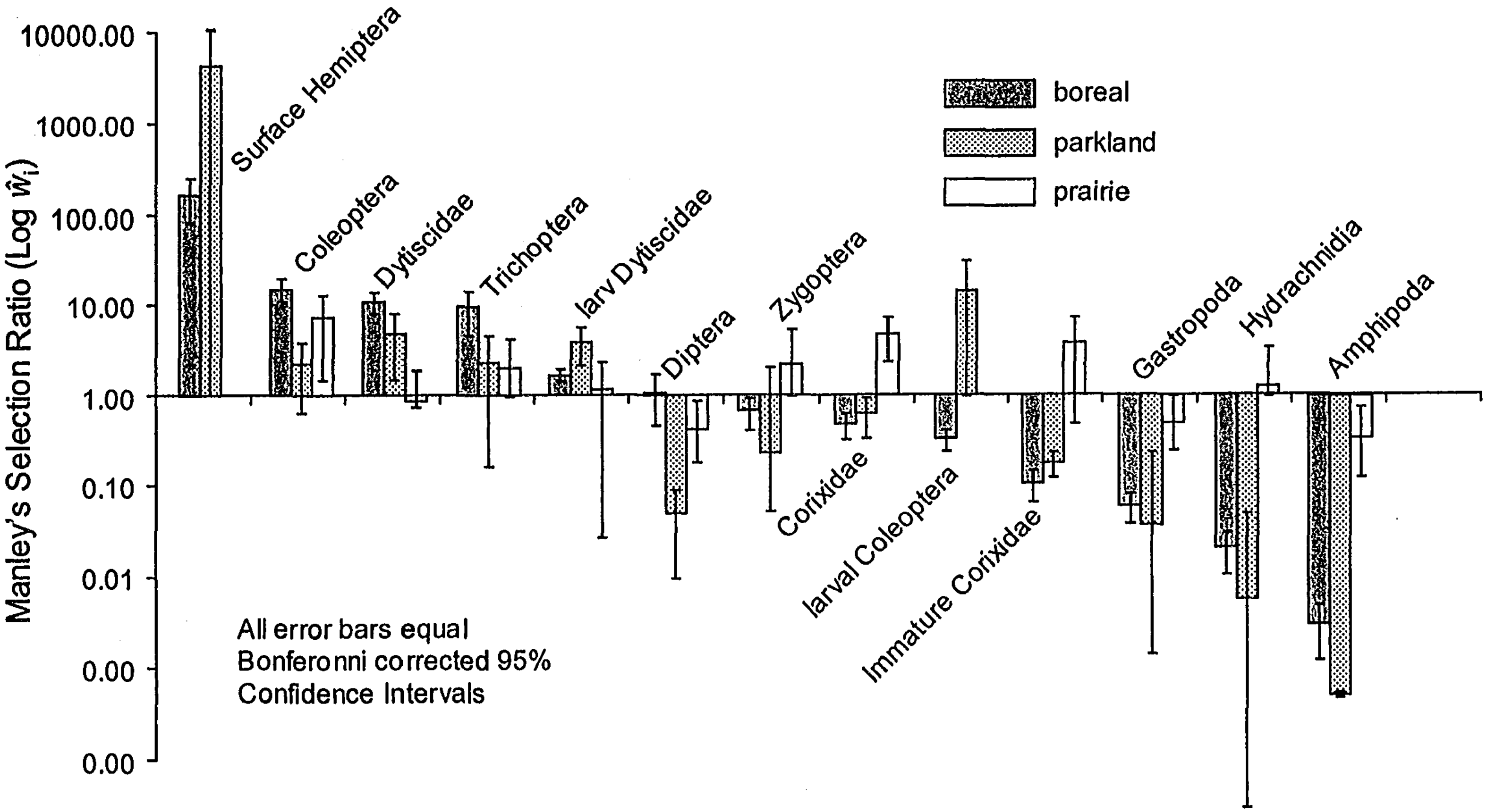


Figure 4.1 - Manley's selection ratio for invertebrate groups found in Mallard duckling diets. Information on whether an invertebrate group is significantly preferred or avoided is included in Table 4.1. Members of each invertebrate group are included in Appendix 4A.

Figure 4.2 - Wetland invertebrate biomass/L of those invertebrate groups found in duckling diets at feeding and non-feeding (alternate) sites using three types of invertebrate sampling methods: scoops of the benthic zone, horizontal sweeps of the water's surface, and vertical hauls of the wetland's nekton.

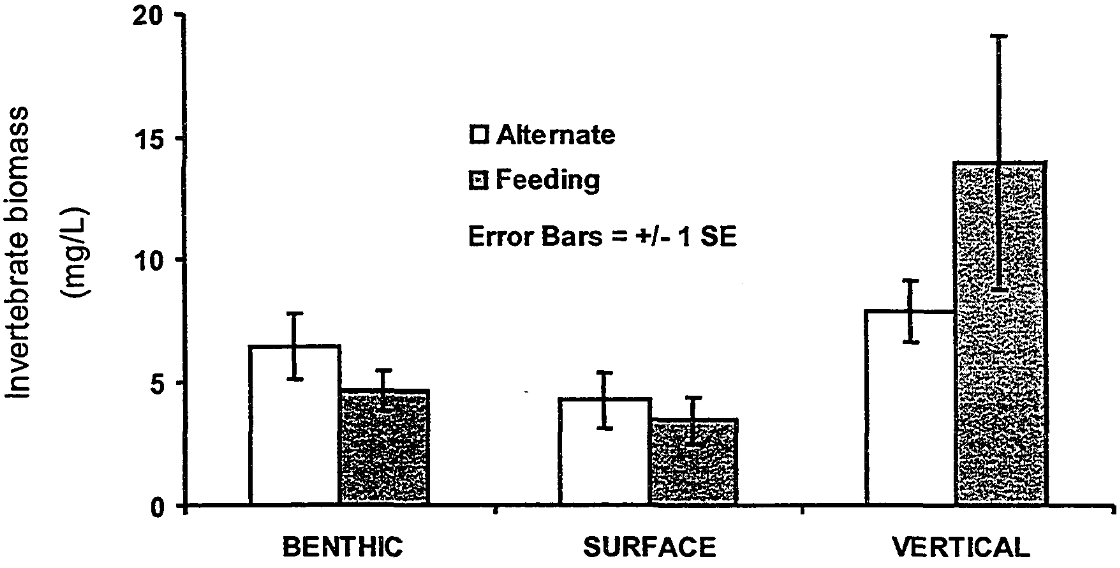


Figure 4.3 - Invertebrate biomass/L during the Mallard brooding season comparing landscapes. Weighted biomass/L is multiplied by the invertebrate group's proportion in duckling diets. Significant differences in means ($\alpha = 0.05$) are denoted by letters above bars.

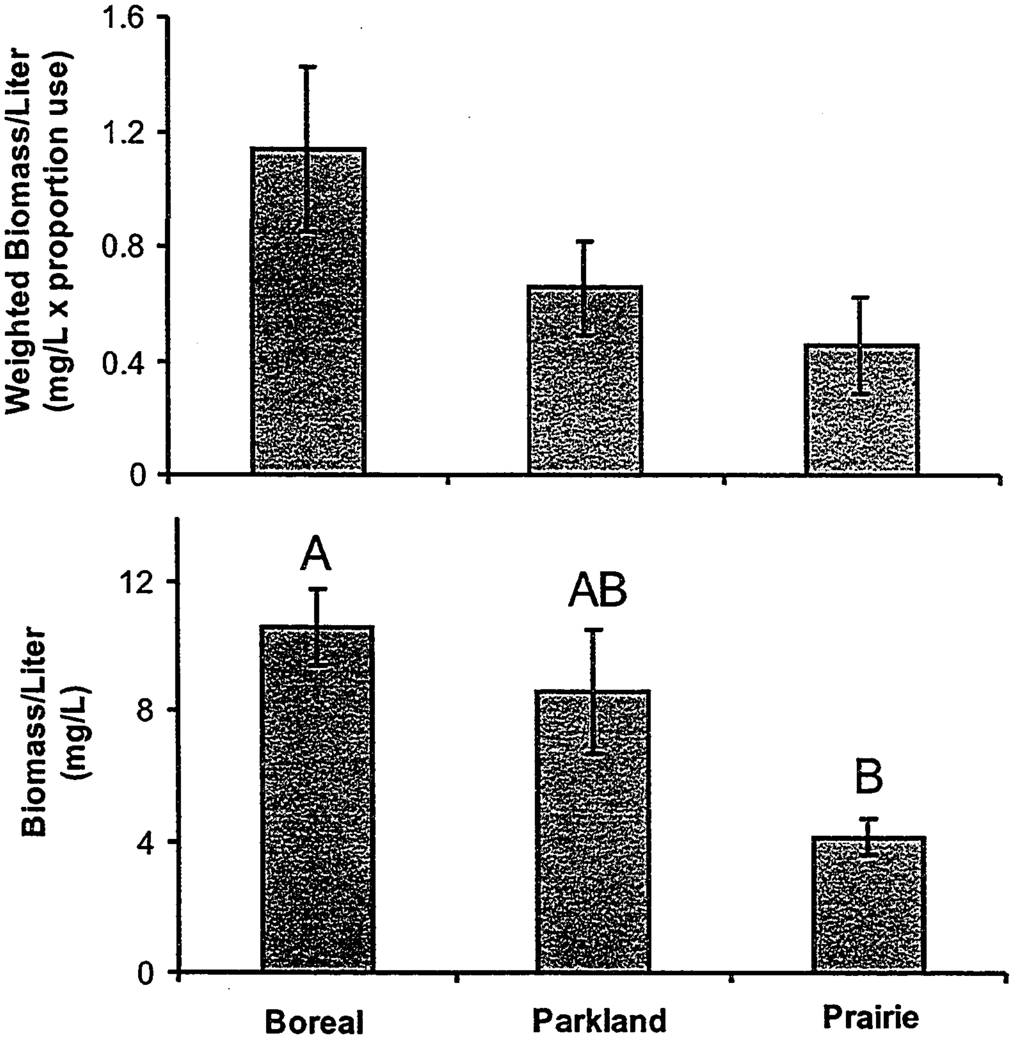


Figure 4.4 - Macrophyte prevalence, cover, depth, and slope at Mallard duckling wetlands comparing measurements at feeding to non-feeding sites. Asterisks indicate a significant difference ($P < 0.05$) using paired t-test.

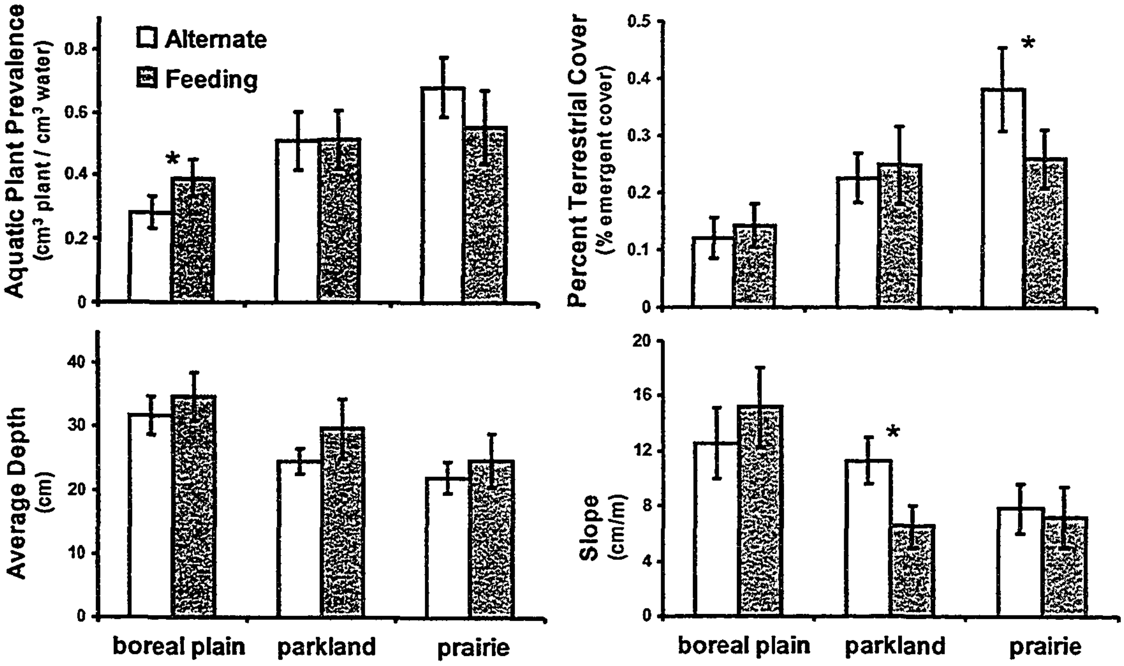


Figure 4.5 - Stable isotope values of Mallard duckling livers and invertebrate predators and grazers.

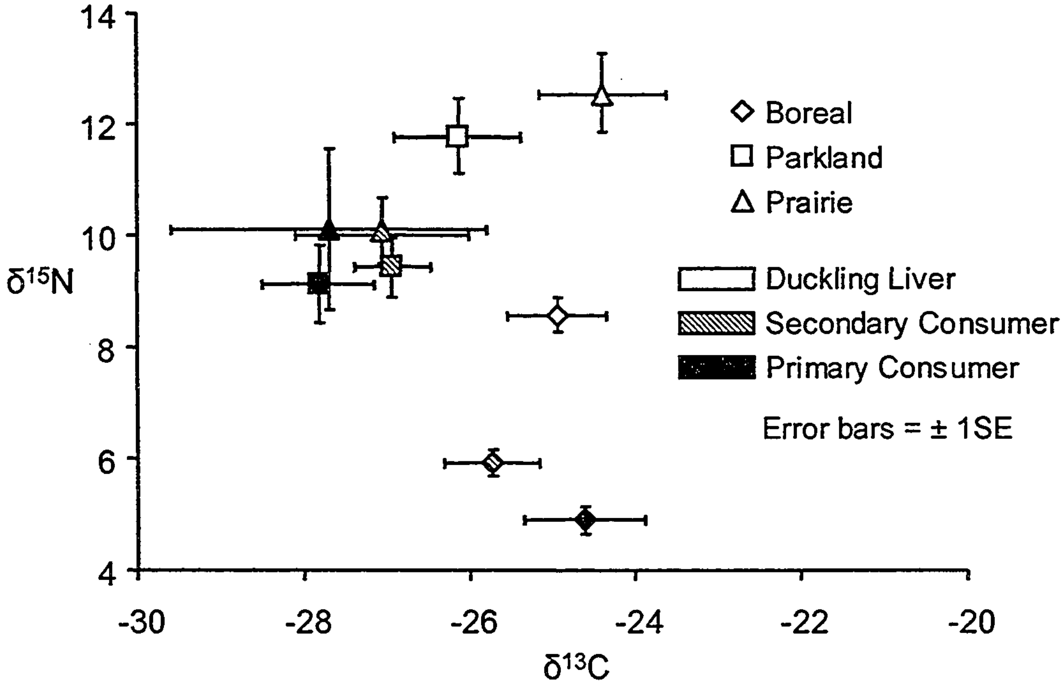
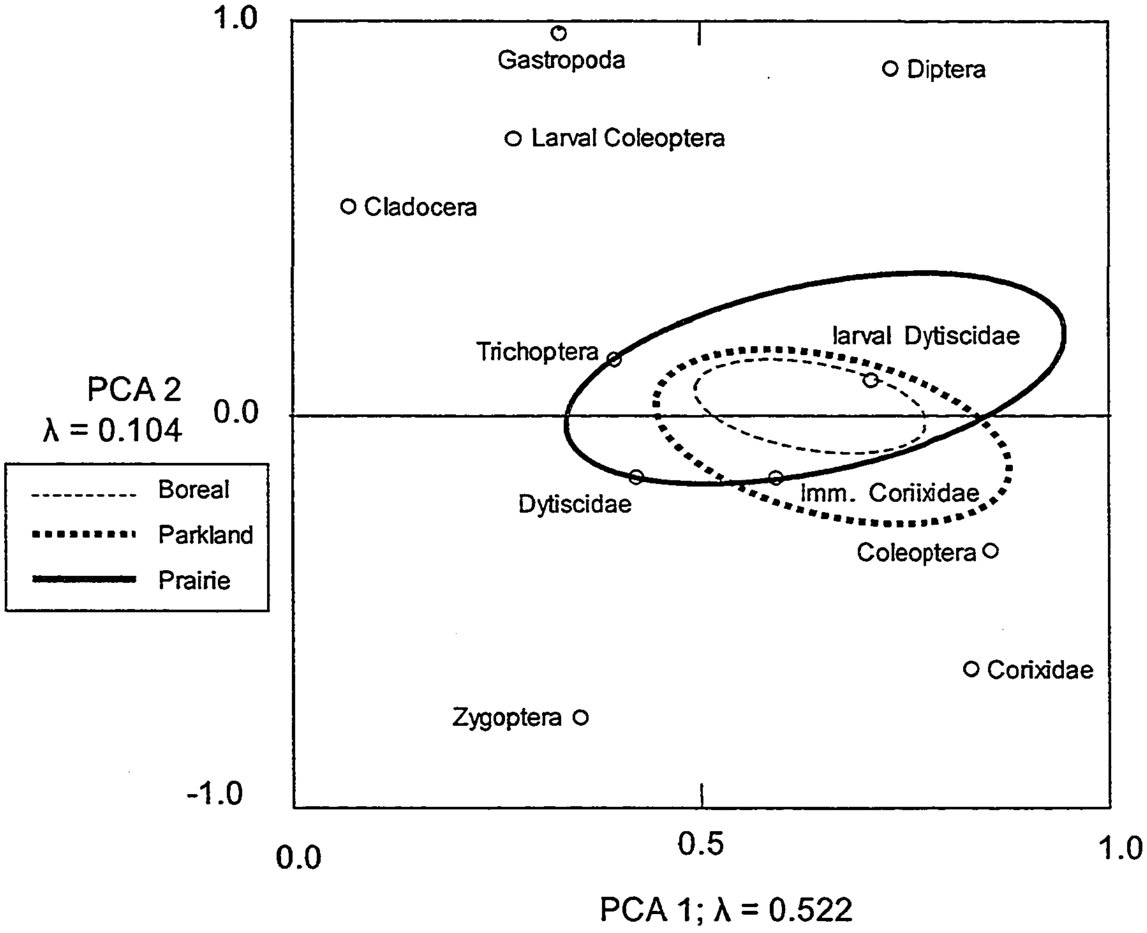


Figure 4.6 - Ordination biplot of invertebrate presence / absence in duckling diets. Ellipses are 95% confidence intervals around the centriods of duckling PCA scores from each landscape. The first axis explained 52.2% of the variation while the second explained an additional 10.4%.



Appendix 4A - Aquatic invertebrate species belonging to the invertebrate groups used in the analysis of duckling diets.

Invertebrate Grouping	Genera or Families in Grouping	Average Size† (mm ± 1SE)
Amphipoda	*Hyalella azteca, Gammarus lacustris*	3.8 (±0.02)
Anisoptera‡	*Aeshna* sp., *Leucorrhinia* sp., *Somatochlora* sp., *Sympetrum* sp., *Cordulia shurtleffi*	8.9 (±0.41)
Cladocera	*Diaphanosoma birgei, Daphnia pulex, Bosmina longirostris, Polyphemus pediculus, Ceriodaphnia quadrangula*	1.9 (±0.01)
Coleoptera (incl. Larval Coleoptera)	*Brychius* sp., *Curculionidae* sp., *Gyrinus* sp., *Haliplus* sp., *Helophorus* sp., *Hydrobius* sp., *Laccobius* sp., *Neohaemeonia* sp., *Paracymus* sp., *Pyrrhalta* sp., Scirtidae*	5.1 (±0.21) Larval: 9.8 (±0.16)
Corixidae (incl. Immature Corixidae)	Corixidae*	7.1 (±0.07) Immature: 4.8 (±0.07)
Diptera‡	*Aedes* sp., *Anopheles* sp., *Chaoborus* sp., *Chrysops* sp., *Dixella* sp., *Prioncera* sp., *Tipula* sp., Ceratopogonidae*, Chironomidae*, Chironomidae pupae*, Sciomyzidae*, Stratiomyidae*	9.3 (±0.04)
Dytiscidae (incl. Larval Dytiscidae)	*Acilius* sp., *Agabus* sp., *Anacaena* sp., *Colymbetes* sp., *Dytiscus* sp., *Graphoderus* sp., *Hydaticus* sp., *Hydroporus* sp., *Hygrotus* sp., *Ilybius* sp., *Laccophilus* sp., *Laccornis* sp., *Liodessus* sp., *Oreodytes* sp., *Rhantus* sp.	7.1 (±0.21) Larval: 8.9 (±0.24)
Ephemoptera‡	*Caenis* sp., *Callibaetis* sp., *Centroptilum* sp., *Siphlonurus* sp.	8.2 (±0.13)
Gastropoda	*Gyraulus* sp., *Helisoma* sp., *Physa* sp., *Pisidium* sp., *Sphaerium* sp., *Stagnicola* sp., *Promenetus exacuous, Promenetus umbilicatellus, Mentus cooperi, Valvata sincera helicoidea , Valvata sincera sincera, Lymnaea stagnalis*	5 (±0.04)
Hirudinea	*Theromyzon* sp., *Glossiphonia complanata, Helobdella stagnalis, Helobdella elongata, Haemopis grandis, Haemopis marmorata, Mooreobdella* sp., *Nephelopsis obscura, Erpobdella punctata*	19.2 (±1.19)
Hydrachnidia	(Hydrachnidia)*	1.9 (±0.02)

Invertebrate Grouping	Genera or Families in Grouping	Average Size[†] (mm ± 1SE)
Notonectidae	*Notonecta* sp.	12.7 (±0.42) Immature: 7.8 (±0.28)
Oligochaets	*Stylaria lacustris* sp., Lumbriculidae*	16.4 (±0.54)
Ostracoda	*Ostracoda* sp.	3.5 (±0.01)
Surface Hemiptera	*Limnoporus* sp., *Mesovelia* sp., *Microvelia* sp.	3.7 (±0.4)
Trichoptera‡	*Agrypnia* sp., *Arctopora* sp., *Asynarchus* sp., *Banksiola* sp., *Cerclea* sp., *Glyphopsyche* sp., *Limnephilus* sp., *Mystacides* sp., *Nectopsyche* sp., *Nemotaulius* sp., *Oecetis* sp., *Orthotrichia* sp., *Phryganea* sp., *Polycentropus* sp., *Ptilostomis* sp., *Rhyacophila* sp., *Triaenodes* sp.	10.1 (±0.33)
Zygoptera‡	*Coenagrion* sp., *Enallagma* sp., *Lestes* sp.	12.9 (±0.24)

* - Indicates taxonomic resolution at the family level only.

† - Average size of those invertebrates measured in this study.

‡ - Includes larval, emergent (teneral) and adult forms.

Appendix 4B – Stable isotope values of invertebrates and Mallard ducklings

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
Amphipoda	2002	Boreal	59	Primary Consumer	-20.1	5.0
Amphipoda	2002	Boreal	121	Primary Consumer	-23.7	3.7
Amphipoda	2002	Boreal	48	Primary Consumer	-20.0	4.8
Amphipoda	2002	Boreal	102	Primary Consumer	-21.3	3.8
Amphipoda	2002	Boreal	37	Primary Consumer	-20.1	2.6
Amphipoda	2003	Boreal	31	Primary Consumer	-23.2	6.4
Amphipoda	2004	Boreal	2	Primary Consumer	-23.4	1.6
Amphipoda	2004	Boreal	12	Primary Consumer	-17.7	3.6
Amphipoda	2004	Boreal	13	Primary Consumer	-15.8	7.4
chironomidae	2004	Boreal	1	Primary Consumer	-33.0	3.8
chironomidae	2004	Boreal	2	Primary Consumer	-26.4	4.5
chironomidae	2004	Boreal	3	Primary Consumer	-34.7	5.2
chironomidae	2004	Boreal	4	Primary Consumer	-31.3	4.8
chironomidae	2004	Boreal	5	Primary Consumer	-33.9	4.0
chironomidae	2004	Boreal	12	Primary Consumer	-20.6	6.4
chironomidae	2004	Boreal	13	Primary Consumer	-17.6	7.3
chironomidae	2004	Boreal	15	Primary Consumer	-14.7	5.5
chironomidae	2004	Boreal	16	Primary Consumer	-37.0	4.6
chironomidae	2004	Boreal	18	Primary Consumer	-34.7	2.6
chironomidae	2004	Boreal	20	Primary Consumer	-20.7	6.4
cladocera	2004	Boreal	13	Primary Consumer	-16.8	4.5
cladocera	2004	Boreal	16	Primary Consumer	-26.6	2.8
Diptera	2002	Boreal	59	Primary Consumer	-19.4	6.1
Diptera	2002	Boreal	121	Primary Consumer	-24.2	4.6
Diptera	2002	Boreal	102	Primary Consumer	-21.5	2.8
Diptera	2002	Boreal	118	Primary Consumer	-31.2	2.4
Diptera	2003	Boreal	11	Primary Consumer	-37.5	6.1
Diptera	2003	Boreal	31	Primary Consumer	-21.3	6.8
Diptera	2003	Boreal	31	Primary Consumer	-21.0	6.1
Diptera	2003	Boreal	31	Primary Consumer	-20.5	6.1
Diptera	2003	Boreal	32	Primary Consumer	-30.9	4.4
Diptera	2003	Parkland	13	Primary Consumer	-24.5	6.4
Diptera	2003	Parkland	14	Primary Consumer	-27.1	14.1
Diptera	2003	Parkland	15	Primary Consumer	-23.7	10.9
Diptera	2003	Parkland	16	Primary Consumer	-28.5	9.3
Diptera	2003	Parkland	23	Primary Consumer	-28.3	6.2
Diptera	2003	Parkland	24	Primary Consumer	-27.8	10.4
Diptera	2003	Parkland	25	Primary Consumer	-29.9	7.7

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
Diptera	2003	Parkland	28	Primary Consumer	-29.8	5.7
Diptera	2003	Parkland	29	Primary Consumer	-32.9	9.0
Diptera	2003	Prairie	1	Primary Consumer	-33.9	14.3
Diptera	2003	Prairie	4	Primary Consumer	-29.9	6.8
Diptera	2003	Prairie	5	Primary Consumer	-31.3	5.1
Diptera	2003	Prairie	7	Primary Consumer	-24.5	13.1
Diptera	2003	Prairie	10	Primary Consumer	-19.6	5.2
Ephemeropteran	2002	Boreal	118	Primary Consumer	-27.6	3.0
Ephemeropteran	2003	Boreal	31	Primary Consumer	-24.5	7.9
Ephemeropteran	2003	Boreal	32	Primary Consumer	-36.1	4.1
Ephemeropteran	2004	Boreal	3	Primary Consumer	-38.4	4.2
Ephemeropteran	2004	Boreal	5	Primary Consumer	-32.2	3.3
Ephemeropteran	2003	Prairie	3	Primary Consumer	-24.3	10.6
Heliosoma	2001	Boreal	168	Primary Consumer	-20.4	5.3
Heliosoma	2001	Boreal	168	Primary Consumer	-21.0	5.2
Lymanalidae	2001	Boreal	59	Primary Consumer	-19.7	5.4
Lymanalidae	2001	Boreal	168	Primary Consumer	-18.7	4.3
Lymanalidae	2001	Boreal	48	Primary Consumer	-19.3	5.3
Lymanalidae	2001	Boreal	48	Primary Consumer	-20.3	5.1
Lymanalidae	2001	Boreal	48	Primary Consumer	-20.0	4.7
Lymanalidae	2001	Boreal	122	Primary Consumer	-21.8	4.6
Lymanalidae	2001	Boreal	1	Primary Consumer	-26.1	4.3
Lymanalidae	2001	Boreal	121	Primary Consumer	-26.4	4.1
Lymanalidae	2001	Boreal	1	Primary Consumer	-27.3	3.8
Lymanalidae	2001	Boreal	122	Primary Consumer	-20.4	3.4
Lymanalidae	2001	Boreal	121	Primary Consumer	-24.2	3.3
Lymanalidae	2001	Boreal	121	Primary Consumer	-23.9	2.9
Lymanalidae	2002	Boreal	37	Primary Consumer	-22.9	3.7
Lymanalidae	2001	Boreal	201	Primary Consumer	-21.8	6.3
Lymanalidae	2001	Boreal	201	Primary Consumer	-21.4	5.8
Lymanalidae	2001	Boreal	201	Primary Consumer	-21.1	5.7
Lymanalidae	2001	Boreal	206	Primary Consumer	-26.8	2.7
Lymanalidae	2001	Boreal	206	Primary Consumer	-26.5	1.4
Lymanalidae	2003	Boreal	31	Primary Consumer	-24.8	10.7
Lymanalidae	2003	Boreal	32	Primary Consumer	-22.0	12.4
Lymanalidae	2003	Boreal	32	Primary Consumer	-32.5	7.0
Lymanalidae	2004	Boreal	4	Primary Consumer	-29.4	1.6
Lymanalidae	2004	Boreal	8	Primary Consumer	-21.3	4.1
Lymanalidae	2004	Boreal	9	Primary Consumer	-17.0	7.9
Lymanalidae	2004	Boreal	16	Primary Consumer	-35.3	3.3

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
Lymanalidae	2003	Parkland	21	Primary Consumer	-26.0	12.4
Lymanalidae	2003	Parkland	22	Primary Consumer	-26.3	10.6
Lymanalidae	2003	Parkland	23	Primary Consumer	-28.9	8.0
Lymanalidae	2003	Parkland	30	Primary Consumer	-28.0	7.9
Lymanalidae	2003	Prairie	1	Primary Consumer	-34.2	15.6
Lymanalidae	2003	Prairie	2	Primary Consumer	-23.9	10.2
Trichoptera	2004	Boreal	2	Primary Consumer	-19.3	3.7
Anisoptera	2001	Boreal	59	Secondary Consumer	-21.7	5.9
Anisoptera	2001	Boreal	168	Secondary Consumer	-22.1	8.8
Anisoptera	2001	Boreal	122	Secondary Consumer	-23.3	8.5
Anisoptera	2001	Boreal	1	Secondary Consumer	-28.1	5.1
Anisoptera	2001	Boreal	121	Secondary Consumer	-27.9	4.2
Anisoptera	2002	Boreal	121	Secondary Consumer	-23.6	4.2
Anisoptera	2002	Boreal	37	Secondary Consumer	-22.8	3.7
Anisoptera	2001	Boreal	201	Secondary Consumer	-21.5	6.9
Anisoptera	2001	Boreal	206	Secondary Consumer	-30.4	2.6
Anisoptera	2001	Boreal	206	Secondary Consumer	-30.5	0.6
Anisoptera	2003	Boreal	11	Secondary Consumer	-28.5	8.4
Anisoptera	2004	Boreal	4	Secondary Consumer	-29.9	5.9
Anisoptera	2004	Boreal	5	Secondary Consumer	-31.3	4.7
Anisoptera	2004	Boreal	7	Secondary Consumer	-31.1	6.2
Anisoptera	2004	Boreal	21	Secondary Consumer	-32.6	3.4
Anisoptera	2004	Boreal	28	Secondary Consumer	-29.2	3.6
Anisoptera	2004	Boreal	28	Secondary Consumer	-29.4	3.4
Anisoptera	2003	Parkland	13	Secondary Consumer	-23.1	9.5
Anisoptera	2003	Parkland	16	Secondary Consumer	-28.9	6.4
Anisoptera	2003	Parkland	21	Secondary Consumer	-24.8	11.3
Anisoptera	2003	Parkland	22	Secondary Consumer	-25.6	9.1
Anisoptera	2003	Parkland	23	Secondary Consumer	-26.4	7.5
Anisoptera	2003	Parkland	24	Secondary Consumer	-28.3	8.9
Anisoptera	2003	Parkland	25	Secondary Consumer	-28.7	7.7
Anisoptera	2003	Parkland	28	Secondary Consumer	-29.8	6.9
corixidae	2002	Boreal	121	Secondary Consumer	-24.2	4.6
corixidae	2002	Boreal	48	Secondary Consumer	-22.1	5.0
corixidae	2002	Boreal	102	Secondary Consumer	-20.8	4.4
corixidae	2003	Boreal	31	Secondary Consumer	-21.2	8.1
corixidae	2004	Boreal	15	Secondary Consumer	-17.4	6.9
corixidae	2003	Parkland	14	Secondary Consumer	-25.0	11.8
corixidae	2003	Parkland	15	Secondary Consumer	-24.6	10.3
corixidae	2003	Parkland	16	Secondary Consumer	-29.2	6.5

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
corixidae	2003	Parkland	21	Secondary Consumer	-28.3	8.7
corixidae	2003	Prairie	9	Secondary Consumer	-30.4	13.1
corixidae	2003	Prairie	10	Secondary Consumer	-27.3	6.6
Dytiscus	2001	Boreal	168	Secondary Consumer	-23.1	9.3
Dytiscus	2001	Boreal	122	Secondary Consumer	-21.8	9.2
Dytiscus	2001	Boreal	48	Secondary Consumer	-22.2	8.3
Dytiscus	2002	Boreal	121	Secondary Consumer	-23.4	4.9
Dytiscus	2002	Boreal	37	Secondary Consumer	-22.4	6.4
Dytiscus	2001	Boreal	206	Secondary Consumer	-31.4	7.3
Dytiscus	2001	Boreal	201	Secondary Consumer	-21.4	6.7
Dytiscus	2004	Boreal	1	Secondary Consumer	-35.0	4.6
Dytiscus	2004	Boreal	7	Secondary Consumer	-30.0	7.5
Dytiscus	2004	Boreal	8	Secondary Consumer	-24.0	6.7
Dytiscus	2004	Boreal	20	Secondary Consumer	-22.0	4.8
Dytiscus	2003	Parkland	14	Secondary Consumer	-27.2	12.0
Dytiscus	2003	Parkland	22	Secondary Consumer	-26.7	9.5
Dytiscus	2003	Parkland	28	Secondary Consumer	-32.4	6.5
Dytiscus	2003	Prairie	2	Secondary Consumer	-26.7	9.7
Dytiscus Larvae	2003	Boreal	32	Secondary Consumer	-37.7	4.0
Dytiscus Larvae	2001	Boreal	59	Secondary Consumer	-23.5	8.8
Dytiscus Larvae	2001	Boreal	168	Secondary Consumer	-19.6	7.5
Dytiscus Larvae	2001	Boreal	168	Secondary Consumer	-19.9	6.9
Dytiscus Larvae	2001	Boreal	48	Secondary Consumer	-25.8	8.2
Dytiscus Larvae	2001	Boreal	121	Secondary Consumer	-21.8	6.8
Dytiscus Larvae	2001	Boreal	121	Secondary Consumer	-24.2	6.4
Dytiscus Larvae	2002	Boreal	59	Secondary Consumer	-19.0	7.2
Dytiscus Larvae	2002	Boreal	59	Secondary Consumer	-21.9	5.9
Dytiscus Larvae	2002	Boreal	121	Secondary Consumer	-24.4	5.5
Dytiscus Larvae	2002	Boreal	48	Secondary Consumer	-20.2	5.9
Dytiscus Larvae	2001	Boreal	201	Secondary Consumer	-20.7	7.4
Dytiscus Larvae	2001	Boreal	206	Secondary Consumer	-29.6	4.9
Dytiscus Larvae	2002	Boreal	118	Secondary Consumer	-29.3	4.0
Dytiscus Larvae	2003	Boreal	31	Secondary Consumer	-21.2	9.1
Dytiscus Larvae	2003	Boreal	32	Secondary Consumer	-31.0	5.1
Dytiscus Larvae	2001	Boreal	1	Secondary Consumer	-27.5	2.8
Dytiscus Larvae	2004	Boreal	1	Secondary Consumer	-31.0	3.0
Dytiscus Larvae	2004	Boreal	3	Secondary Consumer	-33.6	4.9
Dytiscus Larvae	2004	Boreal	9	Secondary Consumer	-17.8	7.4
Dytiscus Larvae	2004	Boreal	12	Secondary Consumer	-19.4	5.2
Dytiscus Larvae	2004	Boreal	18	Secondary Consumer	-34.4	5.4

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
Dytiscus Larvae	2004	Boreal	20	Secondary Consumer	-23.7	5.4
Dytiscus Larvae	2004	Boreal	21	Secondary Consumer	-33.1	3.1
Dytiscus Larvae	2003	Prairie	1	Secondary Consumer	-34.7	12.4
Dytiscus Larvae	2003	Prairie	1	Secondary Consumer	-34.7	12.0
Dytiscus Larvae	2003	Prairie	5	Secondary Consumer	-25.3	5.5
Imm. Corixidae	2003	Boreal	31	Secondary Consumer	-20.1	7.0
Imm. Corixidae	2004	Boreal	8	Secondary Consumer	-27.1	0.4
Imm. Corixidae	2003	Prairie	7	Secondary Consumer	-21.3	11.5
Imm. Notonectidae	2004	Boreal	7	Secondary Consumer	-29.0	7.0
Imm. Notonectidae	2003	Parkland	13	Secondary Consumer	-24.8	8.2
Imm. Notonectidae	2003	Prairie	1	Secondary Consumer	-34.4	14.5
Imm. Notonectidae	2003	Prairie	5	Secondary Consumer	-23.4	5.0
Imm. Notonectidae	2003	Prairie	7	Secondary Consumer	-23.0	10.3
Imm. Notonectidae	2003	Prairie	9	Secondary Consumer	-27.2	9.2
Imm. Notonectidae	2003	Prairie	9	Secondary Consumer	-26.0	7.1
Notonectidae	2002	Boreal	37	Secondary Consumer	-21.0	4.2
Notonectidae	2003	Parkland	13	Secondary Consumer	-25.1	9.4
Notonectidae	2003	Parkland	14	Secondary Consumer	-24.7	11.6
Notonectidae	2003	Parkland	16	Secondary Consumer	-28.2	9.6
Notonectidae	2003	Parkland	24	Secondary Consumer	-26.5	7.5
Notonectidae	2003	Parkland	28	Secondary Consumer	-25.9	7.8
tanypodinae	2004	Boreal	9	Secondary Consumer	-20.8	7.0
Zygoptera	2002	Boreal	59	Secondary Consumer	-19.5	7.7
Zygoptera	2002	Boreal	121	Secondary Consumer	-23.6	5.0
Zygoptera	2002	Boreal	48	Secondary Consumer	-18.9	7.0
Zygoptera	2002	Boreal	102	Secondary Consumer	-20.5	6.5
Zygoptera	2002	Boreal	118	Secondary Consumer	-27.8	4.9
Zygoptera	2003	Boreal	11	Secondary Consumer	-30.2	8.9
Zygoptera	2003	Boreal	31	Secondary Consumer	-20.3	11.6
Zygoptera	2004	Boreal	1	Secondary Consumer	-32.5	3.5
Zygoptera	2004	Boreal	2	Secondary Consumer	-24.5	8.6
Zygoptera	2004	Boreal	3	Secondary Consumer	-34.7	7.4
Zygoptera	2004	Boreal	4	Secondary Consumer	-31.4	6.4
Zygoptera	2004	Boreal	18	Secondary Consumer	-35.1	5.2
Zygoptera	2004	Boreal	21	Secondary Consumer	-33.8	5.6
Zygoptera	2003	Parkland	14	Secondary Consumer	-27.4	13.4
Zygoptera	2003	Parkland	21	Secondary Consumer	-28.0	16.8
Zygoptera	2003	Prairie	1	Secondary Consumer	-35.0	13.0
Zygoptera	2003	Prairie	2	Secondary Consumer	-26.0	13.6
Zygoptera	2003	Prairie	3	Secondary Consumer	-23.0	10.1

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	δ^{13}C	δ^{15}N
Zygoptera	2003	Prairie	4	Secondary Consumer	-24.9	9.8
Zygoptera	2003	Prairie	5	Secondary Consumer	-26.0	7.4
Zygoptera	2003	Prairie	6	Secondary Consumer	-18.4	9.3
Zygoptera	2003	Prairie	9	Secondary Consumer	-27.6	11.4
Zygoptera	2003	Prairie	9	Secondary Consumer	-26.1	10.2
Mallard Duckling liver	2001	Boreal	59	Tertiary Consumer	-21.0	8.8
Mallard Duckling liver	2001	Boreal	59	Tertiary Consumer	-21.5	8.2
Mallard Duckling liver	2001	Boreal	168	Tertiary Consumer	-20.9	9.1
Mallard Duckling liver	2001	Boreal	168	Tertiary Consumer	-24.7	1.0
Mallard Duckling liver	2002	Boreal	59	Tertiary Consumer	-19.9	7.7
Mallard Duckling liver	2002	Boreal	121	Tertiary Consumer	-22.6	7.3
Mallard Duckling liver	2002	Boreal	121	Tertiary Consumer	-22.5	7.2
Mallard Duckling liver	2002	Boreal	48	Tertiary Consumer	-20.7	7.8
Mallard Duckling liver	2002	Boreal	48	Tertiary Consumer	-20.7	7.0
Mallard Duckling liver	2002	Boreal	102	Tertiary Consumer	-20.9	8.5
Mallard Duckling liver	2002	Boreal	102	Tertiary Consumer	-20.8	7.9
Mallard Duckling liver	2002	Boreal	37	Tertiary Consumer	-21.3	6.6
Mallard Duckling liver	2002	Boreal	37	Tertiary Consumer	-21.4	6.6
Mallard Duckling liver	2003	Boreal	11	Tertiary Consumer	-25.3	10.4
Mallard Duckling liver	2003	Boreal	12	Tertiary Consumer	-25.2	8.1
Mallard Duckling liver	2004	Boreal	1	Tertiary Consumer	-31.1	7.4
Mallard Duckling liver	2004	Boreal	2	Tertiary Consumer	-22.5	10.7
Mallard Duckling liver	2004	Boreal	3	Tertiary Consumer	-31.0	8.8
Mallard Duckling liver	2004	Boreal	4	Tertiary Consumer	-30.5	7.8
Mallard Duckling liver	2004	Boreal	5	Tertiary Consumer	-31.5	6.7
Mallard Duckling liver	2004	Boreal	6	Tertiary Consumer	-29.4	7.6
Mallard Duckling liver	2004	Boreal	7	Tertiary Consumer	-26.1	8.8
Mallard Duckling liver	2004	Boreal	8	Tertiary Consumer	-22.2	10.8
Mallard Duckling liver	2004	Boreal	9	Tertiary Consumer	-17.4	12.1
Mallard Duckling liver	2004	Boreal	10	Tertiary Consumer	-17.5	12.8
Mallard Duckling liver	2004	Boreal	11	Tertiary Consumer	-17.5	13.3
Mallard Duckling liver	2004	Boreal	12	Tertiary Consumer	-22.3	11.4
Mallard Duckling liver	2004	Boreal	13	Tertiary Consumer	-21.9	10.5
Mallard Duckling liver	2004	Boreal	14	Tertiary Consumer	-21.0	11.4
Mallard Duckling liver	2004	Boreal	15	Tertiary Consumer	-22.4	10.8
Mallard Duckling liver	2004	Boreal	16	Tertiary Consumer	-30.5	7.4
Mallard Duckling liver	2004	Boreal	17	Tertiary Consumer	-31.6	7.1
Mallard Duckling liver	2004	Boreal	18	Tertiary Consumer	-32.3	9.2
Mallard Duckling liver	2004	Boreal	19	Tertiary Consumer	-32.3	10.4
Mallard Duckling liver	2004	Boreal	20	Tertiary Consumer	-24.0	10.4

Tissue Type	Year	Eco-region	Pond Number	Trophic Level	$\delta^{13}C$	$\delta^{15}N$
Mallard Duckling liver	2004	Boreal	21	Tertiary Consumer	-32.4	6.8
Mallard Duckling liver	2004	Boreal	22	Tertiary Consumer	-32.2	6.9
Mallard Duckling liver	2003	Parkland	13	Tertiary Consumer	-22.9	11.7
Mallard Duckling liver	2003	Parkland	14	Tertiary Consumer	-25.3	16.8
Mallard Duckling liver	2003	Parkland	15	Tertiary Consumer	-24.3	13.6
Mallard Duckling liver	2003	Parkland	16	Tertiary Consumer	-28.6	9.9
Mallard Duckling liver	2003	Parkland	17	Tertiary Consumer	-29.7	11.0
Mallard Duckling liver	2003	Parkland	18	Tertiary Consumer	-30.3	11.5
Mallard Duckling liver	2003	Parkland	19	Tertiary Consumer	-29.8	9.6
Mallard Duckling liver	2003	Parkland	20	Tertiary Consumer	-29.9	8.9
Mallard Duckling liver	2003	Parkland	21	Tertiary Consumer	-26.4	11.0
Mallard Duckling liver	2003	Parkland	22	Tertiary Consumer	-18.2	14.7
Mallard Duckling liver	2003	Parkland	23	Tertiary Consumer	-22.6	11.2
Mallard Duckling liver	2003	Parkland	24	Tertiary Consumer	-28.2	9.7
Mallard Duckling liver	2003	Parkland	25	Tertiary Consumer	-27.8	10.0
Mallard Duckling liver	2003	Parkland	26	Tertiary Consumer	-24.6	10.9
Mallard Duckling liver	2003	Parkland	27	Tertiary Consumer	-22.5	11.2
Mallard Duckling liver	2003	Parkland	28	Tertiary Consumer	-26.4	12.0
Mallard Duckling liver	2003	Parkland	29	Tertiary Consumer	-27.3	8.8
Mallard Duckling liver	2003	Parkland	30	Tertiary Consumer	-25.8	15.5
Mallard Duckling liver	2003	Prairie	1	Tertiary Consumer	-28.9	12.5
Mallard Duckling liver	2003	Prairie	2	Tertiary Consumer	-26.2	13.4
Mallard Duckling liver	2003	Prairie	3	Tertiary Consumer	-22.5	13.8
Mallard Duckling liver	2003	Prairie	4	Tertiary Consumer	-27.6	9.3
Mallard Duckling liver	2003	Prairie	5	Tertiary Consumer	-25.1	11.5
Mallard Duckling liver	2003	Prairie	6	Tertiary Consumer	-25.7	13.6
Mallard Duckling liver	2003	Prairie	7	Tertiary Consumer	-22.2	11.1
Mallard Duckling liver	2003	Prairie	8	Tertiary Consumer	-22.0	12.1
Mallard Duckling liver	2003	Prairie	9	Tertiary Consumer	-25.5	12.3
Mallard Duckling liver	2003	Prairie	10	Tertiary Consumer	-20.0	9.1
Stickleback	2001	Boreal	201	Tertiary Consumer	-20.0	10.6
Stickleback	2001	Boreal	206	Tertiary Consumer	-27.3	5.3
Stickleback	2004	Boreal	16	Tertiary Consumer	-33.7	7.5
Stickleback	2004	Boreal	21	Tertiary Consumer	-32.5	6.1
Stickleback	2003	Prairie	2	Tertiary Consumer	-25.2	16.2
Stickleback	2003	Prairie	7	Tertiary Consumer	-21.7	13.8

Chapter 5

Synthesis: Aquatic Invertebrates and Waterfowl Management in Canada's Western Boreal Forest

Prior Conclusions and Literature Review

Here I synthesize the findings of the previous chapters and relate how the results discussed within this thesis can contribute to wetland and waterfowl management. Conclusions that can help inform managers include:

- Mallard and Bufflehead ducklings showed a strong preference for predaceous macroinvertebrates, specifically Dytiscidae larvae (Figures 3.1, 4.1);
- Predaceous macroinvertebrates were associated with wetlands containing aquatic macrophytes of simple architecture (Figure 2.3); and
- The presence of Brook Stickleback (*Culea inconstans)* significantly decreased the amount of biomass available to developing ducklings in the form of aquatic invertebrates (Figure 2.2).

Coupling these results with other duckling habitat research can further define protection and sustainability criteria. Mortality from freezing or anoxia (winterkill) is a principal determinant of Brook Stickleback distribution in the WBF (Tonn et al. 2004); deeper water can reduce risks of winterkill and allow stickleback populations to persist. Increased road development and soil compaction may promote channelization of upland water flow and runoff to wetlands. This may connect adjacent wetlands with overland flow and increase wetland depth before freeze, resulting in colonization opportunities and increased chance of winter survival, respectively, for stickleback. Field workers in the WBF have observed stickleback swimming up a channel leading to a hillside seep during winter, as much as 50m away from a source wetland, presumably to escape winterkill conditions (K. Devito, *pers. comm.*). Logging of upland forests can increase phosphorus loading to wetlands and lakes within the catchment (Prepas et al. 2001). Increased macronutrient concentrations can lead to wetland domination by *Myriophyllum exalbescens* (Carpenter et al. 1998) or phytoplankton (Annadotter et al. 1999). Both these characteristics would decrease the habitat suitability for Bufflehead and Mallard ducklings on wetlands of the WBF by reducing prey species or by increasing water opacity. To improve access to preferred food resources for Mallard and Bufflehead ducklings, brooding wetlands within the WBF should (1) have clear water, (2) support moderate amounts of simple aquatic macrophytes (preventing algal dominance; Norlin et al. 2005), (3) be fish-free, (4) have water depths of 30 to 40 cm, and (5) not occur within deforested catchments.

Large scale considerations

At a landscape level, WBF managers may want to concentrate on the protection of wetland complexes that are unconnected by surface flows yet maintained by groundwater (low susceptibility to fish colonization) to support abundant invertebrate forage for ducklings, instead of large, connected waterbodies. Small wetlands support a higher edge to open water ratio, that is important for waterfowl (Murkin et al. 1997), and are generally shallower, thereby promoting submerged macrophyte growth and fish winterkill. Predaceous diving beetles are capable of tolerating a wide range of adverse environmental conditions as adults, relative to other invertebrates (Minakawa et al. 2001), because of their sealed exoskeleton and utilization of atmospheric oxygen for respiration (as opposed to adsorption from aqueous medium over a gill structure). Dytiscidae larvae seem to be more susceptible to environmental variation, their abundance decreases as sedimentation from runoff increases (Martin and Neely 2001). The paucity of information specific to this group of macroinvertebrates prevents the demarcation of a definitive range of environmental tolerances. If dytiscid beetle abundance is used to imply Mallard breeding habitat quality, it is important to sample dytiscid larvae, as opposed to adults whose augmented dispersal capability allows for their presence in what could be sub-optimal habitat. Further, to accurately assess a wetland's suitability for dytisicids, the determination whether or not they are breeding there (with the resultant recruitment of new individuals) is important, as this is the most susceptible life stage (Inoda and Kamimura 2004).

The WBF's already significant role in supplying breeding habitat for North American waterfowl will probably increase for those species that now preferentially breed in the Prairie Pothole Region (PPR). Breeding wetlands of the PPR have been significantly reduced, largely through a combination of drought and the farming of marginal cropland. Drought conditions in the late 1980's through to the early 1990's, and locally in southern Alberta during the early 2000's, severely reduced overall waterfowl numbers (Canadian Wildlife Service Waterfowl Committee 2004) and the Mallard population (Bethke and Nudds 1995).

Global warming models predict that warming and drying in the PPR will drastically reduce the number of prairie breeding waterfowl over the next 60 years (Sorenson et al. 1998, Warren 2004). This could result in a greater proportion of North American Mallard populations originating in boreal wetlands, as a result of an increased growing season in northern climates and habitat loss in the PPR.

The Application of Optimal Foraging Theory to Ducklings

Ducklings from the boreal included fewer types of invertebrate prey in their diets (Chapter 4). Predictions from optimal foraging theory hold that diet breadth will contract when highly ranked food is readily available and abundant, and expand when it is not. I conclude that Mallard broods are not limited by food availability in the WBF, as proposed for the nutrient-poor Fennoscadian wetlands (Sjöberg et al. 2000). This indicates that factors other than duckling food availability (most likely limited chances for renesting, hen food availability, or inclement weather; see below) dictate the breeding Mallard numbers in the WBF. Even after considering other factors, the WBF currently plays a large role in the maintenance and sustainability of Mallard populations.

Waterfowl scientists have speculated that reduced waterfowl recruitment on northern wetlands was due to the "lower wetland productivity" (Rogers 1964, Pospahala et al. 1974, Cowardin et al. 1985). Overall (year-long) invertebrate production in southern locales is almost certainly greater, yet during the brooding season northern wetlands seem to have more available invertebrate resources for ducklings (Figure 4.3). The results found here are not consistent with Bethke and Nudds' (1993) assertion that boreal habitats have low resource production during the brooding season and therefore support fewer waterfowl species. I suggest the reduced abundance of waterfowl is influenced more by the length of the brooding season and reduced opportunities for re-nesting attempts.

Research Needs

Mallard duckling preference for particular invertebrate groups on wetlands within the boreal plain is well defined here. How does the composition and abundance of those invertebrate groups preferred by ducklings change when exposed to anthropogenic disturbance like upland forest clearing, oil well-site construction, or road development within the catchments? As the Utikuma area is subjected to additional, and substantial, energy sector development and large-scale forestry, the same wetlands surveyed throughout this study could be revisited to quantify the effects of these practices.

Are available habitats in the WBF fully occupied by breeding Mallards? Chapter 4 provides evidence that the productive wetlands of the WBF satisfy the dietary needs of ducklings. Empirical evidence to answer the above question is lacking, yet important factors such as competitive interactions, tolerance to inclement weather, or the influence of predators could be compared between their preferred habitat and the WBF. These questions are important if the WBF's relative contribution to duck populations increases.

Comparisons of spatial differences in breeding waterfowl numbers on both the WBF and PPR are a logical progression for further ecological study. First, more information is needed to understand the factors influencing migration between these two regions. I compare the WBF and PPR habitat characteristics and resources, yet it is not clear if these factors direct the abundance and distribution of breeding waterfowl on a regional scale.

To isolate local resource factors as the causal mechanism for waterfowl distribution requires a working model that quantifies the "overflight" hypothesis. Although this concept is touted as an important dispersal mechanism, and implicated when local breeding numbers fluctuate, analysis of redistribution is difficult. Researchers have worked to answer large-scale questions regarding continental waterfowl distribution (see Bethke and Nudds 1993, 1995 for example). The necessary information to rigorously explore this issue exist in long-term waterfowl data-sets (Canadian Wildlife Service Waterfowl Committee 2004) the quality of which are being consistently improved (Ducks Unlimited initiative as part of H.E.A.D. study); new sophisticated remote sensing techniques can accurately track waterfowl over local habitats (Pinsat Discovery for Recovery initiative) and advanced modeling techniques could investigate waterfowl distribution as related to changing environmental conditions (Sorenson et al. 1998). The exchange of waterfowl between the WBF and the PPR has important ramifications for waterfowl densities in the boreal, for the evaluation of the WBF's role in sustaining continental waterfowl populations, and especially for the interpretation of data from this region.

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