

A diet analysis of two zooplanktivores, the non-indigenous
rainbow smelt (*Osmerus mordax*) and the native cisco (*Coregonus artedi*),
in Lake Winnipeg, Manitoba

by

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ABSTRACT

Diets of two zooplanktivores were studied in Lake Winnipeg: the non-indigenous rainbow smelt (*Osmerus mordax*) and the native cisco (*Coregonus artedi*). Gut contents of smelt (70-130 mm total length) and cisco (100-200 mm TL) were concurrently collected with zooplankton (integrated vertical tows) from pre-determined locations throughout Lake Winnipeg in 2010 and 2011. When spatially separated, both zooplanktivores showed similar shifts from preference for fast-moving copepods during low total zooplankton density to slow-moving large cladocerans (*Daphnia* spp. and *Eubosmina* sp.) during high total zooplankton density. When spatially overlapped in the North Basin, dietary overlap was high between smelt and cisco, but possible vertical segregation was apparent during daylight-dark trawls. Diel variation in smelt diet was minimal. Overall, impact of smelt on the food web seemed weaker than in other smelt-invaded lakes, potentially owing to the warm, shallow nature of Lake Winnipeg providing a poorer quality habitat than cooler, deeper lakes.

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CHAPTER 1. Introduction

Non-indigenous species are an important conservation issue in many aquatic ecosystems. Invasive zooplanktivorous fish species can directly alter their prey community in a matter of decades (Mills *et al.* 1995; Beisner *et al.* 2003; Amundsen *et al.* 2009). Alterations may occur through selective foraging, for example, causing shifts towards the predominance of less energetically profitable prey species (Amundsen *et al.* 2009). Also, invasive species extend their impacts to native species occupying a similar trophic niche, in terms of dietary overlap and potential competition (Anderson and Smith 1971). Intraniche competition may lead to competitive exclusion and extirpation of native species (Hrabik and Magnuson 1999), or, alternatively, a non-indigenous species may be accommodated within the community through resource partitioning (Urban and Brandt 1993). A third possible scenario is that a non-indigenous species has no measurable impact, due to low competition with native species in a highly productive environment (Gozlan 2008).

One way of understanding the dynamics of trophic structure in response to a non-indigenous zooplanktivorous fish is by studying dietary preferences of the non-native species and niche overlap with native species. Many factors must be considered when investigating dietary preferences of a zooplanktivore, such as differing prey characteristics (Pulliam 1974; Ricklefs and Miller 2000), prey abundance (MacArthur and Pianka 1966; Werner and Gilliam 1984), as well as characteristics of the zooplanktivores themselves (Wong and Ward 1972; Werner and Gilliam 1984). Overall, zooplanktivores are predicted to maximize their fitness by consuming the most energetically profitable prey, thus optimizing their net energy gain (Pulliam 1974).

Environmental variables such as turbidity, temperature and oxygen availability also influence foraging strategies of aquatic species (Harrel and Dibble 2001). Water temperature is generally positively correlated with predator activity, whereas decreased oxygen availability is inversely related (Johnston and Mathias 1994; Pink 2010). It has been proposed that increased turbidity decreases the ability of a visual planktivore to locate and capture prey by increasing search time (Liu and Uiblein 1996), although it also has been suggested that turbid environments may be beneficial to visual zooplanktivores, as decreased predation pressure by piscivores may be experienced (Abrahams and Kattenfeld 1997; De Robertis *et al.* 2003) as well as potentially decreased prey capture energy expenditure due to decreased ability of zooplankton to detect predators (Alajärvi and Horppila 2004; Nurminen and Horppila 2006; Schulze 2011).

One such turbid water body, Lake Winnipeg, is found in southern Manitoba. Being a relict of glacial Lake Agassiz, Lake Winnipeg geologically straddles paleozoic sedimentary rock to the west and Precambrian Shield to the east (Patalas and Salki 1992). The lake itself is composed of two distinct basins: the deeper North Basin (mean depth 13.3 m) and the shallower South Basin (mean depth 9.7 m), connected by a short passage known as the Narrows (Patalas and Salki 1992). Lake Winnipeg is comparable to Lake Erie in terms of surface area but its mean depth is substantially shallower. This results in a warm lake that supports high commercial fish productivity (Lumb *et al.* 2011). As a result of substantial wind-mixing, the lake is extremely turbid and thermal stratification is rare, uncommon for a lake of its size (Franzin *et al.* 1994; Hann *et al.* 2005). Major inflows include the Red, North Saskatchewan, and Winnipeg Rivers, with outflow via the Nelson River into Hudson Bay (Brunskill *et al.* 1980; Patalas and Salki 1992). Lake

Winnipeg currently faces many ecological stressors, including cultural eutrophication and consequently extensive algal blooms, increased commercial fishery activity, and invasion of non-indigenous species (Liu *et al.* 2007). There are a number of non-indigenous species that are currently present in Lake Winnipeg, such as white bass (*Morone chrysops*) and common carp (*Cyprinus carpio*; Lumb *et al.* 2012). Other species are on the verge of entering the system, namely the spiny water flea (*Bythotrephes longimanus*) via the Winnipeg River and the zebra mussel (*Dreissena polymorpha*) via the Red River (Mills *et al.* 1993). However, it is one of the currently established non-indigenous piscine species, the rainbow smelt (*Osmerus mordax*), that is of interest in this project.

The rainbow smelt is native to the three coasts of Canada and the north-eastern coast of the United States (Scott and Crossman 1998). Initially anadromous, this species is capable of establishing non-anadromous land-locked populations (Scott and Crossman 1998; Stewart and Watkinson 2007). The intentional introduction of rainbow smelt to the Laurentian Great Lakes watershed has been documented as early as 1912 in Crystal Lake, Michigan (Evans and Loftus 1987). Subsequently, smelt became established in the Great Lakes themselves in the 1920s (Franzin *et al.* 1994). The range expansion continued west, eventually encompassing Lake Winnipeg, where first observations of the species were made in the South Basin in 1990 (Campbell *et al.* 1991; Franzin *et al.* 1994). Although the direct route of entry remains unresolved, it is possible that this population became established after either live bait release into the South Basin or downstream dispersal from the Winnipeg River via the English River system (Campbell *et al.* 1991; Franzin *et al.* 1994; Stewart *et al.* 2001). Range expansion has continued up the Nelson River, with rainbow smelt currently found in Hudson Bay (Remnant *et al.* 1997; Stewart

et al. 2001; Rooney and Paterson 2009).

In freshwater lakes, rainbow smelt are generally found in mid-water pelagic schools, but some older individuals in populations prefer deeper water (Stewart and Watkinson 2007). Sexual maturity occurs at approximately two years, with a typical lifespan of over seven years (Scott and Crossman 1998; Buckley 1989). In freshwater smelt populations, spawning occurs near-shore or in streams shortly after ice-off (Scott and Crossman 1998; Curry *et al.* 2004). Large post-spawning die-offs are common in late spring and early summer and are typically associated with fungal or disease outbreaks (Rooney and Paterson 2009). Fertilized eggs adhere to the substrata and incubate for 1-4 weeks dependent on water temperature, with a minimum threshold of 6-7 °C and an optimum of approximately 16.5 °C (Buckley 1989; Scott and Crossman 1998).

Larval and young-of-the-year (YOY) smelt may consume exclusively small zooplankters, such as small copepod species, especially nauplius larvae, and rotifers (Evans and Loftus 1987). By late summer, YOY smelt (45 mm fork length) are capable of eating larger zooplankton prey, most likely because of increased gape size (Urban and Brandt 1993). This dietary reliance continues, with adult (<150 mm) diets consisting almost entirely of zooplankton (Scott and Crossman 1998). Feeding is considered visual and selective, with large taxa (and large individuals within taxa) preferred (Johnson *et al.* 2004). In Lake Winnipeg, smelt prefer large cladocerans during the summer months (Sheppard *et al.* 2011). In other water bodies invaded by smelt or similar visually feeding zooplanktivores, selective foraging has restructured the zooplankton community towards one dominated by smaller taxa (Beisner *et al.* 2003; Amundsen *et al.* 2009). Also, smelt invasion has coincided with decreased densities and mean sizes of preferred zooplankton

prey (Johnson and Goettl 1999). These decreases have had detrimental impacts on native zooplanktivore populations, with smelt invasions associated with decreased abundance (Hrabik *et al.* 1998), lower condition (Wain 1993), and diet shifts (Lammens *et al.* 1985), as summarized by Rooney and Paterson (2009). However, smelt may increasingly consume benthic macroinvertebrates and YOY fish as body size increases beyond 150 mm (Stewart and Watkinson 2007; Pothoven *et al.* 2009). This shift is most likely because of increased gape size (Brandt and Madon 1986). In lakes where smelt reach these sizes, intra-guild predation by smelt on larval fish of other species (e.g. cisco, walleye) may cause a decline in abundance of these species owing to overlap in spawning and nursery habitats (Anderson and Smith 1971; Hrabik *et al.* 1998; Kreuger and Hrabik 2005). Rainbow smelt, therefore, indirectly and directly interact with many trophic levels in an invaded ecosystem (Rooney and Paterson 2009).

Cisco (*Coregonus artedi*), a native Lake Winnipeg zooplanktivore, is distributed extensively in freshwater lakes throughout Canada and the north-central and eastern United States (Scott and Crossman 1998). Generally found in the mid-water to benthopelagic zones, it is observed to reach sizes of 350-400 mm total length in Manitoba (Stewart and Watkinson 2007). Sexual maturity is usually reached at three to four years, with spawning occurring during fall, possibly under ice (Scott and Crossman 1998; Stewart and Watkinson 2007). In freshwater lakes, the spawning process usually involves large aggregations of fish and occurs in shallow water (1-3 m), but has been seen to occur in mid- to deep water as well (Scott and Crossman 1998). Eggs are laid on a variety of substrata and subsequently abandoned over winter (Stewart and Watkinson 2007). John and Hasler (1956) found that hatching in southern Canadian lakes most likely occurs

shortly after ice-off in the spring (as cited in Scott and Crossman 1998). Larval cisco begin to consume small zooplankton and algae shortly after hatching (Scott and Crossman 1998). As body size increases (and consequently gape size), they continue to consume pelagic zooplankton prey, but may also feed on benthic macroinvertebrates and insects at the surface (Hanke 1996; Johnson and Kitchell 1996; Stewart and Watkinson 2007).

In Lake Winnipeg, both adult rainbow smelt and cisco, therefore, potentially occupy a similar trophic niche, with overlapping diets according to published literature (Scott and Crossman 1998; Stewart and Watkinson 2007). However, in some lakes where smelt have been established for a longer period of time (i.e. > 50 years), dietary overlap is low (Johnson *et al.* 2004). In these instances, both species have illustrated dietary shifts over time, indicating either niche segregation or changes in the zooplankton community (Johnson *et al.* 2004). Smelt do not often reach sizes >150 mm in Lake Winnipeg (Sheppard *et al.* 2012) and do not feed at trophic levels higher than other forage fish (Gewurtz *et al.* 2006; Hobson *et al.* 2012), inconsistent with other studied lakes (Swanson *et al.* 2003). Both species most commonly occur as adults in the mid-water pelagic zone, leading to high potential for horizontal and vertical spatial overlap. Both species also have similar predators, with both serving as important prey for large piscivores, such as walleye (*Sander vitreus*), sauger (*Sander canadensis*) and northern pike (*Esox lucius*) (Stewart and Watkinson 2007; Sheppard 2010). One main difference between the two species in Lake Winnipeg is that the rainbow smelt occupy predominantly the North Basin and cisco the South Basin possibly due to inter-basin thermal differences; however, there is an area of spatial overlap in the Narrows and the southern portion of the North

Basin (Lumb *et al.* 2012).

Among members of the Lake Winnipeg zooplankton prey community, the cladocerans (predominantly *Daphnia mendotae*, *D. retrocurva*, *D. longiremis*, *Bosmina longirostris*, *Eubosmina coregoni*) move in a conspicuous pattern and have a relatively slow escape response when compared to other zooplankters, especially copepods (Truger *et al.* 1994). In terms of mean body size, in rank order, the smallest prey type is *Bosmina* followed by *Eubosmina*, with copepods and *Daphnia* spp. representing the largest prey types available as well as the largest range of prey sizes because of the amalgamation of a number of species within this taxonomic grouping (Olynyk 2009). Cladocerans generally have both a parthenogenetic and sexual phase in their life cycle (Wetzel 2001). In spring, ephippial eggs hatch producing juvenile females, which after five or six instars (for Daphniidae) become parthenogenetically reproductive adult females (Allan 1976). Throughout the spring and summer, large populations of these individuals may be produced via parthenogenesis (Wetzel 2001). Then, in response to environmental cues, including decreasing photoperiod and temperature, broods of eggs develop into males that produce haploid sperm; adult females then switch reproductive modes from parthenogenesis to gamogenesis, producing ephippial or diapausing (resting) eggs that must be fertilized by sperm from mature males and then enclosed within ephippia (modified carapace) that overwinter in the sediments on the lake bottom (Allan 1976).

Copepods are more sleek-bodied and faster moving than cladocerans (Chang and Hanazato 2003). A typical copepod life cycle involves the hatching of free-swimming naupliar larvae, which after five or six moulting events become known as copepodids (Wetzel 2001). Subsequently, there are five copepodid instars before reaching the adult

form in a typical one-year life cycle (Wetzel 2001). However, individual copepod species within Cyclopoida and Calanoida may have life cycles shorter or longer than one year. Therefore, considering the number of copepod species in Lake Winnipeg, species-specific temporal differences in timing of entering diapause or dormancy and the asynchrony of their life cycles, all life stages (nauplii, copepodids, and adults) may be present at any point in time (Patalas and Salki 1992; Wetzel 2001).

Biotic data originating prior to rainbow smelt invasion in Lake Winnipeg are limited. The only comprehensive open water pre-invasion zooplankton study occurred in 1969. Patalas and Salki (1992) reported that the zooplankton community in 1969 in the North Basin comprised, in order of abundance, calanoid copepods, cyclopoid copepods, *Bosmina longirostris*, and *Daphnia* spp. *Eubosmina coregoni* was not included in their analysis as it did not invade until the late 1980s or early 1990, perhaps coincident with the invasion of rainbow smelt (Suchy *et al.* 2009). The zooplankton community shows strong seasonal patterns, with greatest densities in the summer months (Patalas and Salki 1992). Data from a period of early smelt invasion (1994) showed density increases in all zooplankton groups over 1969 (A. Salki, pers. comm.), most likely attributable to increased eutrophication of the lake (Stainton *et al.* 2003; Liu *et al.* 2007). When comparing 1994 to more recent (2008 and 2009) summer data, densities of copepods were lower in both 2008 and 2009 and *Daphnia* spp. densities were lower in 2009, but not significantly different in 2008 (Sheppard *et al.* 2012). Densities of both *Bosmina* and *Eubosmina* have increased since 1994 (Sheppard *et al.* 2012).

Knowledge of the planktivore fish community before the invasion of smelt is similarly limited. Kristofferson (1985) found that emerald shiner (*Notropis atherinoides*)

dominated the South Basin. Perch (*Perca flavescens*) and cisco (*Coregonus artedi*) were found to be most abundant in the Narrows (Kristofferson 1985). No known pre-invasion description of the North Basin forage fish community exists. The major piscivores present throughout the lake are walleye (*Sander vitreus*) and sauger (*Sander canadensis*), which, along with the benthivorous lake whitefish (*Coregonus clupeaformis*), support a profitable commercial fishery (Kristofferson 1978; Lysack 1986; Lysack 1995). There has been ongoing work monitoring the pelagic fish in Lake Winnipeg since 2002 (Lumb *et al.* 2012). With respect to forage fish biomass, the South Basin is presently dominated by emerald shiners and, to a lesser extent, cisco. In the Narrows, the situation is very similar, with rainbow smelt present in small numbers. In the North Basin, the fish community is comprised overwhelmingly of rainbow smelt, with cisco and emerald shiner at much lower densities (Lumb *et al.* 2012).

The current distribution of non-native smelt in the North Basin and native cisco in the South Basin afforded an opportunity to study diet in these two zooplanktivores presumably using similar dietary niches. Overall, this study aimed to address the knowledge gap in the understanding of the role of rainbow smelt in the food web of Lake Winnipeg, both as a predator on the zooplankton prey community as well as a species sharing a dietary niche with native zooplanktivores. In Chapter 2, parallel consideration of dietary preferences with changing seasonal prey abundance while both species were spatially separated is described. In Chapter 3, diet is studied when both species showed direct spatial overlap in the North Basin, as well as diel dietary differences in smelt.

CHAPTER 2. Seasonal dietary preference of two zooplanktivores in Lake Winnipeg, Manitoba: the North Basin rainbow smelt (*Osmerus mordax*) and the South Basin cisco (*Coregonus artedii*)

2.1 Introduction

An underlying assumption of foraging theory is that individual fish optimize net energy gain to increase overall fitness (Ricklefs and Miller 2000). For a given predator, this involves both energy gain (e.g. caloric content) and loss (e.g. search, handling) for a given prey item (Pulliam 1974). The diet-width model predicts that when prey is abundant, predators will select prey with the highest net energy gain, as overall prey encounter rates are high (MacArthur and Pianka 1966). When prey abundance is low, however, predators are predicted to exhibit a more generalist foraging strategy and consume any encountered prey (MacArthur and Pianka 1966). As reviewed by Werner and Gilliam (1984), many fish species behave as predicted. However, opposing hypotheses do exist where low prey abundance leads to increased interspecific competition and, thus, increased dietary specialization by predators (Schoener 1982). Other predator characteristics, such as body size, must also be taken into account when examining foraging strategies. Ontogenetic changes, such as increased gape size and swimming ability, allow a predator to enhance its ability to capture a wider range of types and sizes of prey (Werner and Gilliam 1984). Thus, larger fish are expected to show increased capture efficiency, allowing for increased foraging specialization of energetically profitable prey types (Wong and Ward 1972; Werner and Gilliam 1984). For example, there is a positive relationship between increasing zooplanktivore body size and the mean size of prey consumed along with an inverse relationship with diet breadth

(Unger and Lewis 1983). In other words, as a zooplanktivore increases in body size, diet generally becomes more specialized on large, energetically profitable prey items.

The non-indigenous zooplanktivore rainbow smelt (*Osmerus mordax*) was first reported in Lake Winnipeg in late 1990 (Campbell *et al.* 1991). Rainbow smelt have since become a predominant member of the forage fish community in Lake Winnipeg (Lumb *et al.* 2012). This population is spatially restricted to the deeper, cooler North Basin, and may be attributed to warmer water temperatures in the South Basin, which are outside the optimal range of this species (Franzin *et al.* 2005; Gewurtz *et al.* 2006). Adult smelt <150 mm total length are entirely zooplanktivorous, with individuals beyond this threshold becoming increasingly piscivorous (Scott and Crossman 1998). Foraging on zooplankton is normally considered to be visual and selective, with large taxa (and large individuals within taxa) preferred (Johnson *et al.* 2004). In Lake Winnipeg, smelt appear to prefer large cladocerans during the summer months (Sheppard *et al.* 2011). In many lakes, smelt invasion has coincided with decreased densities and mean sizes of preferred zooplankton prey (Johnson and Goettl 1999), and the restructuring of the zooplankton community toward one dominated by smaller taxa (Beisner *et al.* 2003; Amundsen *et al.* 2009).

Cisco (*Coregonus artedi*), another zooplanktivore, is native to Lake Winnipeg (Stewart and Watkinson 2007). Cisco are present in both basins, with a decreasing northerly trend in abundance; pelagic trawling indicates a much greater abundance in the South Basin (Lumb *et al.* 2012). Larval cisco begin consuming small zooplankton and algae shortly after hatching (Scott and Crossman 1998). As cisco increase in body size, their diet focuses more on large zooplankton and insect larvae (Scott and Crossman

1998). Arnason (1951) found that cisco diet in Lake Winnipeg was composed predominantly of pelagic zooplankton in the spring, and shifted towards a greater proportion of insect larvae in summer, chiefly midge (Chironomidae) and caddisfly (Trichoptera) larvae. Also, some evidence for piscivory in larger specimens of cisco was noted during winter months.

In Lake Winnipeg, according to pelagic trawl data, rainbow smelt and cisco populations are spatially segregated, with cisco occurring primarily in the South Basin and rainbow smelt in the North Basin (Lumb *et al.* 2012). Stable isotope analysis showed that cisco and smelt occupy similar trophic positions within each basin, but strong inter-basin isotopic differences among all forage fish suggests limited inter-basin movement (Gewurtz *et al.* 2006; Hobson *et al.* 2012). Also, both species have overlapping diets according to published literature (Scott and Crossman 1998; Stewart and Watkinson 2007), further evidence in support of the hypothesis that the two species occupy a similar trophic niche. Although pre-rainbow smelt invasion data do not exist, rainbow smelt may have spatially displaced the native cisco in the North Basin. Spatial displacement has occurred in other invaded lakes, where establishment of smelt has resulted in population decline in native zooplanktivores with overlapping dietary niches (Scott and Crossman 1998); smelt were considered the main cause of the extirpation of cisco in Sparkling Lake, Wisconsin (Hrabik *et al.* 1998). Alternatively, in some lakes where smelt have been established for a long period of time, dietary overlap with cisco is low (Johnson *et al.* 2004). In such cases, both species have illustrated dietary or spatial shifts, indicating possible niche segregation, changes in the zooplankton community, or simply differences in feeding morphology (Johnson *et al.* 2004). As little is known about the diet of either of

these zooplanktivores in Lake Winnipeg, a primary data gap is present in the understanding of the food web. If both species have similar prey preferences even when there occurs separation in the basins, spatial displacement may be a plausible interpretation. An alternative possibility is that the spatial separation occurs because of differences in environmental characteristics of the lake basins that are favourable for each species.

2.2 Objectives and statement of hypotheses

The overall goal of this study was to investigate the current effects of the non-indigenous rainbow smelt on the food web of Lake Winnipeg by considering its diet over the open-water seasons. Also, this study aimed to contrast the dietary preferences of two spatially separated populations of zooplanktivores in Lake Winnipeg: smelt in the North Basin and native cisco in the South Basin. This provided an opportunity to consider the diets of these two species when spatially separated and understand their dietary niches under distinctly different environmental conditions. Composition of the diet of each zooplanktivore was directly compared to proportions of available prey within each season in the given basin. I hypothesized that both species would show dietary preference for large cladocerans (i.e. *Daphnia* spp. and *Eubosmina*) during peak summer zooplankton density, owing to the combination of the conspicuousness and reduced escape ability of this prey type relative to other prey types (e.g. copepods). During periods of relatively low zooplankton density (i.e. spring and fall), I predicted a shift to a more generalist foraging strategy.

2.3 Methods

2.3.1 Field collection

Fish samples were collected from the M.V. *Namao* during three seasonal research cruises (spring, summer and fall) in 2010 and 2011. Fish were collected via trawling during daylight at approximately 65 pre-determined locations throughout Lake Winnipeg as part of Manitoba Conservation and Water Stewardship - Fisheries Branch forage fish monitoring program (for protocol see Appendix 2.6.1). Smelt collected for this study originated from the North Basin and cisco from the South Basin. Trawling occurred at one of three randomly assigned relative depths (shallow, middle and deep) at each station. The trawl was 10.8 m long, with decreasing mesh size towards the cod end (76.2 mm to 19.1 mm stretched mesh). The cod-end was a 1.22 mm PVC pipe (114.3 mm in diameter) with a screw-in plug (as per Lumb *et al.* 2012). Each trawl was carried out for 30 minutes at a towing speed of approximately 3.9 km/hr (Lumb *et al.* 2012). After 30 minutes, the trawl was brought on board and fish were sorted by species. After subsampling the catch for other purposes (Manitoba Conservation and Water Stewardship, Fisheries Branch: 30 fish per species), a random subsample of up to 30 individuals of rainbow smelt (70-130 mm total length) and cisco (100-200 mm total length) was collected for dietary analysis. This size of sub-sample was collected to ensure a minimum of ten full stomachs, as is standard with zooplanktivore diet studies (Parker Stetter *et al.* 2005, Darbyson *et al.* 2003) and has been found to be sufficient in describing variability in piscine diets (Vinson and Budy 2011). Fork and total length of each individual was recorded. The entire digestive tract of the fish was then immediately excised and placed in a 20 mL vial half-filled with 70% ethanol. This halted digestion in

the stomach and preserved the ingested organisms. The remaining gutted carcass was placed in a Whirl-Pak® and immediately frozen onboard (for protocol see Appendix 2.6.2).

All fish collected by Manitoba Conservation and Water Stewardship, Fisheries Branch, were placed in labeled bags and immediately frozen onboard. To supplement the data set collected for this project, additional fish were analyzed for gut contents after they had been thawed, and fork length and weight were measured after each cruise. The gut of each fish was then placed in a 20 mL scintillation vial half-filled with 70% ethanol. Although previously frozen stomachs are not ideal for gut content analysis, they have been used in other studies and are adequate to supplement the other collected stomachs (e.g. Pothoven *et al.* 2009). Stomachs collected in this manner were adequately preserved for the necessary level of identification.

To compare gut contents to available prey, it was critical to compare proportions of zooplankton prey species in smelt diets with those available in the foraging environment. Therefore, the zooplankton community was concurrently sampled at every trawl station where fish were collected. A 73- μ m mesh Wisconsin zooplankton net was hauled from one metre above the bottom to the surface to provide an integrated sample of the prey community of the entire water column at a given station. All zooplankton samples were preserved in 70% ethanol in separate 125 mL containers. A Sea-Bird® SBE 19plus collected environmental profiles throughout the water column, including turbidity and oxygen. Other station-specific data, such as Secchi depth and station depth, were also recorded at each station.

2.3.2 Laboratory processing

i. Zooplankton prey community

Six zooplankton prey groups were considered: calanoid copepods, cyclopoid copepods, nauplius larvae, *Daphnia* spp. (including *D. mendotae*, *D. retrocurva*, *D. longiremis*), *Eubosmina coregoni* (hereafter *Eubosmina*) and *Bosmina longirostris* (hereafter *Bosmina*), as consistent with previous zooplanktivore diet studies (Hrabik *et al.* 1998; Beisner *et al.* 2003). Other groups or consumed items that were encountered in relatively low numbers (e.g. ostracods, *Leptodora kindti*) were combined into an “other” category. For net samples, intact individuals were counted in an etched grid dish for the six prey groups in a 1 mL sub-sample from each station. After three replications, the results were averaged to estimate the zooplankton community composition at a given station. Proportions of zooplankton prey groups were arcsine-root transformed to allow statistical comparison among seasons using *t*-tests. To estimate density of each prey group per station, the number of individuals in the sub-sample was divided by the volume of the sub-sample (1 mL). To calculate the total number of individuals in the sample, this value was multiplied by the total volume of the collected sample (125 mL). Finally, to provide the overall density at a given station, the total number of collected individuals was divided by the volume of water filtered, which is equivalent to the maximum depth of the zooplankton net haul multiplied by the area of the Wisconsin net opening (0.049 m²). Thus, an estimation of the density (individuals/m³) of each prey group at each station was calculated.

To estimate species richness and evenness of the prey groups among stations, Simpson’s index of diversity (*I-D*) was used. In this model, $I-D = 1 - \left(\sum \left(\frac{n_i}{N}\right)^2\right)$,

whereby the number of individuals of a prey group (n_i) is related to the total number of individuals present in a given sample (N ; Simpson 1949). Values of this index range between 0 and 1, with numbers closer to 0 indicating lower diversity (lower species richness and evenness) and numbers closer to 1 higher diversity (higher species richness and evenness). Lengths of the first 25 individuals encountered in a given sample from each of the six prey groups during the summer were measured. A sample of 25 individuals was previously found to be representative of the size range of a given prey group in Lake Winnipeg (Olynyk 2009). To further explore the length-frequency distribution of preferred prey species, up to 25 specimens *Eubosmina* and *Daphnia* spp. from each of the stations sampled in spring and fall were also measured. For copepods, measurements were a straight line length from the most anterior point on the cephalosome medial to the eyespot to the end of the abdomen at which point the rami branch. For *Daphnia* spp., measurements were taken in a straight line from the anterior margin of the eyespot to the base of the tail spine. For *Eubosmina* and *Bosmina*, measurements were from a point on the head shield medial to the eyespot in a straight line to the base of the mucrone. Lengths were measured via digitizing pad associated with a dissecting microscope equipped with a *camera lucida*. One-way ANOVAs with post-hoc Bonferroni tests were used to determine if any length differences among stations were statistically significant.

ii. Zooplanktivore stomach contents

The first ten non-empty stomachs encountered were processed, as these can be considered a random sub-sample based on the nature of the field collection. Using

forceps, each stomach was isolated from the surrounding viscera and the esophagus was severed at its connection to the stomach. Any prematurely ruptured stomachs were not considered. The stomach itself was then medially slit and using 70% ethanol, all gut contents were flushed into a gridded plastic dish. The stomachs were then visually inspected using a dissecting microscope to ensure all contents had been removed and any remaining material in the gut were scraped out using forceps. The total number of individuals in each of the prey groups was then counted using a dissecting microscope. Intact individuals were counted as well as partial organisms only where a head or eyespot was present, as per Stewart *et al.* (2009). Similar to zooplankton tows, proportions of prey were arcsine-root transformed to allow statistical comparison using *t*-tests. Smelt size selection of prey was also explored, with up to 25 intact individuals from preferred prey groups within the gut contents being measured per station. Identical equipment and processes were used as described previously in the determination of mean prey lengths in the zooplankton tows. To investigate size selection, *t*-tests were used to compare the lengths of consumed prey with those found in the environment.

Ivlev's electivity index (E') was calculated to describe dietary preference of each fish for each of the prey groups using the following equation: $E_i = (r_i - p_i) / (r_i + p_i)$ as defined by Ivlev (1961) and described in Lechowicz (1982). This formula computes the electivity (E) index for a given prey item (i) incorporating its proportion in the gut (r) and the environment (p). This index ranges from -1 (dietary avoidance or inaccessibility) to +1 (dietary selection), with a value of 0 indicating random selection (Vanderploeg and Scavia 1979; Lechowicz 1982). Electivities of individual fish were then averaged across each sampling station. A common issue with this index is an absence of an appropriate

statistical test to differentiate among index values (O'Brien and Vinyard 1974; Botts and Cowell 1992). To provide statistical comparisons, the linear selection index (L), was also used (Strauss 1979; Gras and Saint-Jean 1982). It is simply calculated as: $L_i = r_i - p_i$, where the proportion of a given food item (i) is considered in the gut (r) and the environment (p ; Strauss 1979). According to Strauss (1979), this index has an approximately normal distribution, allowing for statistical comparison of values against a null hypothesis of random feeding via t -statistics (Strauss 1979; Hyslop 1980). However, a drawback to the linear index is that statistical comparison is limited to within a given station, not allowing for considerations between stations with differing prey proportions (Lechowicz 1982). Regressions that included mean Ivlev's electivity values and station-specific values for smelt fork length, zooplankton density and turbidity were completed for each sampled season.

2.4 Results

Among stations where fish were sampled for this study when pooled across years, North Basin stations were significantly deeper ($t_{66} = 6.52$, $P < 0.05$), less turbid ($t_{53} = 6.74$, $P < 0.05$) and cooler ($t_{55} = -5.78$, $P < 0.05$) than the South Basin stations (Table 2.1). Station-specific information is given for both the North Basin (Table A1) and South Basin (Table A2). All smelt collected for this study originated from stations in the North Basin and were equally common at all trawl depths. Seasonally, the mean collected fork length was largest in the fall (106.20 ± 0.57 mm), followed by summer (95.26 ± 0.78 mm) and spring (92.60 ± 0.80 mm). All cisco were collected in the South Basin and were most commonly found in shallow trawls. Mean fork length of cisco was largest in the

spring (113.33 ± 3.15 mm) followed by the summer (111.59 ± 0.57 mm) and fall (103.04 ± 1.78 mm).

2.4.1 Zooplankton prey community: mean seasonal densities and proportions

i. North Basin

Overall, zooplankton densities were highest in either summer or fall (Table 2.2). In 2010, a one-way ANOVA revealed significant variation among mean zooplankton density ($F_2 = 8.08$, $P < 0.05$). Bonferroni post-hoc testing revealed significantly higher mean density during the summer than both the spring and fall, with fall mean density not significantly different than spring. In 2011, mean zooplankton density also showed significant variation among seasons ($F_2 = 11.27$, $P < 0.05$), with fall mean density not significantly different than summer, and spring density significantly lower than both fall and summer.

In both 2010 and 2011, the highest proportions of calanoids and lowest proportions of *Daphnia* spp. and *Eubosmina* were observed in spring, whereas *Daphnia* spp. proportions were highest during summer and *Eubosmina* during summer and fall (Table 2.2). In 2010, mean proportions of copepods (i.e. calanoids, cyclopoids, nauplius larvae) were significantly greater than cladocerans (i.e. *Daphnia* spp., *Eubosmina*, *Bosmina*) in spring ($t_{12} = 8.91$, $P < 0.05$) and fall ($t_{16} = 3.87$, $P < 0.05$). Mean cladoceran proportion peaked during summer, but it did not differ from copepods ($t_3 = 2.69$, $P > 0.05$). In 2011, proportions of copepods were significantly higher in spring ($t_{10} = 5.98$, $P < 0.05$) and summer ($t_{11} = 5.20$, $P < 0.05$). Mean proportion of cladocerans was highest during fall and were not statistically different from copepods ($t_{10} = 3.87$, $P > 0.05$).

Station-specific values are given in the appendix (Table A3).

Simpson's index of diversity ($I-D$) revealed a trend of relatively low diversity in spring, peaking in summer and decreasing to an intermediate value in fall (Table 2.2). Seasonal diversity differences in 2010 were not significant ($F_2 = 3.24$, $P > 0.05$), but were in 2011 ($F_2 = 7.58$, $P < 0.05$). Post-hoc Bonferroni testing indicated mean spring diversity was significantly lower than summer and fall, but summer was not significantly different from fall.

ii. South Basin

Mean zooplankton densities were variable in the South Basin, with the highest mean density during summer in 2010 and spring in 2011 (Table 2.2). In 2010, mean zooplankton density of spring and summer did not significantly differ ($t_8 = -1.18$, $P > 0.05$). Fall comparisons were not made as data were available only in 2011. In 2011, mean zooplankton densities did not differ significantly among seasons ($F_2 = 1.91$, $P > 0.05$). Mean zooplankton density was highest in spring, but not significantly different than either summer or fall, with summer and fall also not differing significantly.

Proportionately, copepods dominated the zooplankton community in all seasons (Table 2.2). In 2010, mean proportions of copepods were significantly higher than cladocerans in spring ($t_4 = 28.60$, $P < 0.05$) and summer ($t_{12} = 14.12$, $P < 0.05$), as well as spring ($t_1 = 44.65$, $P < 0.05$), summer ($t_{16} = 10.21$, $P < 0.05$) and fall ($t_{18} = 6.88$, $P < 0.05$) in 2011. Calanoids showed a relative decrease and *Daphnia* spp. an increase from spring to summer 2010. In 2011, calanoid proportions were highest in summer with a minimum in spring and *Daphnia* spp. showed a consistent seasonal increase, highest in fall. Station-

specific values are given in the appendix (Table A4). Overall, mean diversity ($I-D$) values did not differ seasonally in 2010 ($F_1 = 1.95, P > 0.05$) or 2011 ($F_2 = 2.11, P > 0.05$).

2.4.2 Zooplankton prey community: mean body length of prey groups

i. North Basin

Zooplankton from stations where rainbow smelt were caught in the summer were used to provide average lengths of all prey groups. In both years, the ranking of prey group sizes was consistent. Calanoids ($962.11 \pm 15.60 \mu\text{m}$) had the largest mean body length, followed by *Daphnia* spp. ($733.13 \pm 13.17 \mu\text{m}$), cyclopoids ($599.06 \pm 9.50 \mu\text{m}$), *Eubosmina* ($447.82 \pm 5.48 \mu\text{m}$), *Bosmina* ($304.84 \pm 3.63 \mu\text{m}$) and nauplius larvae ($160.12 \pm 3.46 \mu\text{m}$). There were no significant differences in 2010 mean summer lengths among stations for *Daphnia* spp. ($F_2 = 1.07, P > 0.05$), *Eubosmina* ($F_2 = 1.03, P > 0.05$), cyclopoids ($F_2 = 0.55, P > 0.05$) and nauplius larvae ($F_2 = 0.74, P > 0.05$). However, mean length differed significantly among stations for calanoids ($F_2 = 7.63, P > 0.05$) and *Bosmina* ($F_2 = 8.82, P < 0.05$), with larger mean size at northerly relative to southerly stations (Fig. 2.1). In 2011, mean lengths did not differ among stations for *Eubosmina* ($F_7 = 0.77, P > 0.5$) or calanoids ($F_7 = 1.60, P > 0.05$), but significant variation was observed in *Daphnia* spp. ($F_7 = 4.94, P < 0.05$), *Bosmina* ($F_7 = 4.64, P < 0.05$), cyclopoids ($F_7 = 3.37, P < 0.05$) and nauplius larvae ($F_7 = 3.83, P < 0.05$). Similar to 2010, larger mean lengths were found in the more northern stations for cyclopoids (Fig. 2.2a), nauplius larvae (Fig. 2.2b), *Daphnia* spp. (Fig. 2.2c) and *Bosmina* (Fig. 2.2d).

ii. South Basin

At stations where cisco were collected in the summer, zooplankton samples were used to provide mean lengths of South Basin prey groups. Prey group mean body size rankings were again consistent inter-annually. The largest prey group on average were calanoids ($942.47 \pm 10.85 \mu\text{m}$), followed by *Daphnia* spp. ($872.50 \pm 16.99 \mu\text{m}$), cyclopoids ($624.71 \pm 9.06 \mu\text{m}$) and nauplii ($153.76 \pm 2.09 \mu\text{m}$). *Eubosmina* and *Bosmina* were present in some South Basin samples, but were not considered for length measurements due to low densities and, thus, proportion in the environment (Table 2.2). In 2010, significant differences in mean length among stations were observed in *Daphnia* spp. ($F_6 = 6.26, P < 0.05$), cyclopoids ($F_6 = 6.81, P < 0.05$) and nauplii ($F_6 = 3.53, P < 0.05$), but not in calanoids ($F_6 = 0.70, P > 0.05$). Mean sizes of cyclopoids (Fig. 2.3a) were larger in more southern stations and nauplius larvae were larger among more northern stations (Fig. 2.3b). There were no clear latitudinal trends observed among mean sizes of *Daphnia* spp. (Fig. 2.3c). In summer 2011, once again significant differences were observed among stations in mean sizes of *Daphnia* spp. ($F_8 = 9.21, P < 0.05$), cyclopoids ($F_8 = 4.37, P < 0.05$) and nauplius larvae ($F_8 = 3.01, P < 0.05$), but not among calanoids ($F_8 = 2.09, P > 0.05$). There were no clear latitudinal trends in mean size for these species (Fig. 2.4c).

2.4.3 Zooplanktivore stomach contents

2.4.3.1 North Basin rainbow smelt

i. Proportionate stomach contents

Mean proportions of copepods were significantly greater in smelt gut contents

than cladocerans during spring 2010 ($t_{138} = 19.93$, $P < 0.05$) and 2011 ($t_{117} = 7.47$, $P < 0.05$). In 2010, calanoids were the dominant prey group consumed, followed by cyclopoids. In 2011, cyclopoids were dominant followed by calanoids, in total making up over half the prey consumed in both years (Table 2.3a). Cladoceran prey groups and “other” prey made up relatively low proportions. During summer, more cladocerans were consumed, having a significantly greater mean proportion than that of copepods in both 2010 ($t_{58} = -18.67$, $P < 0.05$) and 2011 ($t_{155} = -9.79$, $P < 0.05$). In both years, smelt diet was primarily composed of *Daphnia* spp. (Table 2.3a). In 2010, the second most consumed prey group was *Eubosmina*, and in 2011 it was calanoids followed by *Eubosmina*. The remaining prey groups were consumed in lower proportions. In fall, cladocerans still dominated the smelt diet, with significantly greater proportions than copepods in both 2010 ($t_{178} = 19.93$, $P < 0.05$) and 2011 ($t_{138} = 19.93$, $P < 0.05$). In both years, however, *Eubosmina* was the proportionately dominant prey group (Table 2.3a). More copepods were consumed during fall 2010, with cyclopoids having the second highest proportion as compared to *Daphnia* spp. in 2011. Overall, mean proportions of consumed calanoids peaked during spring in 2010 and summer in 2011. *Daphnia* spp. had the highest proportion in summer in both years, and *Eubosmina* in fall. Also, in all considered years and seasons, no nauplius larvae were detected in smelt. Station-specific values are given in the appendix (Table A5).

ii. Electivity and Linear Indices

Mean seasonal electivity for copepod prey groups in spring 2010 were positive for calanoids and negative for cyclopoids. This switched in spring 2011, with a negative

value for calanoids and a positive value for cyclopoids (Fig. 2.5a). Among cladoceran prey groups, *Daphnia* spp. and *Bosmina* were negative in spring, whereas positive values were observed for *Eubosmina*, albeit weakly in 2010 (Fig. 2.5a). In summer, mean electivity for copepod prey groups was generally negative, with an exception of a weak positive value for calanoids in 2011 (Fig. 2.5b). Among cladoceran prey groups, mean electivity values were consistently positive for *Daphnia* spp. and *Eubosmina* and negative for *Bosmina* in both years (Fig. 2.5b). Mean fall electivities were similar to summer, with negative values for calanoids, cyclopoids and *Bosmina* and positive values for *Daphnia* spp. and *Eubosmina* (Fig. 2.5c). Linear index values showed consistent results with those of Ivlev's electivity index (Table A7). There were no consistent significant inter- or intra-annual correlations between electivities and smelt density, zooplankton density or average turbidity for any prey group (Appendix; Table A9).

iii. Prey size selection

For the two prey groups considered, the mean size of *Daphnia* spp. consumed was significantly larger than found in zooplankton tows in spring (2010: $t_{320} = -11.78$, $P < 0.05$; 2011: $t_{147} = -4.60$, $P < 0.05$), summer (2010: $t_{131} = -10.79$, $P < 0.05$; 2011: $t_{382} = -16.43$, $P < 0.05$) as well as fall (2010: $t_{414} = -12.21$, $P < 0.05$; 2011: $t_{210} = -10.99$, $P < 0.05$). For *Eubosmina*, the mean size of individuals in the gut contents was significantly larger than the environment during spring (2010: $t_{317} = -12.97$, $P < 0.05$; 2011: $t_{333} = 1.84$, $P < 0.05$), summer (2010: $t_{142} = -8.51$, $P < 0.05$; 2011: $t_{396} = -11.83$, $P < 0.05$) and fall (2011: $t_{248} = -9.54$, $P < 0.05$). There was no significant difference in mean consumed and environmental length for *Eubosmina* in fall 2010 ($t_{239} = -0.60$, $P > 0.05$).

2.4.3 South Basin cisco

i. Proportionate gut contents

Similar to rainbow smelt in the North Basin, cisco diets were proportionately dominated by copepods during spring, with mean copepod proportions significantly greater than cladoceran proportions in 2010 ($t_{78} = 22.43$, $P < 0.05$) and 2011 ($t_{38} = 16.17$, $P < 0.05$). Also similar to smelt, spring 2010 calanoids had the highest mean proportion followed by cyclopoids, and in 2011 cyclopoids had the highest mean proportion followed by calanoids (Table 2.3b). In summer, cisco diet shifted to be dominated by cladocerans, in both 2010 ($t_{133} = -6.09$, $P < 0.05$) and 2011 ($t_{70} = -7.08$, $P < 0.05$). *Daphnia* spp. were proportionately dominant in both years (Table 2.3b). In fall 2011, cladocerans had significantly higher proportions in the gut contents when compared to copepods ($t_{196} = -9.34$, $P < 0.05$), with *Daphnia* spp. being the dominant prey group (Table 2.3b). Overall, mean proportion of consumed calanoids decreased from spring to fall, whereas it increased for *Daphnia* spp. (Table 2.3b). As previously noted for rainbow smelt gut contents, no nauplius larvae were observed in guts in any season or year in cisco.

ii. Electivity and Linear Indices

Mean spring electivity values for calanoids and cyclopoids showed weak positive values in 2010 and negative values in 2011 (Fig. 2.6a). In summer, mean electivity values for *Daphnia* were positive in both years, and mean electivity for cyclopoids was weakly positive during summer 2010 with the remainder of the prey groups negative (Fig. 2.6b). No data were collected during fall 2010, but fall 2011 showed positive electivity for

Daphnia spp. and negative values for all other prey groups (Fig. 2.6c). Linear index values showed consistent results with those of Ivlev's electivity index (Table A8). No consistent significant inter- or intra-annual trends were observed between electivities and cisco density, zooplankton density or average turbidity (Appendix; Table A10).

2.5 Discussion

Evidence from this study in Lake Winnipeg suggests that rainbow smelt and cisco occupy similar dietary niches when spatially separated. Both non-indigenous smelt in the North Basin and the native cisco in the South Basin of Lake Winnipeg showed seasonally shifting dietary preferences. For both species, spring diet was dominated proportionately by copepods and shifted towards a cladoceran-dominated diet in summer and fall. This shift in consumed prey proportions was reflected in dietary preferences, where during times of relatively low zooplankton density (i.e. spring), fast-moving copepods had positive electivity values. As overall zooplankton density increased in summer and fall, a shift towards dietary preference for large, relatively slow-moving cladocerans (i.e. *Daphnia* spp. and *Eubosmina*) was observed. Dietary selection of cladocerans by both species seems consistent with selecting prey with the highest net energy gain. These findings were consistent for both species in both basins, even with differing environmental characteristics of the basins.

The dietary selection of both zooplanktivores varied seasonally and seemed to be based upon the energetic quality of prey available. During times of high and intermediate zooplankton density, smelt and cisco selected large-bodied cladocerans and selected larger cladoceran individuals within the environment. This finding is consistent with

other similar zooplanktivore dietary studies (e.g. Urban and Brandt 1993; Hrabik *et al.* 1998; Beisner *et al.* 2003; Johnson *et al.* 2004; Sheppard *et al.* 2012). Prey preferences are assessed in terms of energy gain and loss, with highest quality prey being that which maximized net energy gain to the predator (Pulliam 1974). Larger prey is generally associated with greater net energy gain as caloric values are higher and less energy is expended searching for fewer prey items (Bence and Murdoch 1986; Ricklefs and Miller 2000). In this study, *Daphnia* spp. and calanoid copepods were the largest prey groups available in both basins. This selection of larger prey is consistent with previous findings in summer diet of rainbow smelt in Lake Winnipeg (Sheppard *et al.* 2011) as well as other invaded lakes, where smelt (Johnson *et al.* 2004) as well as other zooplanktivorous fish (Amundsen *et al.* 2009) have shown dietary preference for larger individuals within zooplankton taxa. Caloric content of these prey groups also varies, with copepods providing a higher energy density than that of cladocerans (Cummins and Wuycheck 1971). However, large-bodied cladocerans have a slow swimming speed and non-streamlined body shape, making them relatively conspicuous in the environment and easier to catch (Chang and Hanazato 2003). This typical cladoceran escape response is contrasted with copepods, which have a more rapid escape response coupled with a sleeker body shape (Hambright and Hall 1992). Although large cladocerans provided less energetically valuable input than copepods to Lake Winnipeg zooplanktivores, they resulted in a presumably greater net energetic benefit due to decreased foraging costs. This interpretation is consistent with Johnson *et al.* (2004), where dietary selection of cladocerans was based on slow escape responses. Alternatively, this dietary preference may be due to differential prey escape responses. In a turbid system such as Lake

Winnipeg, copepods may simply have increased avoidance of zooplanktivore predation through their more rapid escape response, being able to move beyond zooplanktivore detection more rapidly (Schulze 2011). However, in both scenarios, large-bodied cladocerans represent the highest energetic quality zooplankton prey available in Lake Winnipeg, likely resulting in the positive electivities for these prey groups during summer and fall (Gliwicz *et al.* 2004).

During low zooplankton density (i.e. spring), however, both rainbow smelt in the North Basin and cisco in the South Basin showed positive electivity for lower energetic quality copepod prey groups. This switch from copepods in the spring to cladocerans in the summer and fall coincides with the annual life cycle of cladocerans, with large populations produced asexually when food is abundant during summer and before the sexual phase and the deposition of ephippial eggs occurs later in fall (Allan 1976; Patalas and Salki 1992). This is consistent with other zooplanktivore populations, such as in Lake Erie, where spring rainbow smelt diets were dominated proportionately by copepods and shifted towards a greater representation of cladocerans in summer and fall (Parker Stetter *et al.* 2005). Pelagic cisco also have shown similar dietary trends in other lakes (Engel 1976), with electivity indices showing a similar seasonal shift from copepods to large-bodied cladocerans (Viljanen 1983).

Dietary preferences based on energetic prey quality also explain the seasonally consistent dietary avoidance of the smallest prey groups, *Bosmina* and nauplius larvae for both zooplanktivores, as these presented the lowest caloric intake. Strong negative electivities for *Bosmina* are consistent with other smelt (Hrabik *et al.* Johnson *et al.* 2004) and cisco (Viljanen 1983; Johnson *et al.* 2004) populations. The absence of nauplius

larvae in gut contents of both fish in this study is also consistent with other zooplanktivore diet studies (Johnson *et al.* 2004). However, this finding is most likely exaggerated in that partial digestion of this particular prey group may make it rapidly unidentifiable when compared to other prey groups, causing a slight underestimate in gut content analyses (Gu *et al.* 1996). As nauplius larvae are thought to represent the lowest energetically valuable prey, this is not a major concern.

Variation in dietary preferences among sampled stations was observed within seasons and is attributed to the large amount of horizontal patchiness of zooplankton in Lake Winnipeg (Patalas and Salki 1992), limiting selectivity in some areas and contributing to increasing variation in zooplanktivore dietary preferences (Stewart *et al.* 2010). Among North Basin smelt, there was also inter-annual variation in dietary preferences. Mean spring electivity index values for copepods were only positive for calanoids in 2010 and only cyclopoids in 2011. This seems to simply reflect the alternating abundance of these two prey groups, with environmental abundances matching smelt dietary preferences. Mean spring electivity index values for *Eubosmina* were weakly positive in all three seasons. As smelt invasion seems to have coincided with *Eubosmina* appearance in Lake Winnipeg, and it has been previously postulated that smelt may have been a vector for *Eubosmina* spread in Lake Winnipeg, this finding is interesting (Suchy *et al.* 2009). This addition of a novel prey group may have supported the initial spread of smelt in the North Basin of Lake Winnipeg. In the South Basin cisco diets, there were negative mean electivity values for both *Eubosmina* and *Bosmina* across all seasons and years. This is attributed to the low abundance of both these cladocerans in the South Basin (Patalas and Salki 1992; Kamada 2012). Also, there is a higher

proportion of “other” prey (predominantly *Diaphanosoma* sp.) relative to the North Basin, which may be related to the reduced abundance of other cladocerans in the South Basin. Among this “other” prey, it is noted that during summer and fall 2011, several spiny water flea (*Bythotrephes longimanus*) individuals were identified in the guts of three cisco in the summer and five in the fall, from stations near the mouth of the Winnipeg River, in the south-west portion of the South Basin, providing some of the first evidence of this invasive zooplankter in Lake Winnipeg. In other lakes where this zooplankter has invaded, both smelt (Pothoven *et al.* 2009) and cisco (Young *et al.* 2009) have shown dietary preference for *Bythotrephes*, with its presence in cisco diet being associated with increased total length (James 2010) and increased trophic position (Rennie *et al.* 2011).

As the two basins of Lake Winnipeg represent very different environments, both in terms of physical characteristics (more turbid, warmer, more shallow in the South Basin) as well as different prey fields for zooplanktivores (e.g. increased abundance of *Eubosmina* and *Bosmina* in the North Basin), direct inter-basin comparisons are difficult. However, due to the similarities in foraging strategy and dietary preferences shown here, I suggest that smelt and cisco occupy similar dietary niches when spatially separated. At the size ranges considered for this study, this is consistent with reports in the literature (Scott and Crossman 1998; Stewart and Watkinson 2007).

Smelt have previously been linked to changes in an invaded system’s zooplankton prey community, such as increased predominance of small-bodied zooplankton species (Reif and Tappa 1966) as well as decreased mean size of preferred prey (Johnson and Goettl 1999). Siegfried (1987) found that in the oligotrophic double-basin Lake George,

New York, the basin with increased smelt coincided with a higher proportion of smaller species. Conversely, larger zooplankton species were more abundant in the other basin where there were less smelt, as reviewed by Rooney and Paterson (2009). The impact of rainbow smelt on the zooplankton community of Lake Winnipeg is not as clear.

Zooplankton community data prior to smelt invasion exists from 1969 (Patalas and Salki 1992). Compared to current zooplankton densities, increases in all prey groups has been observed, but any impact of smelt foraging is most likely masked by the large degree of cultural eutrophication that occurred since 1969 (Stainton *et al.* 2007; Paige 2011). Such an increase in nutrient levels would be expected to be correlated with an increase in zooplankton densities. Long-term changes in zooplankton community structure in Lake Winnipeg were recently summarized by Kamada (2012), and many of the changes observed can be explained by the increased nutrient levels in the lake. Increased food availability for zooplankton has been found to have a greater impact than changes in intensity of zooplanktivore predation on zooplankton abundance (Vanni 1987).

Alternatively, Vanni (1987) found that increased fish predation was linked with decrease in body size and earlier reproduction of cladocerans. Some zooplankton data from early smelt invasion in 1994 also exists (A. Salki, pers. comm.). As described by Sheppard *et al.* (2012), *Bosmina* and *Eubosmina* densities are currently elevated relative to 1994, but this is more likely due to the establishment of *Eubosmina* than the predation by smelt. This increase in *Eubosmina* density is consistent with the findings of Suchy *et al.* (2009), who found that according to sediment cores, *Eubosmina* establishment was occurring, with large increases in abundance during this period. Sizes of zooplankton in the North Basin currently show a general increasing northerly trend, with smelt density

showing the same pattern (Lumb *et al.* 2012). Thus, larger zooplankton individuals within prey groups seem to be present in areas of highest smelt density. Also, smelt maximum mean positive electivity values for cladocerans are weaker than in other invaded systems (Urban and Brandt 1993; Hrabik *et al.* 1998; Pothoven *et al.* 2009). Overall, this suggests that smelt are not currently having a measurable impact on the zooplankton community of Lake Winnipeg. Further work considering long-term temporal trends in mean sizes of zooplankton will be necessary to further support this claim.

Table 2.1. Summary of number of stations sampled, pooled (2010, 2011) seasonal mean (\pm SE) station depth, Secchi depth and surface temperature in the North Basin (NB) and South Basin (SB) of Lake Winnipeg during the open-water season on Lake Winnipeg, MB.

Season	Basin	# of stations	Mean Station Depth (m)	Mean Secchi Depth (m)	Mean Surface Water Temperature ($^{\circ}$ C)
Spring	NB	15	14.22 \pm 0.82	1.11 \pm 0.13	12.32 \pm 0.52
	SB	5	9.69 \pm 0.65	0.68 \pm 0.06	15.94 \pm 0.50
Summer	NB	11	12.69 \pm 1.29	1.00 \pm 0.13	18.11 \pm 0.50
	SB	16	8.32 \pm 0.50	0.53 \pm 0.03	22.75 \pm 0.11
Fall	NB	6	13.09 \pm 0.77	1.01 \pm 0.09	13.49 \pm 0.42
	SB	19	10.18 \pm 0.59	0.53 \pm 0.06	14.96 \pm 0.32

Table 2.2. Summary of mean proportions of (\pm SE) seven prey groups in the environment, mean zooplankton density (\pm SE) and mean Simpson's (*I-D*) index of diversity (\pm SE) in the North Basin and South Basin of Lake Winnipeg during three seasonal research cruises in 2010 and 2011.

Season	Copepods				Cladocerans			Other	1-D	Zooplankton density (individuals/L)
	Calanoids	Cyclopoids	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i>	<i>Bosmina</i>				
North Basin										
Spring 2010	0.36 \pm 0.04	0.33 \pm 0.05	0.11 \pm 0.02	0.05 \pm 0.01	0.05 \pm 0.01	0.10 \pm 0.03	< 0.01	0.70 \pm 0.03	47.51 \pm 10.70	
Summer 2010	0.19 \pm 0.03	0.21 \pm 0.03	0.15 \pm 0.01	0.18 \pm 0.03	0.17 \pm 0.03	0.02 \pm 0.01	0.09 \pm 0.05	0.82 \pm 0.01	124.99 \pm 24.70	
Fall 2010	0.16 \pm 0.03	0.29 \pm 0.04	0.24 \pm 0.06	0.02 \pm 0.01	0.17 \pm 0.06	0.07 \pm 0.02	0.03 \pm 0.01	0.71 \pm 0.02	52.66 \pm 8.78	
Spring 2011	0.15 \pm 0.03	0.13 \pm 0.03	0.60 \pm 0.12	< 0.01	0.02 \pm 0.01	< 0.01	< 0.01	0.49 \pm 0.09	40.81 \pm 9.87	
Summer 2011	0.11 \pm 0.02	0.24 \pm 0.02	0.13 \pm 0.01	0.16 \pm 0.02	0.13 \pm 0.04	0.21 \pm 0.06	< 0.01	0.78 \pm 0.03	155.11 \pm 19.82	
Fall 2011	0.09 \pm 0.02	0.24 \pm 0.03	0.05 \pm 0.02	0.10 \pm 0.04	0.38 \pm 0.09	0.09 \pm 0.01	0.05 \pm 0.03	0.70 \pm 0.05	154.39 \pm 30.69	
South Basin										
Spring 2010	0.57 \pm 0.03	0.18 \pm 0.06	0.21 \pm 0.04	0.02 \pm 6.4x10 ⁻³	< 0.01	< 0.01	< 0.01	0.57 \pm 0.02	51.80 \pm 7.92	
Summer 2010	0.54 \pm 0.03	0.14 \pm 0.03	0.17 \pm 0.02	0.12 \pm 0.02	0.00	< 0.01	0.03 \pm 0.01	0.63 \pm 0.02	72.66 \pm 15.83	
Fall 2010	---	---	---	---	---	---	---	---	---	
Spring 2011	0.18 \pm 0.12	0.31 \pm 0.04	0.49 \pm 0.07	0.02 \pm 9.1x10 ⁻³	0.00	0.01 \pm 7.2x10 ⁻³	< 0.01	0.62 \pm 0.06	161.90 \pm 85.73	
Summer 2011	0.36 \pm 0.03	0.17 \pm 0.03	0.28 \pm 0.04	0.11 \pm 0.04	< 0.01	0.01 \pm 5.0x10 ⁻³	0.07 \pm 0.02	0.71 \pm 0.02	122.69 \pm 20.13	
Fall 2011	0.25 \pm 0.04	0.26 \pm 0.02	0.23 \pm 0.05	0.17 \pm 0.03	0.04 \pm 0.04	0.03 \pm 0.01	0.02 \pm 0.01	0.71 \pm 0.02	91.55 \pm 6.89	

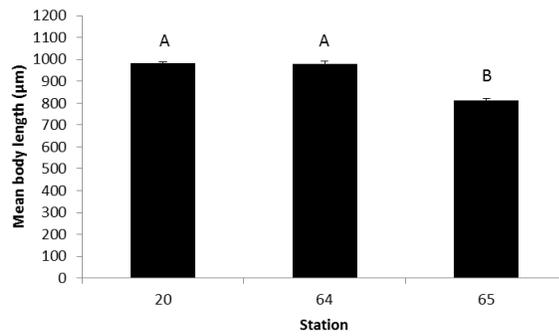
Table 2.3. Mean (\pm SE) proportions of seven zooplankton prey groups consumed by (a) rainbow smelt (*Osmerus mordax*) in the North Basin and (b) cisco (*Coregonus artedii*) in the South Basin of Lake Winnipeg in 2010 and 2011.

(a) *Rainbow smelt*

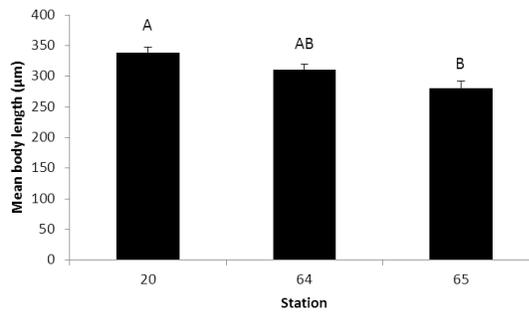
Season	# of stations	Copepods			Cladocerans			
		Calanoids	Cyclopoids	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i>	<i>Bosmina</i>	Other
Spring 2010	7	0.54 \pm 0.03	0.27 \pm 0.02	0.00	0.04 \pm 0.01	0.09 \pm 0.01	0.06 \pm 0.01	< 0.01
Summer 2010	3	0.04 \pm 0.01	0.05 \pm 0.02	0.00	0.56 \pm 0.05	0.30 \pm 0.05	< 0.01	0.04 \pm 0.02
Fall 2010	9	0.13 \pm 0.02	0.29 \pm 0.03	0.00	0.17 \pm 0.02	0.38 \pm 0.04	0.02 \pm 0.01	0.02 \pm 0.01
Spring 2011	6	0.15 \pm 0.03	0.52 \pm 0.04	0.00	0.02 \pm 0.01	0.12 \pm 0.02	0.11 \pm 0.02	0.08 \pm 0.03
Summer 2011	8	0.25 \pm 0.03	0.02 \pm 0.01	0.00	0.50 \pm 0.03	0.19 \pm 0.02	0.02 \pm 0.01	0.02 \pm 0.01
Fall 2011	6	0.03 \pm 0.01	0.09 \pm 0.02	0.00	0.31 \pm 0.04	0.56 \pm 0.05	0.01 \pm 0.01	< 0.01

(b) *Cisco*

Spring 2010	3	0.69 \pm 0.11	0.24 \pm 0.07	0.00	0.07 \pm 0.12	< 0.01	< 0.01	< 0.01
Summer 2010	7	0.19 \pm 0.08	0.10 \pm 0.04	0.00	0.63 \pm 0.12	< 0.01	< 0.01	0.08 \pm 0.08
Fall 2010	0	---	---	---	---	---	---	---
Spring 2011	2	0.39 \pm 0.07	0.54 \pm 0.07	0.00	0.05 \pm 0.04	< 0.01	0.01 \pm 0.01	0.01 \pm 0.01
Summer 2011	9	0.13 \pm 0.03	0.05 \pm 0.02	0.00	0.52 \pm 0.12	0.00	< 0.01	0.31 \pm 0.11
Fall 2011	10	0.07 \pm 0.01	0.24 \pm 0.03	0.00	0.67 \pm 0.03	< 0.01	< 0.01	0.01 \pm 0.01

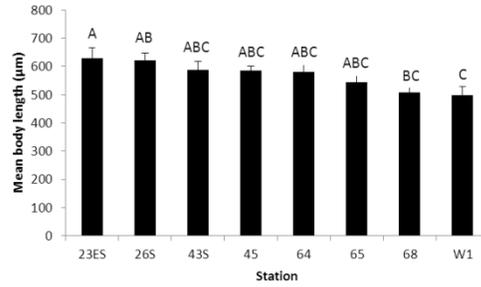


(a) Calanoids

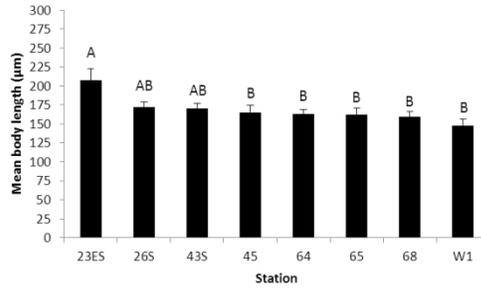


(b) *Bosmina*

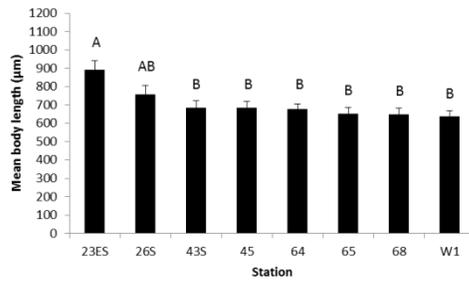
Figure 2.1. Mean body length \pm SE (n=25 per station) of (a) calanoids and (b) *Bosmina* in North Basin of Lake Winnipeg during summer 2010. Three stations arranged in north to south manner. Different letters (above bars) indicate significant differences in Bonferroni post-hoc tests. Note the y axis scale differs in the graphs.



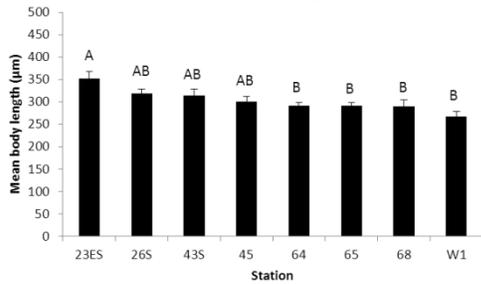
(a) Cyclopoids



(b) Nauplius Larvae

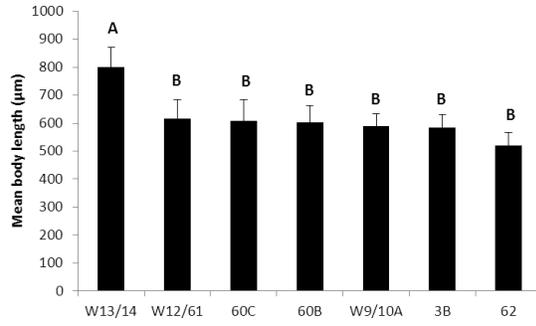


(c) *Daphnia* spp.

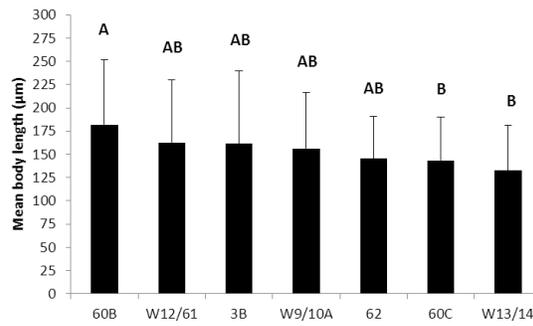


(d) *Bosmina*

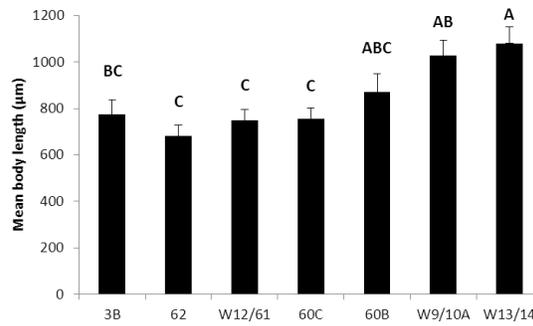
Figure 2.2. Mean body length \pm SE (n=25 per station) of (a) cyclopoids, (b) nauplius larvae, (c) *Daphnia* spp. and (d) *Bosmina* in North Basin of Lake Winnipeg during summer 2011. Eight stations arranged in north to south manner. Different letters (above bars) indicate significant differences in Bonferroni post-hoc tests. Note the y axis scale differs in the graphs.



(a) Cycloids

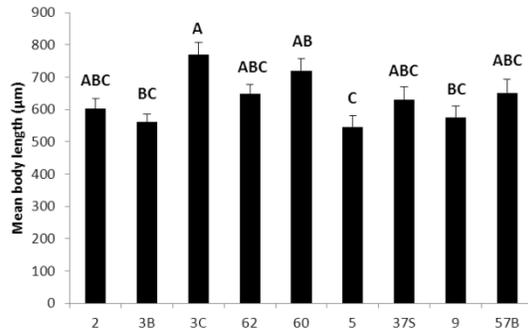


(b) Nauplius Larvae

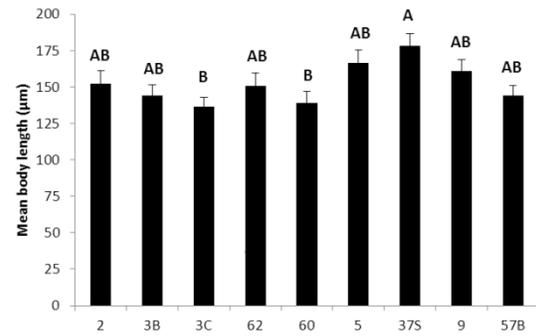


(c) Daphnia spp.

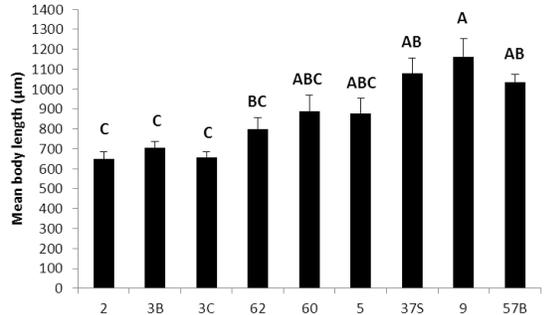
Figure 2.3. Mean body length \pm SE (n=25 per station) of (a) cycloids, (b) nauplius larvae and (c) *Daphnia* sp. collected from South Basin of Lake Winnipeg during summer 2010. Seven stations arranged in south to north manner. Different letters (above bars) indicate significant differences in Bonferroni post-hoc tests. Note the y axis scale differs in the graphs.



(a) Cycloids

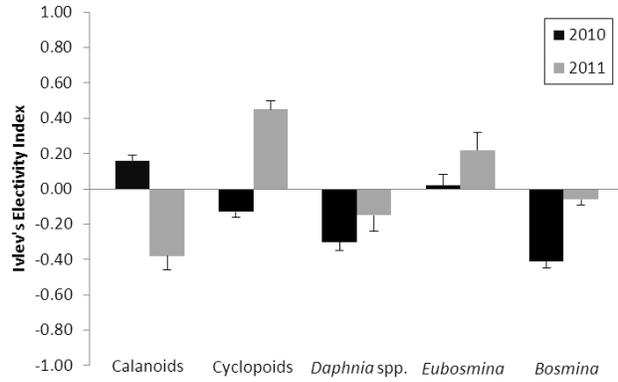


(b) Nauplius Larvae

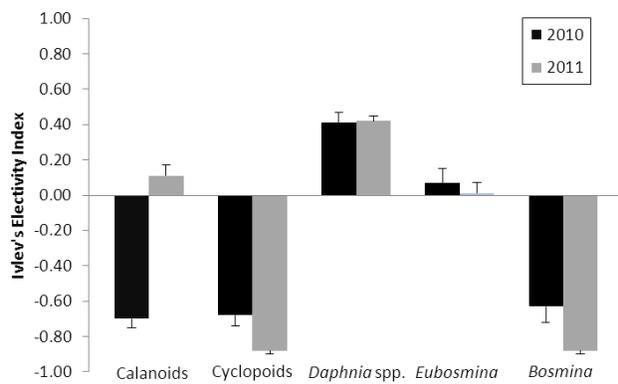


(c) *Daphnia* spp.

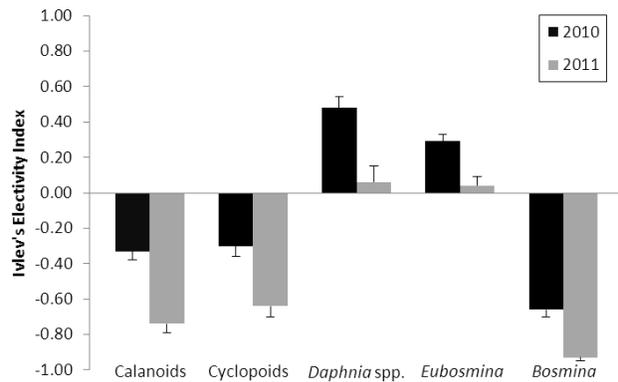
Figure 2.4. Mean body length \pm SE (n=25 per station) of (a) cycloids, (b) nauplius larvae and (c) *Daphnia* spp. collected from South Basin of Lake Winnipeg during summer 2011. Nine stations arranged in south to north manner. Different letters (above bars) indicate significant differences in Bonferroni post-hoc tests. Note the y axis scale differs in the graphs.



(a) Spring

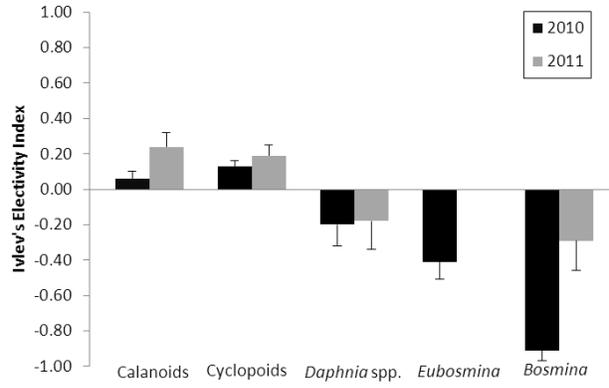


(b) Summer

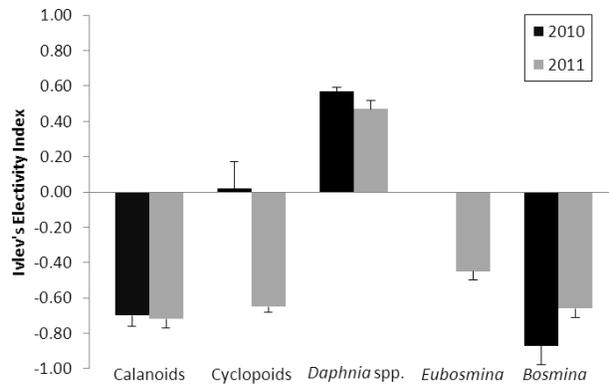


(c) Fall

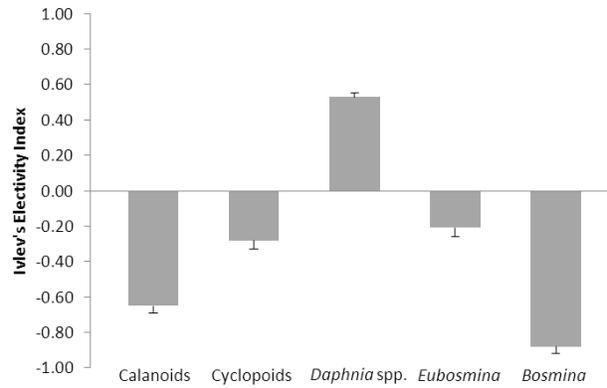
Figure 2.5. Ivlev's electivity index values (mean \pm SE) for five prey groups consumed by rainbow smelt (*Osmerus mordax*) in the North Basin of Lake Winnipeg during the 2010 and 2011 field season: (a) spring, (b) summer and (c) fall.



(a) Spring



(b) Summer



(c) Fall

Figure 2.6. Ivlev's electivity index values (mean \pm SE) for five prey groups consumed by cisco (*Coregonus artedii*) in the South Basin of Lake Winnipeg during the 2010 and 2011 field season: (a) spring, (b) summer and (c) fall. No fall 2010 data were collected.

2.6 Appendix

2.6.1 Pelagic fish trawling protocol

TRAWL PROTOCOL

Trawl Setup

The trawl net is attached to two bars (top and bottom) via cable, with stabilizers hung from the bottom corners. Always ensure that there are no tears in the net, the cod end is screwed on tightly, and the zipper is done up before launching the trawl.

Before you reach the Station

A trawl is performed on the approach to each station, unless the captain informs you it is not safe to do so (too shallow, too windy, etc). Trawls depths are chosen randomly at one of three depths: surface (where the top of the net just breaks the surface of the water), mid-water (half the total depth of the area, which the captain will tell you), or deep (as close to the bottom as is safe). Before you reach the start point of a trawl, randomly decide the depth (flip a coin: 2 heads is surface, 2 tails is deep, and one of each is midwater). Once the trawl depth is determined, use the depth spreadsheet attached to determine how much line will be let out. When counting meters of line let out, only count those that are below the surface of the water. The mid water trawl is conducted from the hook in the South Basin.

Setting the Trawl

Ensure the trawl is laid out on the deck, the cod end is screwed on tightly and the zipper is done up. The crew will lift the trawl up from the cables using the crane, and set it over the side of the ship. Ensure the cod end is dropped cleanly off the side of the ship, far enough back that it is not tangled in the rest of the net. If the crew ask you to step back, then do so. Use the handheld GPS to record start latitude and longitude when trawl started (when fully immersed in water). Save waypoint on GPS and record start lat/long in trawl log book. Make sure the GPS is displaying latitude and longitude in Degrees decimal Minutes (DD MM.MMM) and that the datum is NAD83. It is very important that start and end lat/longs are recorded accurately, because they are used to calculate distance swept by trawl. If there is an error with either the start or end lat/longs, it may not be possible to use data from the trawl.

Retrieving the Trawl

Each trawl is 30 minutes in length. The crew will raise the trawl onto the deck using the crane. Work your way along the trawl, and shake any fish caught in the mesh down into the cod end, removing any that are meshed in the net. Open the cod end over a fish tub that holds an appropriate amount of water for the given catch. Use the handheld GPS to record end latitude and longitude when trawl ended (when trawl begins to be pulled out of water). Save waypoint on GPS and record end lat/long in trawl log book (after haul processed). Make sure the GPS is displaying latitude and longitude in Degrees decimal Minutes (DD MM.MMM) and that the datum in NAD83.

Processing the Catch

Remove larger fish from the tub immediately. Identify them, measure them (fork length), and return them to the water. Sort out all of the species in the trawl and bag each species in an individual whirlpack. Label whirlpack bag with date, trawl number, station, species and bag "1 of 2" or "2 of 2", if more than one bag of a species from a trawl. If walleye/sauger are too small to be able to tell apart by spots on the dorsal fin, use the colour spot technique. Place walleye (fish with bright green spot on top of head) in one small labelled container and sauger (fish without bright green spot on top of head) in different small labelled container (label containers as you would whirlpack bags). Fix specimens of walleye/sauger using formalin. Often there will be large catches of emerald shiners or rainbow smelt. If this is the case, divide the catch by species, fill two 42 ounce whirlpacks with the catch and then place the remainder in the mesh bag. Allow most the water to run out and measure the weight to the nearest 10 grams, and then release these fish.

Use a permanent marker to label each individual species whirlpack, and combine them all in a larger trawl bag with a completed trawl label. Put the catch into the freezer as soon as possible, ensuring it is spread out enough to allow the sample to freeze. Fill out a log book entry for each catch (see attached format guide). When transporting frozen fish samples, use the three large white coolers on board.

At the end of the day, use photocopier onboard the NAMA0 to photocopy pages from trawl log book with information about trawls done during the day. Give these photocopies to the science coordinator, who keeps a binder of all daily activities. These photocopies serve as a back-up in case the trawl log book goes missing (for example, if it goes overboard).

TRAWL DEPTHS

All Line Lengths are in meters, Depths are shown in meters and feet
Use the following formulas to calculate the length of line to let out below the water.

For **Mid Water** Trawls: Length of Line = Total Depth - 3 meters

For **Deep Water** Trawls: Length of Line = (2 X Total Depth) - 5 meters

MID

<i>Depth (ft)</i>	<i>Depth (m)</i>	<i>Line (m)</i>
30	9.1	6
33	10.1	7
36	11.0	8
39	11.9	9
42	12.8	10
45	13.7	11
48	14.6	12
51	15.5	13
54	16.5	14
57	17.4	14
60	18.3	15

DEEP

<i>Depth (ft)</i>	<i>Depth (m)</i>	<i>Line (m)</i>
30	9.1	13
31.5	9.6	14
33	10.1	15
34.5	10.5	16
36	11.0	17
37.5	11.4	18
39	11.9	19
40.5	12.3	20
42	12.8	21
43.5	13.3	22
45	13.7	22
46.5	14.2	23
48	14.6	24
49.5	15.1	25
51	15.5	26
52.5	16.0	27
54	16.5	28
55.5	16.9	29
57	17.4	30
58.5	17.8	31
60	18.3	32

2.6.2. Fish gut contents sampling protocol

RAINBOW SMELT AND CISCO STOMACH SAMPLING PROTOCOL

Datasheets & Labeling

Use one datasheet per trawl/station. The datasheets are divided in half for recording up to 30 fish. Each fish is identified by a unique 4 number ID code (i.e. 1001, 1002, 1003).

THE ID NUMBER ON THE DATASHEET MUST MATCH THE ID NUMBER ON THE VIAL (STOMACH) AND THE WHIRLPAK (FISH).

Random Sample from the Trawl

Fish will be sorted into species on deck. If the smelt catch is sufficient (>60 individuals), randomly select ~30 fish. *The goal is to obtain a random subsample of 30 smelt ~70 mm - 130 mm (total length) and 30 cisco 100 mm - 200 mm (total length) from each trawl/station.*

In the Laboratory

Before removing stomachs, record the following for each fish on a datasheet: total length (in mm; snout to tip of tail) fork length (in mm; snout to fork of tail).

- Length measurements: lay the fish on the measuring board and smooth out the caudal fin to determine total and fork length. Be careful not to push too hard on the fish as stomach contents may be damaged or may come out the anus.

Once these measurements have been recorded, remove the stomach:

1. Use the dissecting scissors to cut from the anus to the gills.
2. Use forceps to grasp the area near the gills and remove the entire digestive tract.
3. Place the stomach immediately into the 20 ml vials (½ filled with 95% ethanol and pre-labeled)

MAKE SURE THAT THE FISH ID NUMBER ON THE DATASHEET CORRESPONDS WITH THE FISH ID NUMBER ON THE LABEL OF THE VIAL!

4. The fish should then be placed in a whirlpak with the corresponding pre-labeled fish ID number.

ZOOPLANKTON SAMPLING PROTOCOL

1. Determine maximum water depth at each station.
2. Make sure zooplankton bucket lever is closed.
3. Lower zooplankton net to 1 m off the bottom (max. depth – 1 m)
4. Slowly and at even speed raise zooplankton net to surface.
5. Release zooplankton sample into sample bottle on board.
6. Close zooplankton bucket lever and rinse net contents into plankton bucket.
7. Release residual zooplankton into sample bottle.
8. Add 95% ethanol (~5 mL) in volume remaining in the sample bottle to narcotize zooplankton.
9. After plankton settles (10 min.), decant volume to half full (take care not to lose any plankton) and refill with 95% ethanol. Cap bottle tightly and replace sample bottle in box.
10. **Label (on the cap) with station number, date, and depth of haul.**

Table A.1. Stations where rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) were collected onboard the M.V. *Nanmo* during three seasonal (spring, summer, fall) research cruises in 2010, including the date, station, arrival time, station depth, Secchi depth, surface water temperature, discrete zooplankton haul depth, basin, relative trawl depth and zooplankton density. South Basin stations precede North Basin stations and are separated by a dotted line.

Date	Station	Arrival Time	Station Depth (m)	Secchi Depth (m)	Surface Water Temperature (°C)	Discrete Zooplankton Haul Depth (m)	Basin	Relative Trawl Depth	Number of fish collected	Species	Zooplankton Density (individuals/L)
06-Jun-10	14	14:31	9.14	0.80	16.74	8.0	South	Shallow	30	Cisco	37.63
07-Jun-10	55	12:33	11.58	0.50	16.57	11.0	South	Shallow	30	Cisco	52.77
07-Jun-10	W14/165	14:07	10.06	0.70	14.59	9.0	South	Shallow	30	Cisco	65.00

10-Jun-10	W7	8:58	15.85	0.90	12.93	15.0	North	Mid	25	Rainbow Smelt	45.29
10-Jun-10	W6	12:35	16.46	1.60	10.59	15.0	North	Mid	30	Rainbow Smelt	28.51
10-Jun-10	W5	14:54	14.63	2.30	10.96	14.0	North	Deep	28	Rainbow Smelt	18.77
10-Jun-10	19	17:25	12.80	0.95	13.93	12.0	North	Shallow	29	Rainbow Smelt	62.15
12-Jun-10	345	11:30	15.24	1.60	10.51	14.0	North	Deep	30	Rainbow Smelt	41.36
13-Jun-10	28	13:59	8.53	1.40	14.35	8.0	North	Shallow	29	Rainbow Smelt	103.64
15-Jun-10	68	15:08	12.19	0.60	16.78	11.0	North	Shallow	30	Rainbow Smelt	32.82
26-Jul-10	60B	16:18	7.92	0.50	23.0	7.0	South	Shallow	30	Cisco	33.82
27-Jul-10	3B	10:30	5.79	0.75	22.7	5.0	South	Shallow	30	Cisco	125.50
27-Jul-10	60C	13:20	8.53	0.65	22.9	8.0	South	Mid	25	Cisco	133.01
29-Jul-10	W12/61	9:54	8.53	0.55	21.9	8.0	South	Shallow	30	Cisco	80.98
29-Jul-10	62	13:53	6.09	0.50	22.3	5.0	South	Mid	30	Cisco	48.17
06-Aug-10	W9/10A	8:38	11.28	0.60	22.8	10.0	South	Mid	27	Cisco	32.99
07-Aug-10	W13/14	10:19	9.14	0.50	22.8	7.0	South	Shallow	30	Cisco	54.17

10-Aug-10	20	15:35	11.89	1.00	21.98	11.0	North	Mid	27	Rainbow Smelt	91.36
17-Aug-10	65	18:25	8.23	0.30	17.63	7.0	North	Shallow	30	Rainbow Smelt	173.16
17-Aug-10	64	20:13	15.54	0.50	18.64	14.0	North	Shallow	31	Rainbow Smelt	110.45
30-Sep-10	W5	10:39	14.33	1.30	12.61	13.0	North	Mid	25	Rainbow Smelt	30.01
01-Oct-10	19	12:59	17.37	0.70	11.94	16.0	North	Shallow	31	Rainbow Smelt	20.25
01-Oct-10	20	14:56	9.14	0.70	12.02	8.0	North	Shallow	30	Rainbow Smelt	33.17
02-Oct-10	W1	7:38	16.76	0.55	12.5	16.0	North	Mid	30	Rainbow Smelt	45.49
02-Oct-10	W2	14:25	14.33	1.20	12.44	13.0	North	Mid	31	Rainbow Smelt	96.61
03-Oct-10	31	18:47	11.28	1.60	12.32	10.0	North	Deep	31	Rainbow Smelt	87.76
04-Oct-10	33	7:43	9.45	0.30	11.41	9.0	North	Deep	33	Rainbow Smelt	68.18
07-Oct-10	22	14:39	15.24	0.90	12.04	14.0	North	Deep	31	Rainbow Smelt	40.52
08-Oct-10	45	18:43	13.41	1.40	12.8	12.0	North	Deep	30	Rainbow Smelt	51.91

Table A.2. Stations where rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) were collected onboard the M.V. *Nanmo* during three seasonal (spring, summer, fall) research cruises in 2011, including the date, station, arrival time, station depth, Secchi depth, surface water temperature, discrete zooplankton haul depth, basin, relative trawl depth and zooplankton density. South Basin stations precede North Basin stations and are separated by a dotted line.

Date	Station	Arrival Time	Station Depth (m)	Secchi Depth (m)	Surface Water Temperature (°C)	Discrete Zooplankton Haul Depth (m)	Basin	Relative Trawl Depth	Number of fish collected	Species	Zooplankton Density (individuals/L)
09-Jun-12	36S	15:02	10.06	0.60	14.86	9.0	South	Mid	22	Cisco	247.63
12-Jun-12	44S	11:07	7.62	0.80	16.96	6.5	South	Mid	22	Cisco	76.17
16-Jun-11	W3/20S	13:55	17.98	0.60	11.23	17.0	North	Shallow	29	Rainbow Smelt	42.92
16-Jun-11	21	18:12	17.98	0.80	13.66	14.0	North	Mid	30	Rainbow Smelt	34.24
17-Jun-11	23B	12:25	17.37	0.80	10.23	17.0	North	Mid	18	Rainbow Smelt	31.83
17-Jun-11	33	16:20	9.14	0.30	10.86	8.0	North	Mid	30	Rainbow Smelt	25.75
17-Jun-11	31	19:05	11.89	1.20	11.97	11.0	North	Mid	19	Rainbow Smelt	105.09
19-Jun-11	28	7:45	9.75	1.50	15.46	9.0	North	Shallow	28	Rainbow Smelt	46.97
19-Jun-11	W2	9:34	16.15	1.20	10.66	15.0	North	Mid	30	Rainbow Smelt	13.91
19-Jun-11	23S	14:52	17.37	0.90	10.67	16.0	North	Shallow	30	Rainbow Smelt	26.28
01-Aug-11	9	14:15	9.75	0.70	23.33	10.0	South	Shallow	30	Cisco	55.36
02-Aug-11	57B	10:35	6.71	0.60	22.26	6.0	South	Shallow	20	Cisco	92.82
08-Aug-11	2	10:40	6.09	0.60	23.03	5.0	South	Shallow	19	Cisco	108.83
08-Aug-11	3B	12:14	6.40	0.40	23.23	5.0	South	Shallow	19	Cisco	115.83
08-Aug-11	3C	13:32	6.40	0.40	23.46	4.5	South	Shallow	20	Cisco	198.30
09-Aug-11	37S	12:46	11.89	0.30	22.26	10.5	South	Mid	15	Cisco	153.35
09-Aug-11	62	15:24	8.23	0.30	22.59	6.0	South	Shallow	27	Cisco	232.33
10-Aug-11	60	9:45	10.22	0.60	22.72	8.0	South	Shallow	23	Cisco	74.89
10-Aug-11	5	12:19	10.97	0.50	22.79	10.0	South	Shallow	30	Cisco	72.53
22-Jul-11	68	17:53	12.80	0.70	19.42	10.0	North	Shallow	30	Rainbow Smelt	244.30
23-Jul-11	65	9:25	5.49	0.60	19.09	5.0	North	Shallow	30	Rainbow Smelt	142.00
23-Jul-11	64	11:30	15.85	1.00	18.35	15.0	North	Mid	30	Rainbow Smelt	86.49
23-Jul-11	45	17:50	13.72	1.50	17.47	13.0	North	Deep	30	Rainbow Smelt	127.47
23-Jul-11	43S	20:10	6.09	1.20	17.33	7.0	North	Mid	30	Rainbow Smelt	154.66
24-Jul-11	23ES	15:00	17.07	1.60	16.44	16.0	North	Deep	30	Rainbow Smelt	224.84
24-Jul-11	W1	16:50	17.07	1.00	16.47	16.0	North	Deep	30	Rainbow Smelt	164.74
25-Jul-11	26S	8:55	15.82	1.60	16.37	15.0	North	Deep	30	Rainbow Smelt	96.34
15-Sep-11	49S	7:57	7.62	0.90	17.36	7.0	South	Shallow	30	Cisco	127.21
18-Sep-11	W14 / 16S	15:15	10.36	0.50	15.39	8.8	South	Shallow	30	Cisco	73.64
27-Sep-11	11	10:09	10.67	0.50	14.74	9.0	South	Shallow	30	Cisco	96.50
27-Sep-11	10S	11:43	12.50	0.50	14.84	10.0	South	Shallow	20	Cisco	85.88
27-Sep-11	W11 / 8	15:15	8.23	0.40	14.77	9.0	South	Shallow	19	Cisco	46.02
28-Sep-11	6	9:28	10.67	0.70	14.97	10.0	South	Mid	32	Cisco	85.71
28-Sep-11	37	11:09	12.50	0.60	15.01	10.0	South	Shallow	26	Cisco	102.72
28-Sep-11	W10	12:32	10.97	0.60	15.05	10.0	South	Shallow	30	Cisco	109.01
03-Oct-11	60	14:34	10.97	0.40	14.20	10.0	South	Shallow	31	Cisco	88.35
04-Oct-11	62	10:44	7.32	0.20	13.28	5.0	South	Mid	29	Cisco	100.50
21-Sep-11	22	8:48	14.63	1.20	15.41	14.0	North	Mid	30	Rainbow Smelt	166.39
21-Sep-11	34S	17:50	15.54	1.10	16.49	14.6	North	Mid	30	Rainbow Smelt	191.49
21-Sep-11	33	19:13	9.14	1.00	15.61	8.0	North	Deep	30	Rainbow Smelt	245.02
24-Sep-11	W2	8:02	14.33	1.10	14.87	12.0	North	Deep	30	Rainbow Smelt	186.52
24-Sep-11	41S	17:20	14.02	1.20	14.95	12.0	North	Deep	15	Rainbow Smelt	105.27
24-Sep-11	43S	19:06	7.32	0.90	14.88	6.0	North	Deep	30	Rainbow Smelt	31.63

Table A.3. Summary of mean proportions of seven zooplankton prey groups in the North Basin (\pm SE) and Simpson's index of diversity (*I-D*) for stations sampled during three seasonal research cruises in (a) 2010 and (b) 2011. Data arranged in a south to north manner.

(a) 2010

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other	<i>I-D</i>
Spring	W7	0.56 \pm 0.01	0.22 \pm 4.0x10 ⁻³	0.05 \pm 1.0x10 ⁻³	0.06 \pm 2.0x10 ⁻³	0.04 \pm 0.01	0.08 \pm 2.0x10 ⁻³	0.01 \pm 0.01	0.62
	W6	0.46 \pm 0.01	0.29 \pm 4.0x10 ⁻³	0.06 \pm 1.0x10 ⁻³	0.08 \pm 0.02	0.05 \pm 0.01	0.06 \pm 0.01	0.00	0.69
	W5	0.37 \pm 0.04	0.24 \pm 0.03	0.08 \pm 0.01	0.06 \pm 0.02	0.06 \pm 0.01	0.18 \pm 0.04	0.01 \pm 0.01	0.76
	19	0.33 \pm 5.0x10 ⁻³	0.45 \pm 0.01	0.14 \pm 1.0x10 ⁻³	0.03 \pm 1.0x10 ⁻³	0.01 \pm 5.0x10 ⁻³	0.04 \pm 0.01	0.00	0.67
	34S	0.29 \pm 2.0x10 ⁻³	0.54 \pm 2.0x10 ⁻³	0.10 \pm 1.0x10 ⁻³	0.01 \pm 2.0x10 ⁻³	0.03 \pm 4.0x10 ⁻³	0.01 \pm 0.01	0.00	0.61
	28	0.22 \pm 0.01	0.27 \pm 0.01	0.16 \pm 4.0x10 ⁻³	0.04 \pm 0.01	0.10 \pm 0.01	0.21 \pm 4.0x10 ⁻³	< 0.01	0.80
	68	0.32 \pm 0.02	0.27 \pm 0.02	0.19 \pm 0.01	0.09 \pm 0.01	0.03 \pm 0.01	0.10 \pm 0.01	0.01 \pm 0.01	0.77
Summer	20	0.13 \pm 0.01	0.15 \pm 0.02	0.15 \pm 0.02	0.12 \pm 3.0x10 ⁻³	0.21 \pm 0.04	0.04 \pm 0.01	0.19 \pm 0.01	0.84
	65	0.21 \pm 2.0x10 ⁻³	0.20 \pm 0.01	0.16 \pm 0.01	0.21 \pm 0.01	0.18 \pm 0.02	0.02 \pm 0.01	0.03 \pm 0.01	0.81
	64	0.23 \pm 4.0x10 ⁻³	0.27 \pm 3.0x10 ⁻³	0.14 \pm 0.02	0.21 \pm 0.02	0.11 \pm 0.01	0.00	0.04 \pm 0.01	0.80
Fall	W5	0.19 \pm 0.01	0.26 \pm 0.01	0.33 \pm 0.01	0.01 \pm 1.0x10 ⁻³	0.11 \pm 0.01	0.01 \pm 1.0x10 ⁻³	0.08 \pm 2.0x10 ⁻³	0.77
	19	0.32 \pm 2.0x10 ⁻³	0.30 \pm 0.01	0.21 \pm 4.0x10 ⁻³	0.04 \pm 3.0x10 ⁻⁴	0.02 \pm 4.0x10 ⁻³	0.03 \pm 3.0x10 ⁻³	0.07 \pm 0.01	0.76
	20	0.12 \pm 0.01	0.47 \pm 4.0x10 ⁻³	0.17 \pm 0.01	0.06 \pm 4.0x10 ⁻³	0.09 \pm 2.0x10 ⁻³	0.05 \pm 4.0x10 ⁻³	0.02 \pm 4.0x10 ⁻³	0.72
	W1	0.24 \pm 0.01	0.16 \pm 0.01	0.57 \pm 0.01	0.01 \pm 1.0x10 ⁻³	0.01 \pm 1.0x10 ⁻³	0.01 \pm 2.0x10 ⁻³	< 0.01	0.59
	W2	0.07 \pm 4.0x10 ⁻³	0.09 \pm 3.0x10 ⁻³	0.09 \pm 5.0x10 ⁻³	0.01 \pm 2.0x10 ⁻³	0.57 \pm 3.0x10 ⁻³	0.17 \pm 3.0x10 ⁻³	0.01 \pm 1.0x10 ⁻³	0.62
	31	0.07 \pm 3.0x10 ⁻³	0.41 \pm 0.01	0.39 \pm 0.02	0.02 \pm 2.0x10 ⁻³	0.07 \pm 4.0x10 ⁻³	0.04 \pm 4.0x10 ⁻³	0.01 \pm 2.0x10 ⁻³	0.67
	33	0.11 \pm 2.0x10 ⁻³	0.21 \pm 0.02	0.05 \pm 4.0x10 ⁻³	0.04 \pm 0.01	0.36 \pm 0.02	0.22 \pm 0.01	0.01 \pm 3.0x10 ⁻³	0.76
	22	0.11 \pm 0.01	0.43 \pm 0.03	0.30 \pm 0.01	0.01 \pm 2.0x10 ⁻³	0.09 \pm 0.01	0.05 \pm 4.0x10 ⁻³	0.02 \pm 5.0x10 ⁻³	0.70
45	0.23 \pm 0.02	0.30 \pm 0.02	0.09 \pm 3.0x10 ⁻³	0.02 \pm 6.0x10 ⁻⁴	0.17 \pm 0.01	0.03 \pm 7.0x10 ⁻³	0.08 \pm 0.01	0.81	

(b) 2011

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other	<i>I-D</i>
Spring	W3	0.05 \pm 0.02	0.03 \pm 0.01	0.91 \pm 0.02	< 0.01	0.00	0.00	0.00	0.17
	23B	0.11 \pm 0.01	0.09 \pm 0.01	0.79 \pm 0.01	0.00	0.01 \pm 2.0x10 ⁻³	< 0.01	0.00	0.36
	33	0.23 \pm 0.01	0.19 \pm 0.02	0.50 \pm 0.02	< 0.01	0.02 \pm 3.0x10 ⁻³	0.05 \pm 0.02	0.01 \pm 0.01	0.66
	28	0.19 \pm 0.01	0.19 \pm 0.01	0.07 \pm 5.0x10 ⁻³	0.06 \pm 0.02	0.09 \pm 0.01	0.40 \pm 0.04	0.01 \pm 4.0x10 ⁻³	0.75
	W2	0.15 \pm 0.01	0.18 \pm 0.01	0.57 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.07 \pm 0.01	0.00	0.62
	23S	0.14 \pm 0.02	0.07 \pm 0.02	0.78 \pm 0.04	< 0.01	0.00	0.00	0.00	0.37
	68	0.09 \pm 4.0x10 ⁻³	0.14 \pm 0.01	0.08 \pm 3.0x10 ⁻³	0.27 \pm 0.02	0.34 \pm 0.03	0.08 \pm 4.0x10 ⁻³	0.01 \pm 5.0x10 ⁻⁴	0.77
Summer	65	0.18 \pm 2.0x10 ⁻³	0.26 \pm 0.02	0.14 \pm 0.02	0.16 \pm 0.02	0.16 \pm 0.02	0.07 \pm 7.0x10 ⁻³	0.02 \pm 5.0x10 ⁻³	0.82
	64	0.14 \pm 0.01	0.18 \pm 0.02	0.14 \pm 0.02	0.18 \pm 0.01	0.21 \pm 0.02	0.13 \pm 0.02	0.02 \pm 2.0x10 ⁻³	0.83
	45	0.06 \pm 4.0x10 ⁻⁴	0.33 \pm 0.01	0.17 \pm 0.01	0.16 \pm 0.02	0.09 \pm 6.0x10 ⁻³	0.19 \pm 2.0x10 ⁻³	< 0.01	0.79
	43S	0.08 \pm 3.0x10 ⁻³	0.30 \pm 6.0x10 ⁻³	0.10 \pm 8.0x10 ⁻³	0.10 \pm 8.0x10 ⁻³	0.08 \pm 4.0x10 ⁻³	0.33 \pm 0.01	< 0.01	0.77
	23ES	0.05 \pm 3.0x10 ⁻³	0.20 \pm 0.01	0.17 \pm 6.0x10 ⁻³	0.17 \pm 6.0x10 ⁻³	0.03 \pm 5.0x10 ⁻³	0.51 \pm 0.01	0.00	0.64
	W1	0.10 \pm 4.0x10 ⁻³	0.31 \pm 0.01	0.17 \pm 0.01	0.17 \pm 0.01	0.06 \pm 0.01	0.28 \pm 0.01	0.00	0.75
	26S	0.21 \pm 0.01	0.20 \pm 0.02	0.08 \pm 0.01	0.08 \pm 0.01	0.08 \pm 0.01	0.05 \pm 0.01	0.00	0.89
Fall	22	0.13 \pm 0.01	0.34 \pm 0.02	0.14 \pm 0.04	0.26 \pm 0.05	0.07 \pm 0.01	0.05 \pm 0.01	0.02 \pm 5.0x10 ⁻³	0.77
	34S	0.17 \pm 0.02	0.26 \pm 4.0x10 ⁻³	0.05 \pm 4.0x10 ⁻³	0.15 \pm 0.01	0.23 \pm 0.02	0.13 \pm 3.0x10 ⁻³	0.01 \pm 5.0x10 ⁻⁴	0.81
	33	0.06 \pm 3.0x10 ⁻³	0.25 \pm 0.01	0.03 \pm 1.0x10 ⁻³	0.05 \pm 0.01	0.52 \pm 0.01	0.09 \pm 4.0x10 ⁻³	0.01 \pm 1.0x10 ⁻³	0.65
	W2	0.02 \pm 2.0x10 ⁻³	0.10 \pm 1.0x10 ⁻³	0.01 \pm 1.0x10 ⁻³	0.05 \pm 6.0x10 ⁻⁴	0.69 \pm 9.0x10 ⁻³	0.12 \pm 3.0x10 ⁻³	< 0.01	0.50
	43S	0.07 \pm 4.0x10 ⁻³	0.24 \pm 4.0x10 ⁻³	0.02 \pm 4.0x10 ⁻³	0.06 \pm 4.0x10 ⁻³	0.38 \pm 0.01	0.12 \pm 3.0x10 ⁻³	0.11 \pm 5.0x10 ⁻³	0.76
	41S	0.06 \pm 5.0x10 ⁻³	0.26 \pm 0.02	0.02 \pm 1.0x10 ⁻³	0.04 \pm 4.0x10 ⁻³	0.41 \pm 0.01	0.05 \pm 3.0x10 ⁻³	0.15 \pm 4.0x10 ⁻³	0.73

Table A.4. Summary of mean proportions of seven zooplankton prey groups in the South Basin (\pm SE) and Simpson's index of diversity ($I-D$) for South Basin stations sampled during three seasonal research cruises in (a) 2010 and (b) 2011. Data arranged in a south to north manner. No fall 2010 stations included as no stations yielded sufficient fish for subsequent analysis.

(a) 2010

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other	$I-D$
Spring	14	0.58 \pm 0.01	0.12 \pm 0.01	0.29 \pm 0.02	0.01 \pm 0.04	0.00	< 0.01	0.01 \pm 2.9x10 ⁻³	0.56
	55	0.63 \pm 0.01	0.10 \pm 0.01	0.24 \pm 0.01	0.01 \pm 4.0x10 ⁻⁴	< 0.01	< 0.01	< 0.01	0.54
	W14/16S	0.51 \pm 0.02	0.31 \pm 0.04	0.14 \pm 0.02	0.03 \pm 3.0x10 ⁻³	< 0.01	0.01 \pm 2.6x10 ⁻³	0.00	0.62
Summer	60B	0.59 \pm 0.03	0.16 \pm 0.01	0.20 \pm 0.02	0.05 \pm 0.01	0.00	0.00	0.00	0.58
	3B	0.46 \pm 0.01	0.22 \pm 4.0x10 ⁻³	0.08 \pm 0.01	0.22 \pm 2.8x10 ⁻³	0.00	0.00	0.02 \pm 4.6x10 ⁻³	0.68
	60C	0.54 \pm 0.01	0.21 \pm 0.01	0.14 \pm 0.01	0.08 \pm 1.1x10 ⁻³	0.00	0.00	0.03 \pm 5.0x10 ⁻⁴	0.64
	W12/61	0.62 \pm 0.03	0.12 \pm 0.01	0.18 \pm 0.03	0.05 \pm 3.6x10 ⁻³	0.00	0.00	0.03 \pm 0.01	0.57
	62	0.57 \pm 0.02	0.06 \pm 0.01	0.22 \pm 0.03	0.14 \pm 0.03	0.00	0.00	0.02 \pm 0.01	0.60
	W9/10A	0.58 \pm 0.04	0.06 \pm 3.2x10 ⁻³	0.22 \pm 0.03	0.10 \pm 0.01	0.00	< 0.01	0.05 \pm 0.02	0.60
	W13/14	0.41 \pm 0.02	0.15 \pm 0.02	0.16 \pm 0.03	0.19 \pm 0.01	0.00	< 0.01	0.09 \pm 0.01	0.74

(b) 2011

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other	$I-D$
Spring	36S	0.06 \pm 0.01	0.35 \pm 0.02	0.56 \pm 0.01	0.03 \pm 0.01	0.00	7.3x10 ⁻⁴ \pm 3.7x10 ⁻⁴	0.00	0.56
	44S	0.29 \pm 0.01	0.26 \pm 3.7x10 ⁻³	0.42 \pm 0.01	0.01 \pm 0.01	0.00	0.02 \pm 4.4x10 ⁻³	2.1x10 ⁻³ \pm 2.1x10 ⁻³	0.67
Summer	9	0.40 \pm 0.02	0.08 \pm 0.02	0.36 \pm 0.02	0.14 \pm 0.01	0.00	0.01 \pm 0.01	0.01 \pm 2.2x10 ⁻³	0.68
	57B	0.43 \pm 0.01	0.04 \pm 0.01	0.50 \pm 0.02	0.01 \pm 1.0x10 ⁻³	0.00	0.00	0.03 \pm 6.9x10 ⁻³	0.56
	2	0.36 \pm 0.02	0.13 \pm 0.01	0.30 \pm 0.03	0.12 \pm 0.01	0.00	0.00	0.09 \pm 7.4x10 ⁻³	0.74
	3B	0.24 \pm 0.01	0.29 \pm 0.02	0.28 \pm 0.02	0.04 \pm 0.01	0.00	2.8x10 ⁻³ \pm 1.4x10 ⁻³	0.16 \pm 4.8x10 ⁻³	0.79
	3C	0.30 \pm 0.01	0.22 \pm 0.01	0.19 \pm 0.01	0.11 \pm 0.01	0.00	0.00	0.17 \pm 1.2x10 ⁻³	0.78
	37S	0.50 \pm 0.01	0.18 \pm 3.9x10 ⁻³	0.27 \pm 0.01	0.01 \pm 5.3x10 ⁻⁴	0.00	4.6x10 ⁻⁴ \pm 4.6x10 ⁻⁴	0.03 \pm 3.4x10 ⁻³	0.64
	62	0.48 \pm 0.06	0.22 \pm 0.03	0.13 \pm 0.02	0.10 \pm 0.02	0.00	1.0x10 ⁻³ \pm 1.0x10 ⁻³	0.07 \pm 0.01	0.69
	60	0.32 \pm 0.07	0.19 \pm 0.01	0.29 \pm 0.03	0.11 \pm 1.8x10 ⁻³	3.2x10 ⁻³ \pm 3.2x10 ⁻³	4.5x10 ⁻³ \pm 2.8x10 ⁻³	0.09 \pm 5.0x10 ⁻³	0.76
	5	0.22 \pm 0.02	0.14 \pm 0.01	0.21 \pm 0.01	0.37 \pm 0.01	0.00	4.6x10 ⁻³ \pm 4.7x10 ⁻³	2.5x10 ⁻³ \pm 2.5x10 ⁻³	0.75
	49S	0.07 \pm 0.01	0.24 \pm 0.01	0.02 \pm 1.2x10 ⁻³	0.06 \pm 0.01	0.38 \pm 0.02	0.12 \pm 0.01	0.11 \pm 0.01	0.76
Fall	11	0.37 \pm 0.02	0.34 \pm 0.01	0.15 \pm 0.01	0.12 \pm 4.6x10 ⁻³	0.00	0.01 \pm 2.2x10 ⁻⁴	0.01 \pm 3.5x10 ⁻³	0.71
	10S	0.52 \pm 0.03	0.15 \pm 0.02	0.17 \pm 0.01	0.15 \pm 0.01	0.00	0.01 \pm 3.6x10 ⁻³	3.0x10 ⁻³ \pm 1.3x10 ⁻⁴	0.66
	W11/8	0.12 \pm 2.1x10 ⁻³	0.28 \pm 0.02	0.29 \pm 4.6x10 ⁻³	0.22 \pm 0.03	0.00	0.08 \pm 0.01	0.01 \pm 3.5x10 ⁻³	0.77
	6	0.37 \pm 0.02	0.18 \pm 0.01	0.15 \pm 0.01	0.28 \pm 0.01	2.0x10 ⁻³ \pm 2.0x10 ⁻³	0.02 \pm 4.4x10 ⁻³	2.0x10 ⁻³ \pm 1.1x10 ⁻³	0.73
	37	0.23 \pm 0.02	0.33 \pm 0.02	0.22 \pm 2.0x10 ⁻³	0.20 \pm 7.1x10 ⁻³	0.00	0.01 \pm 1.5x10 ⁻³	9.4x10 ⁻³ \pm 2.1x10 ⁻³	0.75
	W10	0.25 \pm 0.01	0.30 \pm 0.02	0.08 \pm 5.3x10 ⁻³	0.35 \pm 0.01	0.00	0.01 \pm 4.0x10 ⁻⁴	5.6x10 ⁻³ \pm 1.1x10 ⁻³	0.72
	60	0.13 \pm 0.01	0.16 \pm 4.4x10 ⁻³	0.58 \pm 0.03	0.08 \pm 0.01	0.00	0.02 \pm 7.2x10 ⁻³	0.02 \pm 0.02	0.61
	62	0.17 \pm 0.02	0.28 \pm 0.02	0.45 \pm 0.04	0.09 \pm 0.01	1.5x10 ⁻³ \pm 1.5x10 ⁻³	5.0x10 ⁻³ \pm 2.7x10 ⁻³	3.1x10 ⁻³ \pm 1.6x10 ⁻³	0.68
W14/16S	0.31 \pm 0.01	0.31 \pm 0.01	0.16 \pm 0.02	0.17 \pm 0.01	0.05 \pm 0.01	0.01 \pm 5.5x10 ⁻³	2.4x10 ⁻³ \pm 1.3x10 ⁻³	0.75	

Table A.5. Summary of mean proportions of seven zooplankton prey groups in the gut contents of rainbow smelt (*Osmerus mordax*) (\pm SE) for stations sampled in the North Basin during three seasonal research cruises in (a) 2010 and (b) 2011. Data arranged in a south to north manner.

(a) 2010

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other
Spring	W7	0.78 \pm 0.01	0.16 \pm 0.01	0.00	0.03 \pm 0.01	0.01 \pm 0.01	0.01 \pm 2.3x10 ⁻³	0.00
	W6	0.24 \pm 0.02	0.52 \pm 0.03	0.00	0.02 \pm 2.8x10 ⁻³	0.17 \pm 0.03	0.05 \pm 0.01	< 0.01
	W5	0.36 \pm 0.03	0.37 \pm 0.02	0.00	0.03 \pm 3.8x10 ⁻³	0.15 \pm 0.02	0.09 \pm 0.01	< 0.1
	19	0.79 \pm 0.02	0.08 \pm 0.02	0.00	0.01 \pm 1.3x10 ⁻³	0.01 \pm 1.6x10 ⁻³	0.01 \pm 3.7x10 ⁻³	< 0.01
	34S	0.61 \pm 0.03	0.16 \pm 0.01	0.00	0.06 \pm 0.01	0.19 \pm 0.03	0.01 \pm 3.6x10 ⁻³	< 0.01
	28	0.34 \pm 0.03	0.16 \pm 0.01	0.00	0.06 \pm 0.01	0.19 \pm 0.03	0.24 \pm 0.02	< 0.01
	68	0.65 \pm 0.01	0.17 \pm 0.01	0.00	0.14 \pm 0.01	0.01 \pm 1.8x10 ⁻³	0.02 \pm 3.2x10 ⁻³	< 0.01
Summer	20	0.02 \pm 0.01	0.02 \pm 0.01	0.00	0.36 \pm 0.08	0.50 \pm 0.09	< 0.01	0.10 \pm 0.06
	65	0.07 \pm 0.02	0.12 \pm 0.04	0.00	0.62 \pm 0.09	0.19 \pm 0.07	0.00	< 0.01
	64	0.05 \pm 0.01	0.02 \pm 0.01	0.00	0.71 \pm 0.05	0.20 \pm 0.08	0.00	0.01 \pm 4.7x10 ⁻³
Fall	W5	0.05 \pm 0.01	0.77 \pm 0.03	0.00	0.12 \pm 0.03	0.06 \pm 0.01	0.00	< 0.01
	19	0.09 \pm 0.01	0.74 \pm 0.02	0.00	0.10 \pm 0.02	0.07 \pm 0.01	< 0.01	0.01 \pm 1.8x10 ⁻³
	20	0.07 \pm 0.02	0.55 \pm 0.06	0.00	0.02 \pm 4.0x10 ⁻³	0.34 \pm 0.06	0.01 \pm 3.1x10 ⁻³	< 0.01
	W1	0.49 \pm 0.06	0.09 \pm 0.01	0.00	0.35 \pm 0.05	0.05 \pm 0.01	< 0.01	0.03 \pm 0.01
	W2	< 0.01	0.01 \pm 2.6x10 ⁻³	0.00	0.04 \pm 0.01	0.94 \pm 0.02	< 0.01	< 0.01
	31	0.24 \pm 0.04	0.19 \pm 0.03	0.00	0.32 \pm 0.04	0.24 \pm 0.07	0.01 \pm 0.01	0.01 \pm 3.4x10 ⁻³
	33	0.02 \pm 0.01	0.01 \pm 2.7x10 ⁻³	0.00	0.10 \pm 0.03	0.73 \pm 0.09	0.04 \pm 0.01	0.10 \pm 0.10
	22	0.10 \pm 0.01	0.04 \pm 0.01	0.00	0.05 \pm 0.01	0.73 \pm 0.03	0.07 \pm 0.01	0.01 \pm 3.0x10 ⁻³
45	0.08 \pm 0.01	0.19 \pm 0.03	0.00	0.45 \pm 0.05	0.25 \pm 0.05	0.02 \pm 0.01	< 0.01	

(b) 2011

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other
Spring	W3	0.04 \pm 0.02	0.80 \pm 0.05	0.00	< 0.01	0.15 \pm 0.04	< 0.01	0.01 \pm 0.01
	23B	0.02 \pm 0.01	0.85 \pm 0.09	0.00	0.00	0.02 \pm 0.02	< 0.01	0.11 \pm 0.09
	33	0.09 \pm 0.02	0.37 \pm 0.08	0.00	0.03 \pm 4.7x10 ⁻³	0.15 \pm 0.02	0.37 \pm 0.06	< 0.01
	28	0.58 \pm 0.02	0.31 \pm 0.02	0.00	0.05 \pm 0.01	0.03 \pm 0.01	0.02 \pm 4.8x10 ⁻³	< 0.01
	W2	0.18 \pm 0.02	0.63 \pm 0.02	0.00	0.02 \pm 4.9x10 ⁻³	0.05 \pm 0.01	0.12 \pm 0.03	< 0.01
	23S	0.00	0.17 \pm 0.07	0.00	< 0.01	0.35 \pm 0.11	0.14 \pm 0.05	0.33 \pm 0.13
Summer	68	0.07 \pm 0.04	0.02 \pm 0.01	0.00	0.39 \pm 0.05	0.51 \pm 0.07	< 0.01	0.01 \pm 2.8x10 ⁻³
	65	0.03 \pm 0.01	< 0.01	0.00	0.80 \pm 0.02	0.10 \pm 0.02	< 0.01	0.06 \pm 0.01
	64	0.17 \pm 0.04	0.01 \pm 3.3x10 ⁻³	0.00	0.62 \pm 0.03	0.15 \pm 0.04	< 0.01	0.05 \pm 0.03
	45	0.19 \pm 0.04	0.01 \pm 2.5x10 ⁻³	0.00	0.64 \pm 0.06	0.14 \pm 0.06	0.01 \pm 2.2x10 ⁻³	0.01 \pm 4.0x10 ⁻³
	43S	0.19 \pm 0.03	0.02 \pm 0.01	0.00	0.39 \pm 0.04	0.30 \pm 0.04	0.09 \pm 0.02	< 0.01
	23ES	0.37 \pm 0.06	0.03 \pm 0.01	0.00	0.49 \pm 0.05	0.09 \pm 0.02	0.01 \pm 4.2x10 ⁻³	0.01 \pm 0.01
	W1	0.14 \pm 0.03	0.01 \pm 2.5x10 ⁻³	0.00	0.60 \pm 0.06	0.20 \pm 0.04	0.03 \pm 0.01	0.2 \pm 4.4x10 ⁻³
26S	0.85 \pm 0.02	0.02 \pm 0.01	0.00	0.08 \pm 0.01	0.03 \pm 0.01	< 0.01	0.01 \pm 3.3x10 ⁻³	
Fall	22	0.14 \pm 0.02	0.23 \pm 0.07	0.00	0.59 \pm 0.07	0.04 \pm 0.01	0.00	< 0.01
	34S	< 0.01	0.12 \pm 0.08	0.00	0.03 \pm 0.02	0.85 \pm 0.09	< 0.01	< 0.01
	33	< 0.01	0.03 \pm 0.02	0.00	0.12 \pm 0.06	0.84 \pm 0.08	0.01 \pm 1.3x10 ⁻³	< 0.01
	W2	0.01 \pm 0.01	0.07 \pm 0.03	0.00	0.19 \pm 0.09	0.69 \pm 0.10	0.02 \pm 0.02	0.02 \pm 0.01
	43S	0.01 \pm 0.01	0.06 \pm 0.02	0.00	0.28 \pm 0.09	0.64 \pm 0.09	< 0.01	0.00
	41S	0.01 \pm 2.0x10 ⁻³	0.01 \pm 0.01	0.00	0.66 \pm 0.06	0.32 \pm 0.06	0.00	< 0.01

Table A.6. Summary of mean proportions of seven zooplankton prey groups in the gut contents of cisco (*Coregonus artedii*) (\pm SE) for stations sampled in the South Basin during three seasonal research cruises in (a) 2010 and (b) 2011. Data arranged in a south to north manner.

(a) 2010

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other
Spring	14	0.68 \pm 0.05	0.21 \pm 0.02	0.00	0.10 \pm 0.07	0.00	0.00	< 0.01
	55	0.70 \pm 0.08	0.19 \pm 0.03	0.00	0.11 \pm 0.09	0.00	0.00	0.01 \pm 0.01
	W14/16S	0.69 \pm 0.05	0.30 \pm 0.05	0.00	< 0.01	< 0.01	< 0.01	< 0.01
Summer	60B	0.54 \pm 0.06	0.24 \pm 0.05	0.00	0.22 \pm 0.08	< 0.01	< 0.01	0.00
	3B	0.21 \pm 0.03	0.11 \pm 0.02	0.00	0.67 \pm 0.05	< 0.01	0.00	0.00
	60C	0.05 \pm 0.01	0.03 \pm 4.8 $\times 10^{-3}$	0.00	0.92 \pm 0.01	0.00	0.00	0.00
	W12/61	0.38 \pm 0.09	0.11 \pm 0.03	0.00	0.16 \pm 0.05	0.00	< 0.01	0.35 \pm 0.14
	62	0.05 \pm 0.01	0.02 \pm 4.3 $\times 10^{-3}$	0.00	0.93 \pm 0.02	0.00	0.00	0.00
	W9/10A	0.06 \pm 0.01	0.02 \pm 1.8 $\times 10^{-3}$	0.00	0.73 \pm 0.03	0.00	0.00	0.19 \pm 0.03
	W13/14	0.08 \pm 0.02	0.21 \pm 0.04	0.00	0.71 \pm 0.05	0.00	< 0.01	0.01 \pm 2.6 $\times 10^{-3}$

(b) 2011

	Station	Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.	Other
Spring	36S	0.14 \pm 0.05	0.77 \pm 0.08	0.00	0.09 \pm 0.08	< 0.01	< 0.01	0.01 \pm 3.3 $\times 10^{-3}$
	44S	0.64 \pm 0.04	0.32 \pm 0.04	0.00	0.02 \pm 0.01	0.00	0.01 \pm 0.01	< 0.01
Summer	9	< 0.01	0.01 \pm 6.9 $\times 10^{-3}$	0.00	0.98 \pm 0.01	0.00	0.00	< 0.01
	57B	0.01 \pm 5.7 $\times 10^{-3}$	0.01 \pm 4.3 $\times 10^{-3}$	0.00	0.92 \pm 0.01	0.00	0.00	0.06 \pm 0.01
	2	0.14 \pm 0.07	0.03 \pm 7.6 $\times 10^{-3}$	0.00	0.44 \pm 0.05	0.00	0.00	0.39 \pm 0.04
	3B	0.01 \pm 5.3 $\times 10^{-3}$	0.02 \pm 6.5 $\times 10^{-3}$	0.00	0.16 \pm 0.04	0.00	0.00	0.80 \pm 0.04
	3C	0.10 \pm 0.06	0.07 \pm 0.02	0.00	0.16 \pm 0.02	0.00	0.00	0.68 \pm 0.07
	37S	0.81 \pm 0.03	0.12 \pm 0.02	0.00	0.03 \pm 0.02	0.00	0.00	0.04 \pm 0.01
	62	0.13 \pm 0.05	0.06 \pm 0.02	0.00	0.31 \pm 0.03	0.00	0.00	0.51 \pm 0.05
	60	0.02 \pm 0.01	0.07 \pm 0.01	0.00	0.67 \pm 0.06	0.00	0.00	0.23 \pm 0.06
	5	0.00	0.03 \pm 0.02	0.00	0.97 \pm 0.02	0.00	< 0.01	< 0.01
	49S	0.08 \pm 0.05	0.05 \pm 0.02	0.00	0.83 \pm 0.07	0.00	0.01 \pm 0.01	0.03 \pm 0.02
Fall	11	0.11 \pm 0.03	0.17 \pm 0.04	0.00	0.69 \pm 0.05	0.00	0.01 \pm 0.01	0.01 \pm 0.01
	10S	0.04 \pm 0.01	0.07 \pm 0.02	0.00	0.89 \pm 0.03	0.00	0.00	< 0.01
	W11/8	0.18 \pm 0.04	0.35 \pm 0.06	0.00	0.43 \pm 0.04	0.01 \pm 2.0 $\times 10^{-3}$	0.02 \pm 0.01	0.01 \pm 3.5 $\times 10^{-3}$
	6	< 0.01	0.02 \pm 0.01	0.00	0.98 \pm 0.01	0.00	0.00	< 0.01
	37	0.01 \pm 0.01	0.03 \pm 0.01	0.00	0.96 \pm 0.01	0.00	0.00	< 0.01
	W10	0.01 \pm 2.1 $\times 10^{-3}$	0.10 \pm 0.02	0.00	0.88 \pm 0.02	0.00	0.00	0.01 \pm 3.1 $\times 10^{-3}$
	60	0.10 \pm 0.04	0.56 \pm 0.07	0.00	0.32 \pm 0.05	0.00	0.01 \pm 2.7 $\times 10^{-3}$	0.01 \pm 2.9 $\times 10^{-3}$
	62	0.11 \pm 0.02	0.63 \pm 0.05	0.00	0.22 \pm 0.03	0.00	0.00	0.04 \pm 0.01
W14/16S	0.05 \pm 0.03	0.41 \pm 0.07	0.00	0.51 \pm 0.08	0.01 \pm 0.01	< 0.01	0.01 \pm 0.01	

Table A.7. Summary of linear selection index values (\pm SE) for seven zooplankton prey groups in the gut contents of rainbow smelt (*Osmerus mordax*) in the North Basin for stations sampled during three seasonal research cruises in (a) 2010 and (b) 2011. Data represents stations 7 stations sampled in spring, 3 in summer and 9 sampled in fall, all arranged in a south to north manner. Underlined values indicate no significant difference from 0 (i.e. random feeding; $\alpha = 0.05$).

(a) 2010

	Station	Calanoids	Cyclopoids	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.
Spring	68	0.34 \pm 0.01	-0.10 \pm 0.01	0.05 \pm 0.01	0.02 \pm 0.01	-0.08 \pm 0.01
	W7	0.21 \pm 0.01	-0.06 \pm 0.01	-0.02 \pm 0.01	-0.02 \pm 0.01	-0.07 \pm 0.01
	W6	-0.22 \pm 0.02	0.22 \pm 0.03	-0.06 \pm 0.01	0.12 \pm 0.03	-0.02 \pm 0.01
	W5	<u>-0.01 \pm 0.03</u>	0.13 \pm 0.02	-0.03 \pm 0.01	0.09 \pm 0.02	-0.08 \pm 0.01
	19	0.46 \pm 0.02	-0.27 \pm 0.02	-0.03 \pm 0.01	<u>0.00</u>	-0.03 \pm 0.01
	34S	0.32 \pm 0.03	-0.23 \pm 0.02	<u>-0.01 \pm 0.01</u>	0.02 \pm 0.01	<u>-0.01 \pm 0.01</u>
Summer	28	0.12 \pm 0.03	-0.11 \pm 0.01	0.02 \pm 0.01	0.10 \pm 0.03	0.03 \pm 0.02
	65	-0.14 \pm 0.01	<u>-0.08 \pm 0.01</u>	0.41 \pm 0.08	<u>0.01 \pm 0.01</u>	<u>-0.01 \pm 0.01</u>
	64	-0.18 \pm 0.01	-0.24 \pm 0.01	0.50 \pm 0.08	0.10 \pm 0.09	<u>0.00</u>
	20	-0.12 \pm 0.01	-0.13 \pm 0.01	0.24 \pm 0.08	0.29 \pm 0.09	-0.04 \pm 0.01
	45	-0.15 \pm 0.01	-0.19 \pm 0.03	0.43 \pm 0.05	<u>0.08 \pm 0.05</u>	<u>-0.01 \pm 0.01</u>
	W5	-0.14 \pm 0.01	0.51 \pm 0.03	0.11 \pm 0.03	-0.06 \pm 0.01	-0.01 \pm 0.00
Fall	19	-0.23 \pm 0.01	0.44 \pm 0.02	0.06 \pm 0.02	0.04 \pm 0.01	-0.01 \pm 0.00
	20	-0.05 \pm 0.02	<u>0.08 \pm 0.06</u>	-0.04 \pm 0.01	0.24 \pm 0.06	-0.04 \pm 0.01
	W2	-0.06 \pm 0.01	-0.07 \pm 0.01	<u>0.03 \pm 0.01</u>	0.37 \pm 0.02	-0.17 \pm 0.01
	W1	0.25 \pm 0.06	-0.07 \pm 0.01	0.35 \pm 0.05	0.03 \pm 0.01	-0.01 \pm 0.01
	31	0.16 \pm 0.04	-0.22 \pm 0.03	0.30 \pm 0.04	0.17 \pm 0.07	-0.03 \pm 0.01
	22	<u>-0.01 \pm 0.01</u>	-0.39 \pm 0.01	0.05 \pm 0.01	0.65 \pm 0.03	0.02 \pm 0.01
33	-0.09 \pm 0.01	-0.20 \pm 0.01	<u>0.06 \pm 0.03</u>	0.37 \pm 0.09	-0.18 \pm 0.01	

(b) 2011

	Station	Calanoids	Cyclopoids	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.
Spring	W3	<u>-0.03 \pm 0.02</u>	0.77 \pm 0.05	<u>0.00</u>	0.15 \pm 0.04	<u>0.00</u>
	23S	<u>-0.14 \pm 0.00</u>	<u>0.10 \pm 0.07</u>	<u>0.00</u>	0.35 \pm 0.11	0.14 \pm 0.05
	28	0.39 \pm 0.02	0.12 \pm 0.02	<u>-0.01 \pm 0.01</u>	-0.05 \pm 0.01	-0.38 \pm 0.01
	W2	<u>0.03 \pm 0.02</u>	0.45 \pm 0.02	<u>0.01 \pm 0.01</u>	0.03 \pm 0.01	<u>0.04 \pm 0.03</u>
	23B	-0.10 \pm 0.01	0.76 \pm 0.09	<u>0.00</u>	<u>0.01 \pm 0.02</u>	<u>0.00</u>
	33	-0.14 \pm 0.02	0.17 \pm 0.08	0.03 \pm 0.01	0.12 \pm 0.02	0.32 \pm 0.06
Summer	65	-0.15 \pm 0.01	-0.26 \pm 0.01	0.64 \pm 0.02	-0.07 \pm 0.02	-0.07 \pm 0.01
	68	<u>-0.02 \pm 0.04</u>	-0.13 \pm 0.01	0.13 \pm 0.05	0.17 \pm 0.07	-0.07 \pm 0.01
	64	<u>0.03 \pm 0.04</u>	-0.18 \pm 0.01	0.45 \pm 0.03	<u>-0.06 \pm 0.04</u>	-0.13 \pm 0.01
	45	0.13 \pm 0.04	-0.32 \pm 0.01	0.48 \pm 0.05	<u>0.04 \pm 0.06</u>	-0.18 \pm 0.01
	43S	0.11 \pm 0.03	-0.27 \pm 0.01	0.29 \pm 0.04	0.22 \pm 0.04	-0.24 \pm 0.02
	23ES	0.31 \pm 0.06	-0.17 \pm 0.01	0.32 \pm 0.05	0.06 \pm 0.02	-0.49 \pm 0.01
Fall	W1	<u>0.04 \pm 0.03</u>	-0.30 \pm 0.01	0.43 \pm 0.06	0.14 \pm 0.04	-0.26 \pm 0.01
	26S	0.64 \pm 0.02	-0.18 \pm 0.01	<u>0.00</u>	-0.05 \pm 0.01	-0.05 \pm 0.01
	43S	-0.06 \pm 0.01	-0.17 \pm 0.02	0.22 \pm 0.09	0.26 \pm 0.09	-0.12 \pm 0.01
	41S	-0.05 \pm 0.01	-0.25 \pm 0.01	0.62 \pm 0.06	-0.09 \pm 0.06	-0.05 \pm 0.00
	W2	<u>-0.02 \pm 0.01</u>	<u>-0.02 \pm 0.03</u>	0.13 \pm 0.09	<u>0.00</u>	-0.10 \pm 0.02
	22	<u>0.01 \pm 0.02</u>	-0.11 \pm 0.07	0.33 \pm 0.07	-0.03 \pm 0.01	-0.05 \pm 0.00
34S	-0.17 \pm 0.01	<u>-0.14 \pm 0.08</u>	-0.12 \pm 0.02	0.62 \pm 0.09	-0.03 \pm 0.01	
33	-0.06 \pm 0.01	-0.22 \pm 0.02	<u>0.07 \pm 0.06</u>	0.32 \pm 0.08	-0.08 \pm 0.01	

Table A.8. Summary of linear selection index values (\pm SE) for seven zooplankton prey groups in the gut contents of cisco (*Coregonus artedii*) in the South Basin for stations sampled during three seasonal research cruises in (a) 2010 and (b) 2011. Data represents stations 7 stations sampled in spring, 3 in summer and 9 sampled in fall, all arranged in a south to north manner. Underlined values indicate no significant difference from 0 (i.e. random feeding; $\alpha = 0.05$).

(a) 2010

	Station	Calanoids	Cyclopoids	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.
Spring	14	0.10 \pm 0.05	0.10 \pm 0.02	0.10 \pm 0.07	<u>0.00</u>	<u>0.00</u>
	55	0.06 \pm 0.08	0.09 \pm 0.03	0.09 \pm 0.09	<u>0.00</u>	<u>0.00</u>
	W14/16S	0.18 \pm 0.05	-0.01 \pm 0.05	-0.03 \pm 0.01	<u>0.00</u>	<u>-0.01 \pm 0.01</u>
Summer	60B	<u>-0.04 \pm 0.06</u>	<u>0.08 \pm 0.05</u>	0.16 \pm 0.07	<u>0.00</u>	<u>0.00</u>
	3B	-0.25 \pm 0.03	-0.11 \pm 0.02	0.46 \pm 0.05	<u>0.00</u>	<u>0.00</u>
	60C	-0.50 \pm 0.01	-0.18 \pm 0.01	0.84 \pm 0.01	<u>0.00</u>	<u>0.00</u>
	W12/61	-0.24 \pm 0.08	<u>-0.01 \pm 0.03</u>	0.11 \pm 0.05	<u>0.00</u>	<u>0.00</u>
	62	-0.52 \pm 0.01	-0.04 \pm 0.01	0.80 \pm 0.02	<u>0.00</u>	<u>0.00</u>
	W9/10A	-0.52 \pm 0.01	<u>-0.03 \pm 0.01</u>	0.63 \pm 0.03	<u>0.00</u>	<u>0.00</u>
	W13/14	-0.33 \pm 0.02	0.06 \pm 0.04	0.52 \pm 0.05	<u>0.00</u>	<u>0.00</u>

(b) 2011

	Station	Calanoids	Cyclopoids	<i>Daphnia</i> spp.	<i>Eubosmina</i> sp.	<i>Bosmina</i> sp.
Spring	36S	0.07 \pm 0.05	0.42 \pm 0.02	0.06 \pm 0.08	<u>0.00</u>	<u>0.00</u>
	44S	0.35 \pm 0.04	0.05 \pm 0.04	<u>0.02 \pm 0.01</u>	<u>0.00</u>	<u>0.00</u>
Summer	9	-0.39 \pm 0.00	-0.07 \pm 0.01	0.84 \pm 0.01	<u>0.00</u>	<u>-0.01 \pm 0.00</u>
	57B	-0.41 \pm 0.01	<u>-0.03 \pm 0.00</u>	0.91 \pm 0.01	<u>0.00</u>	<u>0.00</u>
	2	-0.22 \pm 0.07	-0.10 \pm 0.01	0.32 \pm 0.05	<u>0.00</u>	<u>0.00</u>
	3B	-0.22 \pm 0.01	-0.26 \pm 0.01	0.12 \pm 0.04	<u>0.00</u>	<u>0.00</u>
	3C	-0.20 \pm 0.06	-0.16 \pm 0.02	0.05 \pm 0.02	<u>0.00</u>	<u>0.00</u>
	37S	0.31 \pm 0.03	-0.07 \pm 0.02	<u>0.02 \pm 0.02</u>	<u>0.00</u>	<u>0.00</u>
	62	-0.34 \pm 0.05	-0.17 \pm 0.02	0.20 \pm 0.03	<u>0.00</u>	<u>0.00</u>
	60	-0.30 \pm 0.01	-0.12 \pm 0.01	0.57 \pm 0.06	<u>0.00</u>	<u>0.00</u>
	5	0.22 \pm 0.00	-0.11 \pm 0.02	0.59 \pm 0.02	<u>0.00</u>	-0.05 \pm 0.00
	49S	-0.36 \pm 0.05	-0.20 \pm 0.02	0.67 \pm 0.07	<u>0.00</u>	<u>0.00</u>
Fall	11	-0.27 \pm 0.03	-0.17 \pm 0.04	0.57 \pm 0.05	<u>0.00</u>	<u>0.01 \pm 0.01</u>
	10S	-0.48 \pm 0.01	-0.08 \pm 0.02	0.74 \pm 0.03	<u>0.01 \pm 0.00</u>	<u>-0.01 \pm 0.00</u>
	W11/8	0.06 \pm 0.04	0.08 \pm 0.06	0.20 \pm 0.04	<u>0.01 \pm 0.00</u>	-0.06 \pm 0.01
	6	-0.36 \pm 0.00	-0.16 \pm 0.01	0.70 \pm 0.01	<u>0.00</u>	<u>-0.02 \pm 0.00</u>
	37	-0.23 \pm 0.01	-0.30 \pm 0.01	0.76 \pm 0.01	<u>0.00</u>	<u>-0.01 \pm 0.00</u>
	W10	-0.24 \pm 0.00	-0.20 \pm 0.02	0.01 \pm 0.08	<u>0.00</u>	<u>-0.01 \pm 0.00</u>
	60	<u>-0.03 \pm 0.04</u>	0.40 \pm 0.07	0.24 \pm 0.05	<u>0.00</u>	<u>-0.02 \pm 0.00</u>
	62	-0.06 \pm 0.02	0.34 \pm 0.05	0.13 \pm 0.03	<u>0.00</u>	<u>0.00</u>
	W14/16S	-0.26 \pm 0.03	0.10 \pm 0.07	0.35 \pm 0.08	<u>-0.03 \pm 0.01</u>	<u>-0.01 \pm 0.00</u>

Table A.9. Summary of regression analysis results between Ivlev's electivity index and: mean fork length of rainbow smelt (*Osmerus mordax*), mean water column turbidity and zooplankton density during the spring cruise in the North Basin of Lake Winnipeg during (a) spring, (b) summer and (c) fall. Significant relationships ($\alpha = 0.05$) are indicated with an asterisk.

(a) Spring

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	70	0.14		7	0.54		7	0.36	
	Cyclopoids	70	0.42	*	7	0.52		7	0.60	
	Nauplii	70	---		7	---		7	---	
	<i>Daphnia</i> spp.	70	0.03		7	0.26		7	0.33	
	<i>Eubosmina</i>	70	0.19		7	0.86	*	7	0.03	
	<i>Bosmina</i>	70	0.11		7	0.77		7	0.42	
2011	Calanoids	60	0.46	*	6	0.34		6	0.22	
	Cyclopoids	60	0.27	*	6	0.13		6	0.19	
	Nauplii	60	---		6	---		6	---	
	<i>Daphnia</i> spp.	60	0.04		6	0.52		6	0.36	
	<i>Eubosmina</i>	60	0.03		6	0.59		6	0.30	
	<i>Bosmina</i>	60	0.12		6	0.65		6	0.52	

(b) Summer

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	30	0.09		7	---		7	0.99	
	Cyclopoids	30	0.19		7	---		7	0.67	
	Nauplii	30	---		7	---		7	---	
	<i>Daphnia</i> spp.	30	0.24		7	---		7	0.76	
	<i>Eubosmina</i>	30	0.07		7	---		7	0.94	
	<i>Bosmina</i>	30	0.10		7	---		7	0.16	
2011	Calanoids	80	0.13		8	0.93	*	8	0.14	
	Cyclopoids	80	0.10		8	0.50		8	0.44	
	Nauplii	80	---		8	---		8	---	
	<i>Daphnia</i> spp.	80	0.06		8	0.20		8	0.08	
	<i>Eubosmina</i>	80	0.20		8	0.31		8	0.65	
	<i>Bosmina</i>	80	0.19		8	0.23		8	0.01	

(c) Fall

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	90	0.10		9	0.31		9	0.01	
	Cyclopoids	90	0.35	*	9	0.11		9	0.67	*
	Nauplii	90	---	---	9	---		9	---	
	<i>Daphnia</i> spp.	90	0.15		9	0.43		9	0.13	
	<i>Eubosmina</i>	90	0.02		9	0.05		9	0.01	
	<i>Bosmina</i>	90	0.04		9	0.25		9	0.13	
2011	Calanoids	60	0.08		6	0.28		6	0.04	
	Cyclopoids	60	0.26	*	6	0.37		6	0.18	
	Nauplii	60	---		6	---		6	---	
	<i>Daphnia</i> spp.	60	0.15		6	0.12		6	0.18	
	<i>Eubosmina</i>	60	0.26	*	6	0.57		6	0.42	
	<i>Bosmina</i>	60	0.33	*	6	0.40		6	0.23	

Table A.10. Summary of regression analysis results between Ivlev's electivity index and: mean fork length of cisco (*Coregonus artedi*), mean water column turbidity and zooplankton density during the spring cruise in the North Basin of Lake Winnipeg during (a) spring, (b) summer and (c) fall. Significant relationships ($\alpha = 0.05$) are indicated with an asterisk.

(a) Spring

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	30	0.32		3	0.65		3	0.44	
	Cyclopoids	30	0.24		3	0.05		3	0.88	
	Nauplii	30	---		3	---		3	---	
	<i>Daphnia</i> spp.	30	0.05		3	0.11		3	0.96	*
	<i>Eubosmina</i>	30	0.08		3	0.99	*	3	0.27	
	<i>Bosmina</i>	30	0.29		3	0.81		3	0.85	
2011	Calanoids	20	0.08		2	---	---	2	---	---
	Cyclopoids	20	0.25		2	---	---	2	---	---
	Nauplii	20	---		2	---	---	2	---	---
	<i>Daphnia</i> spp.	20	0.16		2	---	---	2	---	---
	<i>Eubosmina</i>	20	0.11		2	---	---	2	---	---
	<i>Bosmina</i>	20	0.37		2	---	---	2	---	---

(b) Summer

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	55	0.32		7	0.07		7	0.10	
	Cyclopoids	55	0.19		7	0.48		7	0.51	
	Nauplii	55	---		7	---		7	---	
	<i>Daphnia</i> spp.	55	0.15		7	0.23		7	0.17	
	<i>Eubosmina</i>	55	<0.01		7	---		7	---	
	<i>Bosmina</i>	55	0.32		7	0.20		7	0.47	
2011	Calanoids	89	0.01		9	0.60		9	0.46	
	Cyclopoids	89	0.27		9	0.42		9	0.31	
	Nauplii	89	---		9	---		9	---	
	<i>Daphnia</i> spp.	89	0.04		9	0.74	*	9	0.54	
	<i>Eubosmina</i>	89	0.32		9	0.23		9	0.22	
	<i>Bosmina</i>	89	0.19		9	0.09		9	0.24	

(c) Fall

	Prey Group	Mean fork length (mm)			Turbidity (NTU)			Zooplankton density (individuals/L)		
		<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
2010	Calanoids	99	0.03		10	0.66	*	10	0.52	
	Cyclopoids	99	0.36	*	10	0.81	*	10	0.40	
	Nauplii	99	---		10	---		10	---	
	<i>Daphnia</i> spp.	99	0.33	*	10	0.56		10	0.53	
	<i>Eubosmina</i>	99	0.24	*	10	0.24		10	0.10	
	<i>Bosmina</i>	99	0.07		10	0.12		10	0.36	

CHAPTER 3: Diel diet variation and dietary overlap in rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) in North Basin of Lake Winnipeg, Manitoba

3.1 Introduction

When two species sharing a dietary niche are present in a given habitat, there are two ultimate outcomes. Through concurrent use of similar and limited resources, the competitive exclusion principle predicts that one species may develop an advantage over the other, causing an eventual out-competition and possible extirpation of that species (Hardin 1960; Hutchinson 1961). Alternatively, Hardin (1960) postulates that the disadvantaged species may undergo an ecological shift (e.g. spatial, dietary) to reduce the degree of overlap with the dominant species. This second scenario would lead to coexistence of the two species through differentiation of their niches (Armstrong and McGehee 1980). An updated competitive niche shift principle focuses more on the limitation of similarity rather than out-competition, as increased niche overlap is predicted to result in decreased possibility of coexistence (Roughgarden 1983; den Boer 1986; Meszena *et al.* 2006).

Overlap in dietary niches is an important consideration in ecosystem studies (Azevedo *et al.* 2006). Considering dietary overlap through quantitative gut content analysis among established populations allows for estimations of potential resource partitioning by two sympatric species (Smith 1985). Understanding shared dietary niche use between species is important when describing trophic structure and competitive relationships in a system (Wallace 1981; Lopez *et al.* 2012). Dietary overlap is predicted to be positively correlated with competition (Schoener 1983). Thus, two species sharing the same habitat with highly overlapped diets are considered interspecific competitors

(Sih *et al.* 1985). When dietary overlap is low, this may indicate past competition owing to niche differentiation (Holt 1977). In both cases, however, it is important to consider that this may not be competition, as a particular niche could be productive enough for both species to coexist without reduced fitness, at least until a shared resource becomes limited (Bastolla *et al.* 2005). This misinterpretation of competition where there is none, or the “ghost” of present or past competition is an important consideration in all studies of this nature (Connell 1980).

In aquatic species, such as zooplankton and fish predators, dietary overlap can vary with other factors, such as diel patterns in prey abundance (Appenzeller and Leggett 1995). Zooplanktivorous fish are commonly seen to move within the water column to increase the relative spatial-temporal overlap with their zooplankton prey (Wurtsbaugh and Li 1985). Diurnal or nocturnal ascents (Begg 1976) as well as horizontal movement are often observed (Bohl 1980). Although zooplanktivore feeding rates during dark are generally lower than during the day (Sømes and Aksnes 2004; Pothoven *et al.* 2009), and dietary preferences may show a shift towards lower quality energetic prey presumably due to decreased detection (Urban and Brandt 1993), this movement may also minimize predator detection (Jacobsen *et al.* 1997). This pattern of movement can also increase spatial overlap with competitors (Savino and Stein 1989; Appenzeller and Leggett 1995), leading to shared dietary niche use during dark (Goldschmidt *et al.* 1990).

These trophic structures and regimes of established systems can be widely altered by the introduction of a non-indigenous species (Ricklefs and Miller 2000). Rapid population growth relative to native species is possible, as vulnerability to predation or environmental tolerances may be different in a non-indigenous species compared with a

native species (Tilman 1999; Sakai *et al.* 2001). Thus, heightened competitive ability (e.g. as a consequence of larger body size) and possible dramatic increases in population density may impart competitive benefits to a non-indigenous population (Declerck *et al.* 2005; Mills *et al.* 2004). However, some non-indigenous species may also be beneficial to native species, through such means as competitive or predatory release (Rodriguez 2006). An example of a non-indigenous species expanding its range into an aquatic ecosystem is the rainbow smelt (*Osmerus mordax*). This species has been linked to decreases in populations of sympatric zooplanktivores such as yellow perch (*Perca flavescens*) and cisco (*Coregonus artedii*; Hrabik *et al.* 1998; Hrabik *et al.* 2001). Native zooplanktivores may consequently consume lower quality prey as they are out-competed by smelt, leading to decreases in overall fitness and abundance of these native fish (Rooney and Paterson 2009). Smelt have also been linked to extirpation of native fish species through direct predation on eggs and larvae (Brandt and Madon 1986; Hrabik *et al.* 1998; Myers *et al.* 2009). However, as summarized by Rooney and Paterson (2009), native zooplanktivore populations in other systems may compensate by thermal (Crowder *et al.* 1981), spatial (Urban and Brandt 1993), or dietary (Lammens *et al.* 1985) segregation from the non-indigenous smelt.

In Lake Winnipeg, rainbow smelt were first reported in Lake Winnipeg in late 1990 (Campbell *et al.* 1991). The adult population is generally spatially limited to the cooler waters of the North Basin, showing a northerly increase in biomass with a patchy pelagic distribution (Lumb *et al.* 2012). This spatial limitation is most likely a consequence of the higher mean annual water temperature during the open water season in the South Basin, a low quality thermal habitat for adult smelt (Franzin *et al.* 2005).

Low numbers of young-of-the-year (YOY) smelt, however, are found in the South Basin (Lumb *et al.* 2012), likely due to their broader thermal tolerance (Brandt *et al.* 1980; Dodson and Ingram 1989). Cisco show a contrasting distribution to that of smelt, with a northerly decrease in biomass (Lumb *et al.* 2012). Cisco are also present in the North Basin, however, providing an opportunity to consider dietary overlap between these two zooplanktivores (Arnason 1951; Lumb *et al.* 2012). Abundance of cisco within the North Basin is highest in summer and fall, which coincides with maximum zooplankton density (Patalas and Salki 1992; Lumb *et al.* 2012). When considered within their separate basins, these species occupy a similar dietary niche in Lake Winnipeg, as documented in Chapter 2. As no fish community data exist prior to rainbow smelt invasion, an interesting opportunity presents itself to provide a description of current niche overlap where smelt and cisco occur together and, thus, the possible impact of rainbow smelt on one of the main native zooplanktivores of Lake Winnipeg.

3.2 Objectives and statement of hypotheses

The primary objective of this study was to investigate the diet of two Lake Winnipeg zooplanktivores, the non-indigenous rainbow smelt and the native cisco, in an area of direct spatial overlap (i.e. the North Basin) as well as diel dietary differences within species. To do this, I analyzed gut contents of the two species at locations where they were concurrently collected, as well as during daylight and dark trawls. I predicted that there would be a large degree of overlap between cisco and rainbow smelt where they were spatially overlapped, as both species showed similar dietary preferences when spatially separate (as seen in Chapter 2). I also predicted little diel dietary variation in the

diets, as there are no clear and consistent diel patterns in species composition and relative abundances of the zooplankton community (Kamada 2012).

Methods

3.3.1 Study area and design

3.3.1.1 Daylight-dark sampling

To investigate diel dietary patterns in rainbow smelt and cisco and possible dietary overlap between these two species in the North Basin of Lake Winnipeg, I collected both species during daylight and dark hours by trawling from the M.V. *Namao* during the summer research cruise of 2011 (July 25-26). The work was carried out in the north-west portion (53°18.988 N, 98°55.220 W) of the North Basin of Lake Winnipeg and based out of Grand Rapids, MB (Fig. 3.1). Daylight work began at 10:00, allowing for the sun to have fully risen above the horizon as sunrise was at 05:44. With sunset at 21:44, dark work began one hour after sunset to allow for the sun to be fully below the horizon. This project, initiated by Manitoba Conservation and Water Stewardship – Fisheries Branch, was the first of its kind on Lake Winnipeg. Their primary goal was to determine diel variation in the composition or biomass of pelagic fish species between dark and daylight periods (for protocol see Appendix 3.6.1).

Three parallel transects at a 2 km north-south spacing were completed, each consisting of three consecutive depth-relative trawls (shallow, mid and deep) and beginning at a pre-determined station. All station sampling and transects were replicated during daylight and dark to provide diel comparisons. Selected stations were a minimum 8 m deep and had previously been chosen due to relatively large numbers of fish caught

in previous years in the vicinity of these stations. At each station prior to trawling, basic site information (i.e. depth, air and surface water temperature) and depth profiles (i.e. photosynthetically active radiation (PAR), temperature, oxygen, conductivity and turbidity) were collected. The zooplankton prey community was also sampled at each station with a 73- μ m mesh Wisconsin zooplankton net hauled from 1 m above the bottom to the surface, thus sampling the entire water column. After collection, the sample was transferred into a 125 mL glass container and preserved with 70% ethanol.

Three sequential trawls at increasing trawl depth occurred as the ship moved away from a station, beginning with a shallow trawl, followed by mid, and finally a deep trawl (Fig. 1). Trawling was carried out with a 3 m (square) side beam trawl, 10.8 m long, with decreasing mesh size towards cod end (76.2 mm to 19.1 mm stretched mesh). The cod-end of the trawl was a 1.22 mm PVC pipe (114.3 mm in diameter) with a screw-in plug (as per Lumb *et al.* 2012). Each trawl lasted for 30 minutes at a towing speed of approximately 3.9 km/hr. After 30 minutes, the trawl was brought on board, emptied, and fish were sorted by species. After sorting, all fish collected were frozen onboard by Manitoba Conservation and Water Stewardship personnel.

3.3.1.2 Seasonal small pelagic fish monitoring

In addition to the daylight-dark sampling procedure, fish were also collected as part of the Manitoba Conservation and Water Stewardship – Fisheries Branch seasonal pelagic fish monitoring program, as described in Lumb *et al.* (2012). This program, using the same trawling protocol as described in the daylight-dark design, collects fish from approximately 65 pre-determined locations across Lake Winnipeg during daylight hours

(07:00 – 20:30) throughout three seasonal research cruises (i.e. spring, summer, fall) every year. Data described in Chapter 2 originated from these trawls, but focused on spatially separate diets of smelt and cisco. In this study, cisco and smelt that were caught concurrently in a given trawl were considered for gut content analysis. As described previously, fish were sorted on board and then frozen.

3.3.2 Laboratory processing

All frozen fish samples were subsequently returned to the lab for processing. Sub-samples of 30 rainbow smelt (70-130 mm total length) and 30 cisco (100-200 mm) were collected where available from each trawl. This was done to ensure that a minimum of 10 full stomachs was collected, standard protocol with zooplanktivore diet studies (Parker Stetter *et al.* 2005, Darbyson *et al.* 2003). The sampled size ranges for each fish species were selected to provide comparisons of fish with similar gape sizes and, thus, similar physical limits to size-based prey selection (Schmitt and Holbrook 1984), as shown by a gape size-total length linear regression analysis (rainbow smelt: $R = 0.937$, $P < 0.05$, $n = 61$; cisco: $R = 0.970$, $P < 0.05$, $n = 60$). Gut contents of fish described the prey consumed during the diel period in which they were caught, as zooplanktivores show an exponential rate of digestion (Adams and Breck 1990; Karnitz 1992), with generally fully evacuated guts after 2 – 2.5 hours in 15-16 °C water (Mills *et al.* 1984; Boisclair and Marchand 1994). Specifically, rainbow smelt in the lab show a greater than 80% evacuation after 1 hour and entire evacuation after 3 hours at 15 °C (Karnitz 1992), with lab-based rates being generally consistent to those estimated in the environment (Beseres *et al.* 2006).

After each fish was given a unique four-digit identifying number, its body cavity

was opened via a ventral incision along the midline beginning from the anus to the mouth. The stomach was then removed with the use of forceps and the entire digestive tract placed in a 20 mL scintillation vial half-filled with 70% ethanol. This halted any further digestion and degradation allowing for the identification of the gut contents.

To provide a description of diet, the first ten non-empty stomachs were examined for each species. First, the stomach was separated from other viscera and the esophagus. Then, the stomach was slit medially and the contents rinsed into an etched grid dish. After settling, half the volume of this sample was counted for six prey groups, namely: *Daphnia* spp. (which included *D. mendotae*, *D. retrocurva*, *D. longiremis*), *Eubosmina coregoni*, *Bosmina longirostris*, calanoid copepods, cyclopoid copepods and nauplius larvae. These prey groups are consistent with previous freshwater zooplanktivore diet studies (e.g. Hrabik *et al.* 1998, Beisner *et al.* 2003; Sheppard *et al.* 2012). Other groups or consumed items that were encountered inconsistently or in relatively low numbers (e.g. *Leptodora kindti*, ostracods) were combined into a separate seventh “other” category. Half the volume of a 5 mL sub-sample of each integrated zooplankton samples was analyzed in a similar manner to gut contents (see Chapter 2 for details) to provide a description of the zooplankton prey community existing in the water column in the vicinity of where sampled fish were feeding. All proportions were arcsine-square root transformed to allow for statistical comparisons among prey groups.

To estimate the degree of dietary overlap between these two zooplanktivores, Schoener’s (1969) Index was used, which is common in studies of this nature (e.g. Johnson *et al.* 2004; Moncayo-Estrada *et al.* 2011). Using this index, the proportion (p) of a prey type (i) in a given rainbow smelt (x) diet (p_{xi}) is directly compared to that of the

same prey group in cisco (y) diet (p_{yi}) at a given location, or station. The index (α) ranges from +1 (complete dietary overlap) to 0 (no dietary overlap) is calculated in the following manner: $\alpha = 1 - 0.5 \sum_i |p_{x,i} - p_{y,i}|$. With similar indices, values >0.6 are generally considered biologically meaningful (Zaret and Rand 1971; Mathur 1977), as summarized by Johnson *et al.* (2004).

3.4 Results

During the daylight-dark study, smelt were collected from three stations during daylight trawls for dietary analysis, all originating from deep trawls. Smelt were caught from four stations and cisco from three stations during dark. Rainbow smelt were caught in two mid trawls and two deep trawls, and cisco were found in all three deep trawls, resulting in two stations where smelt and cisco were sampled concurrently (Table 3.1).

Smelt collected during daylight (109.46 ± 0.94 mm) were significantly smaller than those collected during dark (112.38 ± 1.04 mm; $t_{207} = -2.08$, $P < 0.05$). During dark, cisco (158.20 ± 1.67 mm) were significantly larger than smelt ($t_{207} = -23.32$, $P < 0.05$). Pooled mean density data for the three stations (provided by C. Lumb) revealed non-significantly higher biomass of both smelt ($t_2 = 0.99$, $P > 0.05$) and cisco ($t_2 = 0.82$, $P > 0.05$) during dark trawls relative to daylight trawls. Specifically, rainbow smelt daylight biomass was lowest in shallow (0.41 ± 0.22 g/1000 m³) and mid trawls (0.73 ± 0.19 g/1000 m³), with the highest biomass collected in deep trawls (4.46 ± 0.32 g/1000 m³). For cisco, the numbers of individuals caught during daylight at each station were not sufficient for subsequent dietary analysis, but mean biomass of shallow (0.37 ± 0.38 g/1000 m³) and mid (1.20 ± 0.65 g/1000 m³) trawls during daylight were low and no

cisco were caught in deep trawls. During dark trawls, smelt biomass increased with trawl depth, with lowest observed biomass collected in shallow (2.15 ± 0.16 g/1000 m³), followed by mid (4.39 ± 0.10 g/1000 m³) and highest in deep (4.71 ± 0.20 g/1000 m³) trawls. For cisco collected during dark, low biomass was still caught in shallow (0.92 ± 0.92 g/1000 m³) and mid (0.70 ± 0.70 g/1000 m³) trawls, but the deep trawls (5.38 ± 0.19 g/1000 m³) provided the maximum mean biomass of any trawl depth for the two considered species during daylight or dark.

3.4.1 Zooplankton prey community

Zooplankton densities were not higher during dark in all three transects ($t_2 = -1.64$, $P > 0.05$). During both diel periods, cyclopoid copepods consistently had the highest proportion of considered prey groups (Table 3.2). Mean proportions revealed that copepod prey groups had higher proportions than cladoceran prey groups during daylight ($t_{15} = 6.54$, $P < 0.05$), but not during dark ($t_{16} = 1.64$, $P > 0.05$). Dark zooplankton samples had similar proportionate prey group rankings to that of daylight samples; however, proportions of *Eubosmina* ($t_{16} = -2.72$, $P < 0.05$) were higher during dark and *Bosmina* proportions were higher during daylight ($t_{10} = 1.93$, $P < 0.05$; Table 3.2).

3.4.2 Zooplanktivore stomach contents

Fork lengths of rainbow smelt analyzed for gut contents ranged from 83-176 mm and cisco ranged from 73-192 mm. During the day, rainbow smelt diet consisted predominantly of large cladocerans (*Eubosmina* and *Daphnia* spp.) followed by calanoids, *Bosmina*, cyclopoids and “other” (Table 3.3). *Eubosmina* was also dominant in mean proportions in dark smelt diet, but calanoids were found at a greater mean

proportion than that of *Daphnia* spp., followed by “other” prey, cyclopoids and *Bosmina* (Table 3.3). Most mean proportions of prey groups in the guts did not significantly differ between daylight and dark, but *Bosmina* was consumed at a significantly greater proportion during daylight ($t_{61} = -5.75, P < 0.05$) and calanoids ($t_{61} = 1.71, P < 0.05$) as well as “other” prey ($t_{61} = 4.44, P < 0.05$) significantly greater during dark. Diet of cisco collected during dark was mostly composed of *Eubosmina*, followed by calanoids, cyclopoids, *Bosmina*, *Daphnia* spp. and “other” prey (Table 3.3). When compared to dark smelt mean prey group proportions, cisco had significantly larger proportions of cyclopoids ($t_{68} = -4.26, P < 0.05$), *Eubosmina* ($t_{58} = -3.61, P < 0.05$) and *Bosmina* ($t_{65} = -5.59, P < 0.05$) in their diet, whereas smelt had significantly greater proportions of *Daphnia* spp. ($t_{50} = 4.81, P < 0.05$).

3.4.3 Dietary overlap

The previously-described daylight-dark trawling of summer 2011 provided two stations on the western side of the North Basin where smelt and cisco were caught concurrently (Fig. 3.2). Both these trawls were deep trawls during dark (Table 3.4). During fall 2010, cisco and smelt were concurrently caught at an additional five stations. These were predominantly shallow trawls (Table 3.4) and were spread along the eastern side of the North Basin (Fig. 3.2). Schoener’s Index values from both seasons revealed a high degree of dietary overlap (>0.9) across all prey groups (Table 3.5).

Discussion

Rainbow smelt diet showed no clear differences between daylight and dark. Where sampled concurrently in an area of spatial overlap and during times of high (i.e. summer) and intermediate (i.e. fall) zooplankton density, diets of the non-indigenous rainbow smelt and the native cisco had a high degree of overlap, with both species depending entirely on zooplankton prey. Overall, this suggests that smelt and cisco share a dietary niche in the North Basin of Lake Winnipeg. The two species, however, showed possible spatial segregation vertically within the water column. Cisco densities showed a large increase at night in deep trawls, suggesting that during daylight cisco were more associated with near-bottom waters than smelt.

Few significant diel differences were observed among prey groups in smelt diet and the zooplankton prey community. Zooplankton samples revealed that mean proportions of smaller prey groups (e.g. *Bosmina*) decreased and larger prey groups (e.g. calanoids) increased in dark relative to daylight. These differences were most likely caused by differential catchability among the prey groups with time of day. Larger-bodied prey groups commonly show increased proportions during dark, as they have presumably decreased capacity to detect and subsequently avoid a sampling apparatus when compared to daylight (Robinson and Ware 1994; Shaw and Robinson 1998). Diel dietary differences in smelt were most likely due to changes in the relative abundance of these prey groups, as an increased mean proportion of *Bosmina* during daylight coincided with increased presence in smelt diet. Overall, these differences do not seem to indicate a major diel shift in smelt diet, suggesting that foraging strategies did not vary with time of day.

Often daily vertical movement within the water column, or zooplankton diel vertical migration (DVM), is observed in freshwater lakes in response to food availability (Lampert and Taylor 1985) or predator avoidance (Lampert 1993). DVM normally involves individuals spending daylight hours in deeper waters and then moving near the surface during the dark hours (Lampert 1989), although reverse DVM has also been observed (Ohman 1990). However, in Lake Winnipeg, Kamada (2012) found there were no consistent changes in vertical distribution of zooplankton when considering depth-stratified samples, although density increased during dark sampling. This in turn supports the idea that zooplanktivores in Lake Winnipeg are presented with a relatively similar prey community throughout the day. The distribution of zooplanktivores may itself be reducing the ability of zooplankton to avoid predation through DVM, as smelt are present throughout the water column during daylight and dark periods. These dietary findings agree with other similar non-indigenous smelt populations, such as in Crystal and Sparkling Lake, Wisconsin where smelt dietary preferences for large-bodied cladocerans were consistent between day and night (Hrabik *et al.* 1998). Also, in many deeper lakes, DVM of zooplankton leads to differences in diet (e.g. Pothoven *et al.* 2009).

The daylight-dark trawling procedure also provided sites where both smelt and cisco were concurrently caught. These sites, along with stations from fall 2010, illustrated that when smelt and cisco are spatially overlapped and, thus, likely exposed to the same zooplankton community, their diets have an extremely high degree of overlap. Thus, in Lake Winnipeg, it seems that smelt and cisco are occupying extremely similar dietary niches, at least during times of high prey densities. A high degree of dietary overlap among zooplanktivores has been seen in other large lakes, such as in Lake Ontario where

smelt had similar diets with alewife (*Alosa pseudoharengus*) during times of high zooplankton density (Urban and Brandt 1993). Urban and Brandt (1993) found, however, that alewife and smelt were spatially segregated, with smelt occupying deeper waters than the alewife. Similarly, smelt in Lake Michigan showed a high degree of dietary overlap with alewife, but low overlap with other zooplanktivores, such as yellow perch (*Perca flavescens*) and trout-perch (*Percopsis omiscomaycus*; Crowder *et al.* 1981). In this case, smelt and alewife were spatially segregated into divergent thermal habitat, compensating for high dietary overlap. When species were found together with smelt, dietary overlap was low (Crowder *et al.* 1981). In their literature review, Rooney and Paterson (2009) suggest that large lakes present multiple niches (e.g. spatial, thermal, dietary) that can provide adequate opportunities for niche differentiation. In cases where smelt have had detrimental impacts on native zooplanktivores, this seems to be a consequence of direct predation of smelt on eggs and larval fish of those species, not from interspecific competition (Crowder 1980; Hrabik *et al.* 1998; Johnson *et al.* 2004).

In Lake Winnipeg, niche differentiation may occur by occupying different vertical habitats in the water column. Mean densities of both cisco and smelt were higher at all depths during dark relative to daylight periods, except cisco caught in mid trawls. Alternatively, the higher fish density at night could be an artifact of increased susceptibility to being caught in a trawl, as fish are presumably less able to detect and, thus, avoid the trawl due to decreased visibility during dark (Casey and Myers 1998). Low densities of cisco in all trawl depths during daylight and relatively high densities during dark strongly suggest that cisco exhibit diel vertical movement within the water column. They may be near the bottom during daylight (i.e. below trawl depth) and then

move upwards during dark. As with smelt and alewife in Lake Michigan and Ontario (Crowder *et al.* 1981; Urban and Brandt 1993), this vertical movement suggests that smelt and cisco are spatially segregated in the North Basin of Lake Winnipeg. Similar zooplanktivore movement is relatively common in freshwater lakes, with densities of fish in the pelagic zone often increasing at night through upward vertical movement relative to the day (Burczynski *et al.* 1987; TeWinkel and Fleischer 1999). Diel horizontal movement from the littoral to pelagic zone has been documented as well (Wurtsbaugh and Li 1985). Both types of movement may increase foraging efficiency by following the movement patterns of zooplankton prey (Bohl 1980), as well as to avoid piscivore predators (Clark and Levy 1988; Appenzeller and Leggett 1995).

As rainbow smelt are generally found in deeper cooler waters in other lakes (Argyle 1982; TeWinkel and Fleischer 1999; Simonin 2001), it is interesting that cisco seem to occupy this spatial niche in Lake Winnipeg. This may leave smelt excluded from the bottom, possibly leading to increased susceptibility to piscivore predation by walleye (*Sander vitreus*) and sauger (*Sander canadensis*); these predator species include a large proportion of smelt relative to cisco in their diet in the North Basin (Sheppard 2013). Future investigations could address the spatial and thermal distribution of zooplanktivores on a larger scale, with seasonal considerations to further elucidate zooplanktivore habitat use. It would also be interesting to look at dietary and spatial overlap between smelt and cisco during times of low prey abundance (i.e. spring), at which time cisco may show a greater dependence on other prey sources, such as benthic invertebrates.

Table 3.1. Summary of daylight-dark trawling conducted onboard the M.V. *Namao* on 25-26 July, 2011, showing collection date, transect number, relative trawl depth, site depth and number of collected rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedi*).

Station	Date	Time	Trawl Start Time	Relative trawl depth	Station depth (m)	Number of smelt collected	Number of cisco collected
T1	25-Jul-11	dark	23:30	Mid	14.63	30	---
T1	26-Jul-11	dark	00:00	Deep	14.63	---	30
T2	26-Jul-11	dark	02:00	Mid	14.94	30	---
T2	26-Jul-11	dark	02:30	Deep	14.94	30	30
T1	26-Jul-11	daylight	10:10	Deep	14.63	30	---
T2	26-Jul-11	daylight	13:00	Deep	14.94	30	---
T3	26-Jul-11	daylight	15:00	Deep	15.24	30	---
T3	26-Jul-11	dark	23:00	Deep	15.24	30	30

Table 3.2. Mean environmental proportion (\pm SE) and density for seven zooplankton prey groups collected during daylight and dark at the beginning of three fish trawling transects in the North Basin of Lake Winnipeg.

Station	Time	<i>Environmental Proportion (\pm SE)</i>							<i>Density (individuals/L)</i>
		Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i>	<i>Bosmina</i>	Other	
T1	daylight	$0.12 \pm 4.9 \times 10^{-3}$	0.34 ± 0.02	0.07 ± 0.01	0.15 ± 0.01	0.07 ± 0.01	$0.24 \pm 9.7 \times 10^{-3}$	$0.01 \pm 3.2 \times 10^{-3}$	108.94
	dark	$0.15 \pm 9.2 \times 10^{-3}$	$0.28 \pm 7.2 \times 10^{-3}$	$0.08 \pm 6.0 \times 10^{-3}$	0.18 ± 0.01	0.12 ± 0.01	0.19 ± 0.02	$0.01 \pm 3.0 \times 10^{-3}$	159.60
T2	daylight	$0.16 \pm 7.8 \times 10^{-3}$	0.26 ± 0.02	$0.18 \pm 1.9 \times 10^{-3}$	$0.13 \pm 8.9 \times 10^{-3}$	$0.09 \pm 6.2 \times 10^{-3}$	$0.17 \pm 7.7 \times 10^{-3}$	$0.01 \pm 3.0 \times 10^{-3}$	94.75
	dark	0.29 ± 0.01	0.29 ± 0.03	0.16 ± 0.03	0.13 ± 0.01	$0.08 \pm 7.1 \times 10^{-3}$	$0.03 \pm 1.7 \times 10^{-3}$	$0.01 \pm 1.8 \times 10^{-3}$	103.56
T3	daylight	$0.19 \pm 7.4 \times 10^{-3}$	0.26 ± 0.01	0.14 ± 0.01	$0.18 \pm 9.6 \times 10^{-3}$	$0.05 \pm 6.3 \times 10^{-3}$	$0.18 \pm 6.7 \times 10^{-3}$	< 0.01	113.79
	dark	0.13 ± 0.01	$0.22 \pm 2.8 \times 10^{-3}$	$0.07 \pm 6.0 \times 10^{-3}$	0.28 ± 0.02	$0.09 \pm 8.1 \times 10^{-3}$	$0.20 \pm 5.3 \times 10^{-3}$	$0.01 \pm 2.3 \times 10^{-3}$	140.02

Table 3.3. Mean proportion of seven zooplankton prey groups (\pm SE) consumed by rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) collected during daylight-dark trawling of three fish trawl transects in the North Basin of Lake Winnipeg.

Station	Time	Relative trawl depth	Species	Gut proportions (\pm SE)						
				Calanoid	Cyclopoid	Nauplii	<i>Daphnia</i> spp.	<i>Eubosmina</i>	<i>Bosmina</i>	Other
T1	dark	Mid	Rainbow smelt	0.41 \pm 0.08	0.09 \pm 0.02	0.00	0.18 \pm 0.03	0.20 \pm 0.06	0.01 \pm 0.01	0.12 \pm 0.04
T1	dark	Deep	Cisco	0.30 \pm 0.05	0.09 \pm 0.01	0.00	0.03 \pm 0.01	0.50 \pm 0.04	0.03 \pm 0.01	0.05 \pm 0.01
T2	dark	Mid	Rainbow smelt	0.15 \pm 0.05	0.05 \pm 0.01	0.00	0.18 \pm 0.06	0.43 \pm 0.13	0.01 \pm 0.01	0.18 \pm 0.06
T2	dark	Deep	Cisco	0.09 \pm 0.01	0.08 \pm 0.02	0.00	0.05 \pm 0.01	0.69 \pm 0.02	0.08 \pm 0.01	0.02 \pm 0.01
T2	dark	Deep	Rainbow smelt	0.04 \pm 0.02	0.01 \pm 0.01	0.00	0.13 \pm 0.04	0.68 \pm 0.07	0.01 \pm 0.01	0.12 \pm 0.04
T1	daylight	Deep	Rainbow smelt	0.32 \pm 0.09	0.05 \pm 0.02	0.00	0.24 \pm 0.06	0.33 \pm 0.07	0.05 \pm 0.01	0.02 \pm 0.01
T2	daylight	Deep	Rainbow smelt	0.02 \pm 0.01	0.01 \pm 0.01	0.00	0.12 \pm 0.02	0.73 \pm 0.03	0.08 \pm 0.01	0.02 \pm 0.01
T3	daylight	Deep	Rainbow smelt	0.12 \pm 0.05	0.02 \pm 0.01	0.00	0.21 \pm 0.06	0.55 \pm 0.08	0.04 \pm 0.01	0.06 \pm 0.02
T3	dark	Deep	Rainbow smelt	0.31 \pm 0.08	0.02 \pm 0.01	0.00	0.12 \pm 0.03	0.43 \pm 0.09	0.05 \pm 0.02	0.07 \pm 0.02
T3	dark	Deep	Cisco	0.07 \pm 0.02	0.07 \pm 0.02	0.00	0.05 \pm 0.02	0.72 \pm 0.05	0.07 \pm 0.02	0.01 \pm 0.01

Table 3.4. Summary trawls where smelt and cisco were concurrently caught onboard the M.V. *Namao*. Date, relative trawl depth, site depth and number and fork length size range of rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedi*) collected are included. The two summer 2011 stations represent dark trawls, whereas all other trawls were performed during daylight.

	Station	Date	Relative trawl depth	Site depth (m)	Number of smelt collected	Number of cisco collected	Smelt fork length range (mm)	Cisco fork length range (mm)
Fall 2010	19	01-Oct-10	Shallow	17.37	30	20	96 - 114	126 - 158
	20	01-Oct-10	Shallow	9.14	30	8	91 - 129	128 - 144
	345	04-Oct-10	Shallow	15.85	25	31	71 - 123	120 - 142
	21	07-Oct-10	Shallow	16.76	20	26	84 - 104	126 - 146
Summer 2011	45	08-Oct-10	Deep	13.41	29	30	76 - 110	94 - 152
	72	26-Jul-11	Deep	14.94	30	30	93 - 125	138 - 175
	73	26-Jul-11	Deep	15.24	30	30	90 - 176	118 - 176

Table 3.5. Mean Schoener's Index (\pm SE) for six prey groups between rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) in the North Basin of Lake Winnipeg.

		<i>Schoener's Index (\pm SE)</i>					
	Station	Calanoids	Cyclopoids	<i>Daphnia</i> spp.	<i>Eubosmina</i>	<i>Bosmina</i>	<i>Other</i>
Fall 2010	19	$0.97 \pm 9.3 \times 10^{-3}$	0.93 ± 0.01	0.96 ± 0.01	0.97 ± 0.01	$0.99 \pm 4.0 \times 10^{-4}$	$0.99 \pm 9.2 \times 10^{-4}$
	20	0.97 ± 0.01	0.84 ± 0.04	$0.78 \pm 2.9 \times 10^{-3}$	0.84 ± 0.04	$0.99 \pm 2.2 \times 10^{-3}$	$0.99 \pm 1.3 \times 10^{-3}$
	34S	$0.99 \pm 2.1 \times 10^{-3}$	0.98 ± 0.01	$0.99 \pm 3.3 \times 10^{-3}$	0.94 ± 0.05	$0.99 \pm 2.3 \times 10^{-3}$	1.00 ± 0.00
	21	$0.98 \pm 4.8 \times 10^{-3}$	0.93 ± 0.01	0.97 ± 0.01	0.95 ± 0.01	$0.99 \pm 7.5 \times 10^{-4}$	$0.99 \pm 4.6 \times 10^{-4}$
	45	0.95 ± 0.01	0.92 ± 0.02	0.90 ± 0.02	0.94 ± 0.01	$0.99 \pm 2.7 \times 10^{-3}$	$0.99 \pm 4.8 \times 10^{-3}$
	Average	$0.97 \pm 4.2 \times 10^{-3}$	0.92 ± 0.01	0.96 ± 0.01	0.93 ± 0.01	$0.99 \pm 9.9 \times 10^{-4}$	$0.99 \pm 1.1 \times 10^{-3}$
Summer 2011	T2	$0.97 \pm 4.4 \times 10^{-3}$	0.96 ± 0.01	0.95 ± 0.02	0.91 ± 0.02	0.97 ± 0.01	0.94 ± 0.02
	T3	0.86 ± 0.04	0.97 ± 0.01	0.96 ± 0.01	0.84 ± 0.04	0.97 ± 0.01	0.97 ± 0.01
	Average	0.91 ± 0.02	0.97 ± 0.01	0.95 ± 0.01	0.87 ± 0.03	$0.97 \pm 4.1 \times 10^{-3}$	0.95 ± 0.01

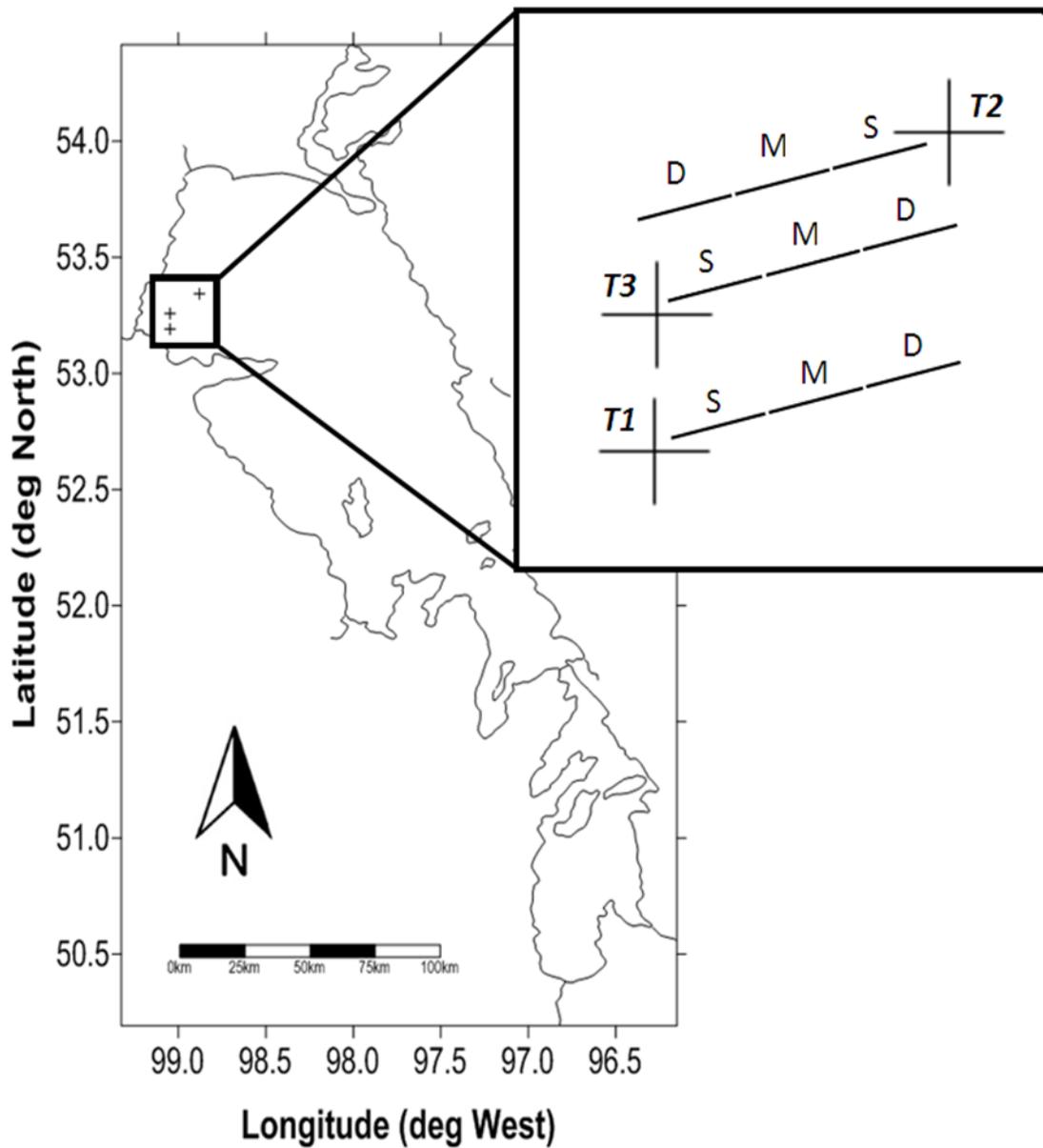


Figure 3.1. Schematic of day-night trawling study design during 25-26 July, 2011 onboard the M.V. *Namao* in the North Basin of Lake Winnipeg. Enlarged section depicts the sampling area: numbered crosses indicate stations, lines represent trawls, each labelled with its relative depth (S -shallow, M - mid and D - deep).

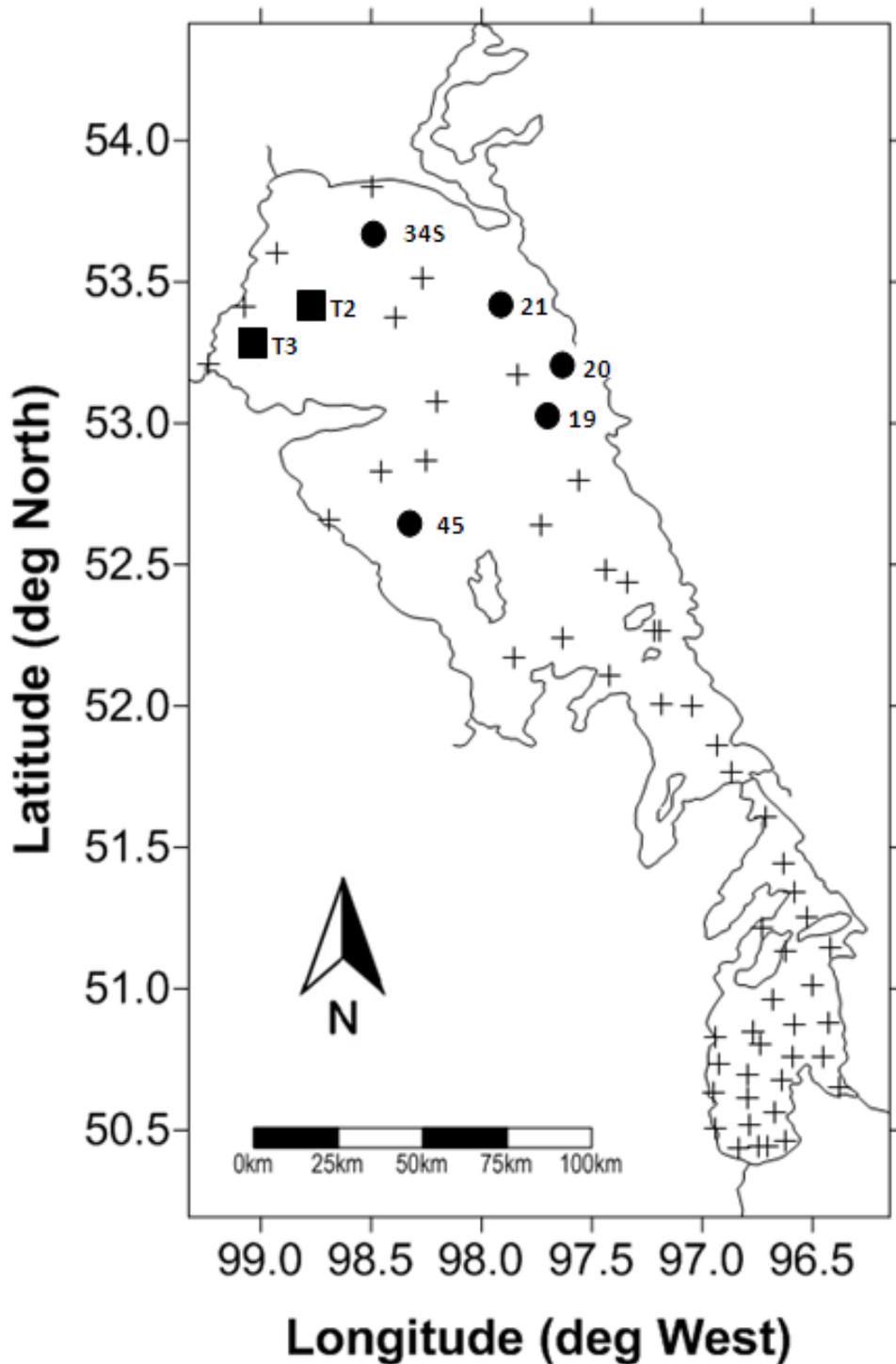


Figure 3.2. Map of Lake Winnipeg with crosses indicating all long-term monitoring stations where fish trawling occurred over 2010 and 2011. Labeled circles (fall 2010) and squares (summer 2011) indicate stations where both rainbow smelt (*Osmerus mordax*) and cisco (*Coregonus artedii*) were concurrently caught. Summer 2011 stations are consistent with those presented in daylight-dark sampling data.

2.6 Appendix

2.6.1 Daylight-dark sampling protocol

Objectives:

- a) to compare trawl catches from two diel periods (day and night) to see if there are differences in catch composition or fish biomass estimates
- b) to describe how environmental variation influences fish distribution (vertically, horizontally and within diurnal period)

Daytime samples:

- 1) begin data collection at 10:00am

North Basin:

July 26, in Grand Rapids Sunrise: 5:44 Sunset: 21:44, noon = 13:44, civil twilight = 5:00

South Basin:

Aug. 2, in Winnipeg Sunrise: 5:59 Sunset: 21:09, noon = 13:35, civil twilight = 5:22

Note: times of sunrise and sunset from website:

<http://www.sunrisesunset.com/calendar.asp>

- 2) On arriving at site (minimum 8 m depth, soft bottom not necessary if no bottom trawls) collect light (PAR) profile, temperature profile, oxygen profile (dissolved oxygen (mg/L) & %sat), conductivity profile and turbidity (NTU) profile at 1m intervals from surface to bottom. Also record lake depth, lat/longs, Secchi disc depth, and cloud cover when arrive at site.

- 3) Conduct 30 minute surface tow with beam trawl, as normally would **except** for ship fork lengths and weights, and ship bulk weights – bag and freeze catch instead

- Record unique number for Trawl # - something like D-1 for Day trawl # 1, N-1 for Night trawl #1
- Record trawl type (surface/mid/deep) and line out (if applicable)
- Record trawl as normally would: mark start time, start waypoint, trip odometer, log track, mark end waypoint, and end time, **also record site (1, 2 or 3)**
- Process catch as normally would except for ship lengths and weights
- Record in trawl log book information from ships log usually record: depth of lake where trawl went into water, speed of boat, wind speed and direction, air temperature and water temperature

- 4) Conduct 30 minute mid-water tow with beam trawl (deploy at 1/2 depth of the water column), as normally would **except** for ship fork lengths and weights, and ship bulk weights – bag and freeze catch

- 5) Conduct 30 minute deep trawl as normally would **except** for ship fork lengths and weights, and ship bulk weights – bag and freeze catch

- 6) Repeat the process, beginning with point 2, until 3 sets of collections of all variables has been made. Return to start point (W2) and wait for darkness to begin sampling again, so that trawl depth kept consistent within a site, between day and night.

Night collections should begin no earlier than 60 minutes after full sunset (sun's disk entirely drops below the horizon), so night sampling in north basin can begin at 23:00 (check time sun's disk entirely drops below the horizon), south basin 22:30, night work should be done by civil twilight.

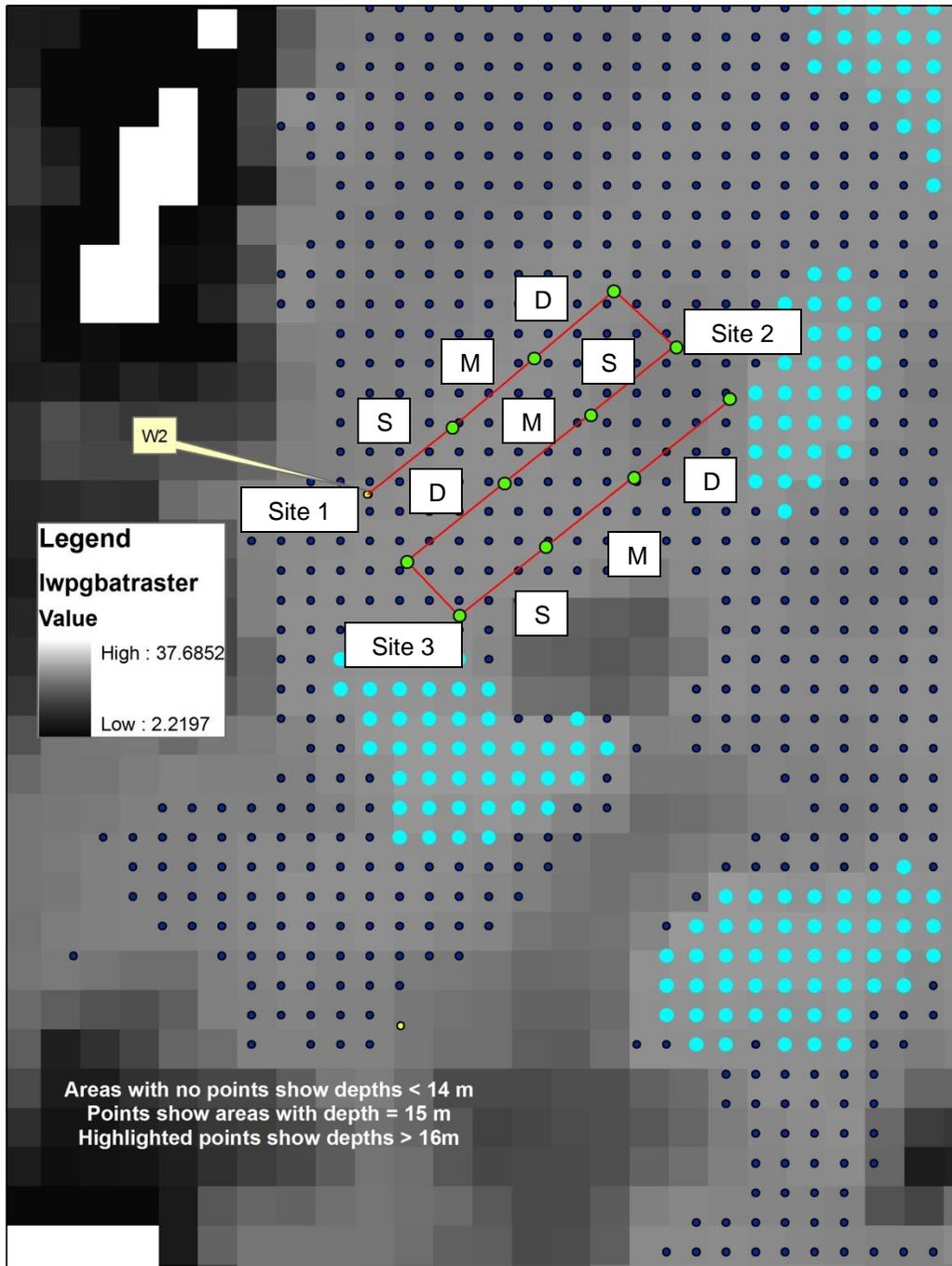
Cautionary notes about working at night:

- safety risk to working at night due to less than ideal lighting conditions
- easier to get feet caught up in a rope hidden by a shadow
- depth perception is not as precise
- when a trawl is retrieved it will be hard to see the edge hidden in the shadow of the hull until it is literally within a few inches or feet of the deck
- advisable to have all persons on deck equipped with some sort of life preserver
- if there's light rain and everything looks shiny under the lights that will make things even more complicated
- simple things that are routinely and easily done during daylight become a lot more challenging under these conditions
- need to keep things as quick, clean and as simple as possible

Especially for the night trawls, it is possible that catches will be MUCH higher than staff and crew normally deal with (up to 10 fold increase). It is possible that shorter trawls than suggested will be required at night. Will have to be assessed on the water. Modifications to trawl protocol may be necessary as you see what it's like to work at night (light conditions, as people get increasingly tired), and when you see what trawl catches are like.

It's Brian's preference to see entire catch from each trawl bagged and frozen, for simplicity and safety especially when working at night. If processing trawl regular way (euthanizing and fixing walleye and sauger, sub-sampling trawls for diet studies) is too difficult, **bag and freeze catch**

North basin proposed sites (S = surface trawl, M = midwater trawl, D = deepwater trawl):



South Basin site considerations:

- would like to fish “deepwater” trawls (in the past, deepwater trawls fished in SB near sites 60, 10S, 37S, 6, 60C, 61)
- would like to fish deep trawl roughly from depth of about 6m (19.7ft) to 9m (29.5ft) in water column, so need spot with about 11 (36ft) or 12 (39.4ft) of water
- need an area large enough for three transects (surface, mid, and deep trawls), depending on trawl tow duration, could be an area as large as roughly 7km x 4km
- use equation to calculate how much line to let out for deep trawl in north basin, to select standard amount of line to let out for “deep” trawls in south basin (use marked line)
- for midwater trawls, let out 7m of line, for “deep” trawls, let out 13.5m of line.

For Mid Water Trawls:

$$\text{Length of Line} = \text{Total Depth} - 3 \text{ meters}$$

MID

Depth (ft)	Depth (m)	Line (m)
30	9.1	6
33	10.1	7
36	11.0	8
39	11.9	9
42	12.8	10
45	13.7	11
48	14.6	12
51	15.5	13
54	16.5	14
57	17.4	14
60	18.3	15

For Deep Water Trawls: Length of Line = (2 X Total Depth) - 5 meters

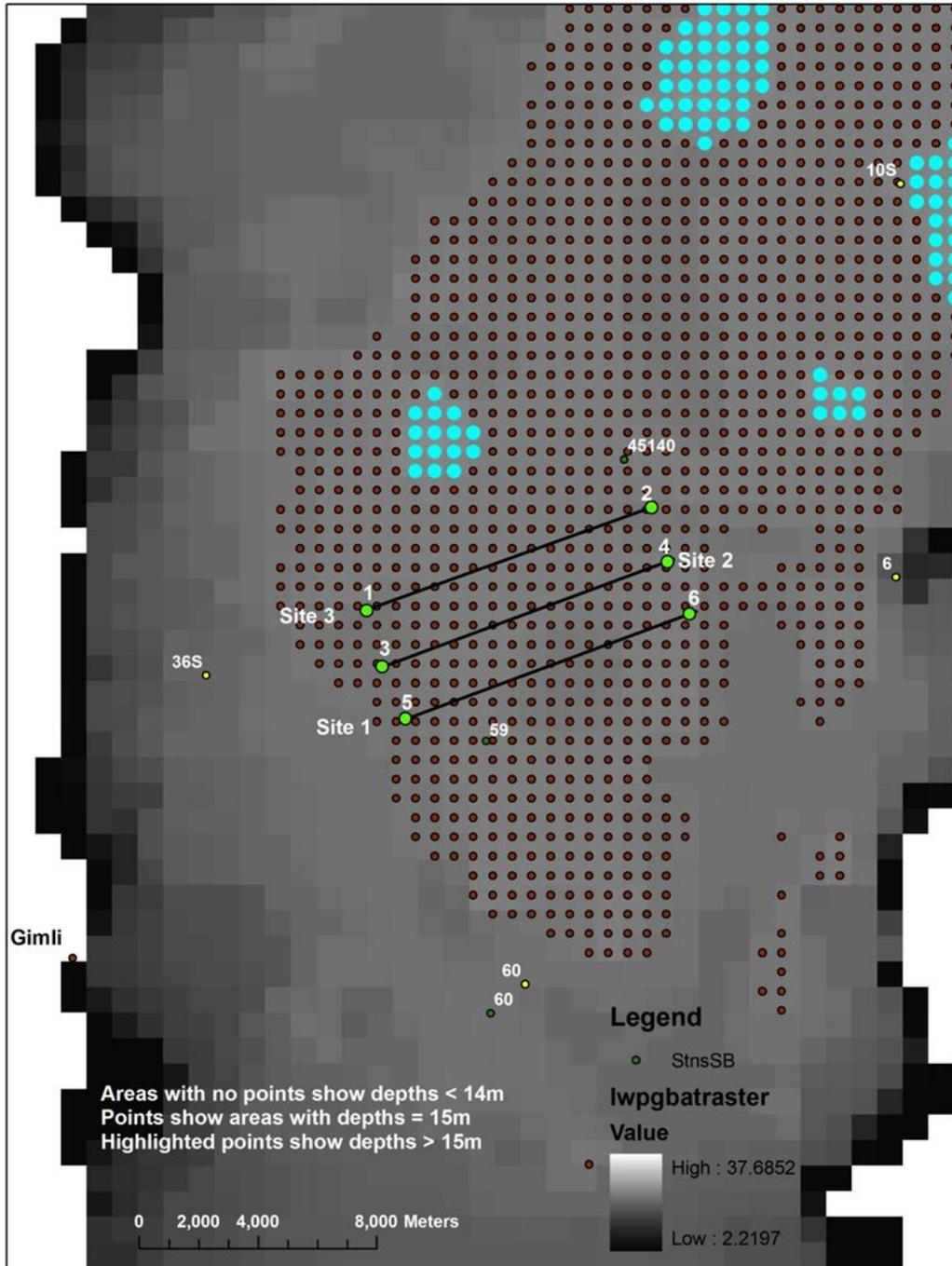
DEEP

Depth (ft)	Depth (m)	Line (m)
30	9.1	13
31.5	9.6	14
33	10.1	15
34.5	10.5	16
36	11.0	17
37.5	11.4	18
39	11.9	19

Notes about sites:

- minimum 8 m depth (soft bottom not necessary if no bottom trawls)
- keep lake depth as consistent as possible among sites within north basin and among sites within south basin, so that sampling same depth strata (i.e. about 15m in NB, 12m in SB, if possible, or deepest possible for SB “deep” trawls)
- in north basin, commence sampling at stn W2
- stations where lots of fish caught in trawls near Grand Rapids in previous years: 2004 – near stn. W2/25S (south east side of Selkirk Island), 23ES, 23S, 39 (all depths > 10m in 2007 to 2009), and 28 (9m depth summer 2009)
- stations where lots of fish and lots of species of fish caught in trawls in South Basin in previous years: stn. **60** (9.5-10m depth), 36S (9.5m depth), 11, 10S, 6 (stns 11, 10S and 6 - all about 10m depth)
(Stns bottom trawled spring 2010: 37S, W10, 57, 59, **60**)

Map shows sampling sites as well as stations nearby where most species caught in trawls were caught in previous years (except stn 59) and fish densities were high. Map shows deeper areas of south basin



CHAPTER 4. Synthesis

In this study I found that when considered in spatially distinct populations, rainbow smelt (*Osmerus mordax*) in the North Basin and cisco (*Coregonus artedi*) in the South Basin show similar seasonal dietary preferences. Although both species face different environmental conditions in their separate basins, both smelt and cisco seem to base their diet on energetic quality of prey, shifting from preference of low energetic quality copepods during times of low zooplankton densities to large-bodied high energetic quality cladocerans in times of higher zooplankton densities. High dietary overlap suggests that each species is filling a similar dietary niche in their given basin. When the two species were considered within areas of direct spatial overlap in the North Basin, there also was high dietary overlap, suggesting that both smelt and cisco utilize the same dietary niche even when found together in the North Basin. They appeared, however, to be distributed differently in the water column, with cisco more associated with bottom waters.

The daylight-dark sampling program executed during this study revealed a deficiency in the existing forage fish sampling program. As current sampling protocols include only the pelagic zone (i.e. 1-4 m off the bottom to surface) during daylight, fish residing near the bottom of the lake during the day are not adequately sampled. With increased effort placed on pelagic dark and daylight bottom trawling, a more comprehensive understanding of the composition and distribution of the fish community in the North Basin will be possible. Specifically, this will further clarify the abundance of cisco in the North Basin and, thus, the spatial overlap of smelt and other native zooplanktivores throughout the lake. This study raises the question as to the process

through which the current distribution of these zooplanktivores arose, at least in the pelagic zone. Without historical zooplanktivore abundances in the North Basin, it is unclear whether the invasion of smelt caused extirpation or niche shifts in cisco and other native species, or if the lake was productive enough to support the addition of a non-indigenous species without much change to the native fish community. Insufficient evidence is available to describe a pelagic distribution of cisco in the North Basin, but it is noteworthy that cisco were routinely harvested by commercial fishers in gill nets in the 1950s (Hewson 1959a; Hewson 1959b) and seen in stomach contents of other fish (Hewson 1955). Also, other species of cisco (e.g. *Leucichthys zenithicus*, *Leucichthys nigripinnis*, *Leucichthys nipigon*) were identified historically but have since not been found (Bajkov 1930). In other lakes where cisco were present prior to the invasion of rainbow smelt, after invasion rainbow smelt often fed directly on larval cisco, causing cisco population crashes (Hrabik *et al.* 1998; Gorman 2007). In the absence of more recent pre-smelt invasion forage fish community data, it is tempting to speculate that invasive rainbow smelt may have led to the demise of these other species of cisco, with only one species, *Coregonus ardeti*, remaining extant, occupying less optimal habitat in the lake. Only further sampling of the forage fish communities in the entire lake will permit assessment of the ultimate impact of the invasion of the non-indigenous rainbow smelt.

My findings suggest that rainbow smelt are not having as strong an impact on the zooplankton community as in other invaded lakes. Although rainbow smelt show dietary selectivity and size selection, the electivity values are lower and more variable than those observed in other non-native smelt populations (e.g. Urban and Brandt 1993; Hrabik *et*

al. 1998; Pothoven *et al.* 2009). Many of the changes in zooplankton composition since smelt invasion instead can be correlated with the large influx of nutrients in the past decades (Kamada 2012). This nutrient loading may be contributing to a “bottom-up” effect that creates a sufficiently productive environment to support all zooplanktivores, including the large numbers of invasive smelt, and maintain the zooplankton community.

This particular population of smelt may be experiencing reduced recruitment in relation to other similar populations, as a result of Lake Winnipeg’s unique characteristics (Franzin *et al.* 1994). This interpretation is consistent with the findings of this study. The main factors that seem to restrict smelt distribution include lake depth, lake area and turbidity (Mercado-Silva *et al.* 2006). The large surface area of Lake Winnipeg suggests this lake provides ideal habitat for smelt; however, it is relatively shallow compared to other similarly sized water bodies, such as the Laurentian Great Lakes, including Lake Erie (Patalas and Salki 1992). This leads to elevated water temperature in Lake Winnipeg in comparison to similar sized lakes with greater mean depth. The mean surface water temperature during the summer in North Basin from 1999-2007 was 19.7°C, with little evidence of persistent thermal stratification (McCullough and Lévesque 2011). Temperature preference of adult rainbow smelt in the field is variable, but ranges from 6°C-16°C, as summarized by Simonin (2010). Also, in other invaded lakes such as Lake Oahe (Burczynski *et al.* 1987) and Lake Champlain (Parker Stetter *et al.* 2006), smelt are concentrated in the cooler waters (5-14°C) of the lower metalimnion and hypolimnion. Thermal habitat quality seems to be a major driver of the success of invasive populations of rainbow smelt, to the point that it has been suggested that manual destratification of Crystal Lake, Wisconsin would result in the

eradication of the non-indigenous population of rainbow smelt, through increased water temperature and the elimination of optimal thermal habitat (Gaeta *et al.* 2012). For smelt, a species that shows preference to cooler and deeper waters, the difference in inter-basin smelt distribution in Lake Winnipeg shows densities concentrated almost exclusively in the coolest, deepest and clearest parts of the lake (Lumb *et al.* 2012). Despite this, Lake Winnipeg's mean summer temperature is above what is predicted to be optimal for smelt.

Another important factor that may be limiting smelt success is turbidity, as Lake Winnipeg is an extremely turbid lake when compared to other invaded lakes. The average summer Secchi depth in the North Basin of Lake Winnipeg from 1999-2007 was 1.4 m (McCullough and Léveque 2011). Secchi depths in lakes where smelt have had a large impact, such as the Laurentian Great Lakes: Lake Erie (4.0 - 6.0 m), Lake Ontario (4.0 – 5.0 m) and Lake Huron (7.0 – 8.0 m) (Dobiesz and Lester 2009) as well as other oligotrophic lakes such as Crystal and Sparkling Lakes in Wisconsin (6.0 m; Beisner *et al.* 2003) represent higher water clarity habitats than those in Lake Winnipeg. Although it has been hypothesized that turbidity may facilitate dietary selectivity in zooplanktivores as a consequence of decreased vulnerability to piscivores (Abrahams and Kattenfeld 1997; DeRobertis *et al.* 2003), it has also been suggested that high turbidity will result in increased search time for zooplanktivores and a possible lower energetic quality diet (Liu and Uiblein 1996; De Robertis *et al.* 2003).

Other evidence that Lake Winnipeg may not be optimal habitat for smelt relates to the mean size of rainbow smelt found in the lake. Landlocked populations of rainbow smelt commonly grow to 150-200 mm in other systems (Scott and Crossman 1973) but fish rarely reach 150 mm in Lake Winnipeg. Smaller fish will be limited in the prey types

and sizes they can ingest due to smaller gape size and, thus, may show reduced dietary specialization (Werner and Gilliam 1984; Hambright and Hall 1992). This may explain the reduced dietary selectivity when compared to other lake systems (e.g. Urban and Brandt 1993; Hrabik *et al.* 1998; Pothoven *et al.* 2009). Finally, densities of smelt are lower in Lake Winnipeg than in other invaded lakes. Although the units of measurement are not directly comparable, in other invasive populations such as Lake Champlain (1.2 fish/m²; Stritzel Thomson *et al.* 2011), Lake Michigan (2010: 0.17 kg/ha, 24 fish/ha; 2011: 0.12 kg/ha, 13 fish/ha; Madenjian *et al.* 2012), Lake Huron (5.0 fish/ha; Schaeffer *et al.* 2012) and Lake Superior (up to 3.0 kg/ha; Gorman 2007), smelt densities are higher than those observed in Lake Winnipeg over the past decade (0.001-0.003 kg/1000 m³; Lumb *et al.* 2012). As they may experience a lower quality habitat than other native zooplanktivores (i.e. cisco), this may leave smelt more susceptible to piscivore predation. In the North Basin, smelt is the predominant prey for walleye and sauger (Sheppard 2010). Alternatively, it is possible that the high predation pressure may be correlated with the lower maximum sizes and densities of smelt. Walleye and sauger are adapted to be more active in low-light conditions, possibly giving them an advantage over this zooplanktivore in the low transparency conditions present in Lake Winnipeg (Ali and Anctil 1977; Ryder 1977; Braekevelt *et al.* 1989).

This study has described a non-indigenous population of rainbow smelt that may have a weaker impact than in other lakes where they have become established. No dramatic disruptions in either the zooplankton prey or native zooplanktivore community is predicted with the continued presence of smelt in Lake Winnipeg. Further work incorporating bioenergetics modeling programs would be advantageous to investigate this

prediction. The future use of stable isotope analysis of fish muscle tissue could also provide potential confirmation to the interpretations of this study. To test whether smelt have had minimal impact on the zooplankton community, it will be necessary to examine archived zooplankton samples (2000-2012) in parallel with smelt invasion timeline, with particular emphasis on long-term temporal changes in mean body size of preferred prey groups. As no evidence of piscivory or consumption of eggs of other fish during the open-water seasons was observed in this study, investigation of smelt diet during winter could be revealing when there would be low zooplankton abundance and potential exposure to coregonid (i.e. cisco, lake whitefish) eggs laid prior to ice formation (Scott and Crossman 1998). Although pre-smelt invasion biotic data would be ideal in the consideration of the ecological impact of this non-indigenous species, this study has ultimately filled an important knowledge gap in the understanding of species interactions in the unique and economically important food web of Lake Winnipeg.

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