

Spatial and seasonal variation in diet, growth and condition of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye (*Sander vitreus*) in Lake Winnipeg, Manitoba

By

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Abstract

Lake Winnipeg has the second largest walleye fishery in North America. The North and South Basins of the lake differ in many ways, e.g. water temperature, turbidity, and fish community. The study objectives were to determine if (a) growth, condition or diet of walleye, sauger or dwarf walleye differed between basins, (b) among seasons, and (c) whether the invasive rainbow smelt are associated with these differences. Walleye, sauger and dwarf walleye were caught using gill-nets and analysed for growth, condition and diet in all seasons. Walleye and sauger in the North Basin showed higher growth rates and condition than in the South Basin. Diet in the South Basin had more diverse species composition, whereas in the North Basin, the diet consisted almost entirely of rainbow smelt. Some seasonal variation was also documented and the impact of rainbow smelt seems to be positive for these piscivorous fish in Lake Winnipeg.

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Chapter 1: General Introduction

Animals consume prey in a way that maximizes their energy intake while minimizing energy expenditure, resulting in enhanced fitness (MacArthur and Pianka 1966). The net profitability of a prey item is determined by the amount of energy ingested and expended while searching for and handling the prey item (MacArthur and Pianka 1966; Estabrook and Dunham 1976). Handling involves the pursuit, capture and ingestion of a prey item, after which the predator can resume searching for its next prey item (Estabrook and Dunham 1976). Prey characteristics such as morphology, size and behaviour influence the time and energy spent handling, while prey density influences search time (Breck 1993). When prey density is high, foraging theory predicts that predators will become specialists, where only one or two of the most energetically profitable prey types will be incorporated into the diet (Pulliam 1974). In contrast, predators are predicted to become generalists when prey density is low, incorporating many prey types into the diet often in similar proportions to their abundance in the environment (Pulliam 1974). Other factors influencing the switch between generalist and specialist foraging strategies are predation risk, starvation probability (e.g. amount of energy stores), and competitor density (Caraco 1981; Partridge and Green 1985; Magnhagen and Magurran 2008).

In the context of foraging theory, poikilothermic predators, including most fishes, have different foraging behaviour relative to homeothermic predators as a consequence of the direct influence of environmental temperature on internal biochemical processes, such as metabolism (Huh et al. 1976; Quist et al. 2002). For this reason, fish will adjust their body temperature by occupying different thermal habitats, which will in turn influence

rates of digestion and growth. Many piscivorous fishes in north temperate zone lakes consume only a few prey items in a day and, thus, search time may be more important than handling time in determining the net profitability of prey types because few prey are handled (Breck 1993). Many prey characteristics influence the net energetic profitability of different prey types, including prey length, weight, morphology, behaviour and energy density, because of their influence on search and handling time (Knight et al. 1984; Breck 1993). According to foraging theory, diets consisting of fewer large prey (length, weight), and/or more energy dense prey (i.e. calories per gram), are more energetically profitable relative to many small prey, because the predator maximizes energy consumption while minimizing energy expenditure to search and handle fewer prey items (Breck 1993; Kaufman et al. 2009). Larger prey usually swim faster which increases their conspicuousness and decreases the time and energy spent searching (Breck 1993). Although increased prey length and weight can decrease the number of prey required, there is a threshold at which the prey will be too large to ingest, typically dictated by gape limitations of the predator, as well as other physical constraints (Knight et al. 1984; Einfalt and Wahl 1997; Porath and Peters 1997; Little et al. 1998; Bur et al. 2008). A prey item that is within the physical constraints of a piscivorous fish is one with soft fin rays and a fusiform body (or an easily crushed broad body) that occurs in the area of the water that the predator occupies and stays within a length and/or body depth that is consumable for the predator (Hoyle and Keast 1987; Hartman and Margraf 1992; Einfalt and Wahl 1997; Quist et al. 2002).

Abiotic factors, such as turbidity and light levels, can also affect the net energy intake of a visual predator who must first encounter and identify prey to determine whether it

will be eaten (Breck 1993; De Robertis et al. 2003). High turbidity can impair the visual acuity and contrast of potential prey for a predator, which can decrease the rate at which fish pursue prey and the number of successful captures a predator has (Vineyard and O'Brien 1976; Gardner 1981; Barrett et al. 1992; Breck 1993; De Robertis et al. 2003). For example, prey intake rates by rainbow trout (*Oncorhynchus mykiss*) and other piscivores on salmon (*Oncorhynchus* spp.) declined with increased turbidity under laboratory and field conditions (Ginetz and Larkin 1976; Gregory and Levings 1998). Alternatively, Abrahams and Kattenfield (1997) found that prey capture rates of a piscivorous predator, yellow perch (*Perca flavescens*), did not change with increased turbidity; however, this could be attributed to less effective anti-predator behaviour of the prey with increased turbidity. Piscivorous predators may have minimal visual impairment relative to planktivores when foraging in turbid waters (De Robertis et al. 2003). For instance, laboratory experiments with walleye (*Sander vitreus*) showed that prey detection and capture was not altered under high levels of turbidity, likely a consequence of the presence of *tapetum lucidum* in their retina which increases their ability to see in highly turbid water (Vandenbyllaardt et al. 1991). The *tapetum lucidum*, also possessed by sauger (*Sander canadensis*; Ali and Ancil 1977), is apparently not fully developed in walleye and sauger during their juvenile, zooplanktivorous years but becomes fully developed during their switch to piscivory (Braekevelt et al. 1989).

There are many methods for determining dietary composition of animals, including stable isotopes of various tissue types and gut content analysis. Stable isotopes are a popular method as they can determine dietary composition over the long-term, depending on the tissue chosen for analysis. Stable isotopes, however, cannot determine the propor-

tion of the diet made up of different prey items with similar isotopic values, while gut contents can. Often, hard calcified objects, such as otoliths, in the gut contents of piscivores are used to identify prey items. Otoliths are composed of calcium carbonate and there are three pairs (sagittae, lapilli and asteriscii) in the inner ear canals of the skull of a fish. The structure and shape of sagittae otoliths are species-specific, allowing the identification of each prey item consumed by a predator (Jobling and Breiby 1986; Campana and Thorrold 2001). Otolith length, from post-rostrum to rostrum, can also be used to estimate the length of the fish consumed when an otolith length-fork length regression is developed (Jobling and Breiby 1986). Gut contents at any given time likely represent one feeding episode owing to the large amount of motion in the intestinal tract (Jobling and Breiby 1986) and, thus, otoliths found in a stomach can provide an estimate of meal size and feeding behaviour (Jobling and Breiby 1986). The identification of the type and size of prey consumed allows researchers to interpret in what proportion predators are consuming different prey types and sizes as well as the importance of those prey items. Empty stomachs can also provide information about foraging behaviour. For instance, there is a higher occurrence of empty stomachs in piscivores compared to fishes feeding on invertebrate prey (e.g. planktivores or benthivores; Paradis et al. 2008). Although gut contents provide short-term information about the diet and foraging behaviour, when paired with seasonal sampling, a longer-term picture can be assembled.

Dietary composition can result in variation in growth among individuals of a population (Werner and Hall 1974; Hartman and Margraf 1992; Jones et al. 1994; Einfalt and Wahl 1997; Porath et al. 2003; Cade et al. 2008; Kaufman et al. 2009). Growth is a cumulative measure of length at a particular age, and thus, growth is determined by ex-

amining relationships between age and length (Busacker et al. 1990). Otoliths can be used to determine the age of a fish by counting the annuli rings (Erickson 1983; Campana 2001; Campana and Thorrold 2001; Walsh et al. 2008). Growth of large piscivorous fishes tends to increase with increased densities of profitable prey such as bluegill (*Lepomis macrochirus*), cisco (*Coregonus artedi*), rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*) and gizzard shad (*Dorosoma cepedianum*; Swenson and Smith 1976; Knight et al. 1984; Hartman and Margraf 1992; Jones et al. 1994; Madenjian et al. 1996; Einfalt and Wahl 1997; Porath and Peters 1997; Porath et al. 2003; Hoxmeier et al. 2006; Cade et al. 2008; VanDeValk et al. 2008; Kaufman et al. 2009). Similar to other predators, piscivorous fishes show a functional response, whereby a higher proportion of individuals achieve maximum prey intake rates as prey densities increase (Holling 1959). This results in increased growth (Breck 1993), owing to lower time and energy searching for prey. Faster growing individuals achieve a larger size at a given age than slower growing individuals, giving them a competitive advantage during foraging and reproduction (Werner 1974; Hoxmeier et al. 2006; Kaufman et al. 2009).

Growth is also linked to condition for many piscivores in many systems, where increased growth is positively correlated with increased condition (Hartman and Margraf 2006; Lumb et al. 2007; VanDeValk et al. 2008; Vassilopoulou and Haralabous 2008). Condition is the net profitability of an animal's diet relates directly to the amount of energy stored in the body (VanDeValk et al. 2008). Generally, if two fish have the same body length but one weighs more than the other, the heavier fish is said to be in better condition (VanDeValk et al. 2008), and has more energy to allocate to reproduction or growth. Condition in fish can be measured using morphometric, bioenergetic, or bio-

chemical methods (McPherson et al. 2011). Morphometric measures include Fulton's Condition Factor (Kaufman et al. 2007), the relative weight index (Kaufman et al. 2007; VanDeValk et al. 2008), the adjusted relative weight index (Hansen and Nate 2005), and the relative condition index (Kaufman et al. 2007). Morphometric analyses have been criticized as not being direct measures of body condition because they measure the size or girth of the fish rather than energy reserves (McPherson et al. 2011). This is why morphometric analyses are often validated with another method of analyzing body condition (Hansen and Nate 2005; Kaufman et al. 2007; McPherson et al. 2011). Bioenergetic techniques include the liver condition index as well as measurement of mesenteric fat levels (McPherson et al. 2011). These techniques are useful in categorizing condition based on deposits of fat in specific areas and organs of a fish such as the liver or mesentery (McPherson et al. 2011). Biochemical techniques, including quantifying total muscle fatty acid and body lipid content analysis (Kaufman et al. 2007; McPherson et al. 2011), are used less often because they are expensive and time-consuming; however, they more accurately measure body condition because they directly measure fat or protein content of the fish (McPherson et al. 2011). The tissue used in a bioenergetic analysis will depend on the species in question because fat should be measured in the tissue where most is stored (Kaufman et al. 2007; McPherson et al. 2011).

Condition of fishes that live in north temperate regions varies with season, age, diet, as well as other factors in their environment such as fishing pressure. For instance, fish that spawn in the spring are usually in their peak condition during late summer and fall because they have been storing as much fat as possible after spawning to over-winter and spawn the next spring (Quist et al. 2002). During the winter, and particularly the

spring, fish condition drops because of lower food consumption in addition to energy reserves being allocated to gonadal development and spawning (Quist et al. 2002). Age may be an important variable because as fish age they deposit more body fat, i.e., better condition until senescence (Jobling 1994 IN VanDeValk et al. 2008). When profitable prey are abundant in the environment, increases in condition are often documented (Hartman and Margraf 1992; Knight and Vondracek 1993; Porath and Peters 1997). Some research has indicated that body condition of walleye could be used as an indicator of prey availability in that system (VanDeValk et al. 2008). Condition has been linked to the level of commercial and recreational fishing in a system (Kaufman et al. 2007). Individuals in more heavily exploited populations tend to be in better condition (have a higher body lipid content; Kaufman et al. 2007), possibly due to lower densities of predators and, thus, higher densities of prey per predator.

Study Species

In many ecosystems (e.g. riverine, estuarine, lake), walleye (*Sander vitreus*) and sauger (*Sander canadensis*) are top predators, often playing important roles in structuring food webs, and are target species for commercial and recreational fisheries. Sauger and walleye are closely related but there are a few distinguishing characteristics (Scott and Crossman 1998; Stewart and Watkinson 2004). Walleye lack black spots on the dorsal fin or scales on the cheeks whereas sauger have spotted fins and scaly cheeks (Stewart and Watkinson 2004). Walleye have a white tip on the anal and caudal fin whereas sauger do not (Stewart and Watkinson 2004). Both species show variation in their colour

which may be attributable to differences in habitat and body size (Scott and Crossman 1998; Stewart and Watkinson 2004). Sauger are usually dull brown or grey with large dark blotches on their sides (Scott and Crossman 1998; Stewart and Watkinson 2004). Walleye exist in two colour morphs, the yellow form and the greenback form (Stewart and Watkinson 2004). There is also a slow growing morphotype within the walleye species, called dwarf walleye, which is identified by examining the size of the fish at a particular age (Kaufman et al. 2007; Moles et al. 2010). These fish mature at a smaller size and have a smaller, more sloped head, shorter snout, and larger eyes (Moles et al. 2010).

Walleye and sauger differ in size with sauger reaching shorter lengths of 254-406 mm compared to walleye, which reach lengths of 350-500 mm (Scott and Crossman 1998; Stewart and Watkinson 2004). Normally, young-of-the-year walleye grow more quickly than sauger (Scott and Crossman 1998). Growth rates of walleye also appear to be higher in prairie lakes than those in Precambrian Shield lakes (Scott and Crossman 1998). Additionally, there are sex-based differential growth rates in walleye, as in many fish species, where females grow faster than males (Scott and Crossman 1998; Purchase et al. 2005; Kaufman et al. 2007; Madenjian et al. 2009).

Walleye mature between 2 and 5 years of age and roughly 200 mm in length (Henderson and Morgan 2002; Johnston et al. 2010). Sauger live until an average age of 7 years in the Lake of the Woods (Stewart and Watkinson 2004) and mature at 2 years of age (roughly 200 mm; Johnston et al. 2010). Walleye spawn when the ice begins to melt, which is mid-April to late May in north temperate regions, whereas sauger spawn in late May and early June (Scott and Crossman 1998; Stewart and Watkinson 2004; Gillenwater et al. 2006; Balon 1975; Jones et al. 2003; Manny et al. 2010).

Walleye are a pelagic species that tend to inhabit deep, cool, less turbid, offshore waters while sauger usually inhabit shallower, more turbid, nearshore waters (Stewart and Watkinson 2004). In Lake Winnipeg, walleye are often caught in trawls which are usually performed off-shore in pelagic water while fewer sauger are caught, which may be the result of them inhabiting nearshore, more benthic water (Pers. Obs.). Walleye are distributed in the water column according to temperature or turbidity in stratified lakes, but distribute evenly throughout the water column in unstratified lakes (Olson et al. 2007).

The diets of adult walleye and sauger are similar in most systems, with both being predominantly piscivorous (Scott and Crossman 1998). Sauger and walleye may show dietary overlap with other fishes in the same ecosystems, e.g. northern pike (*Esox lucius*), goldeye (*Hiodon alosoides*), yellow perch, smallmouth (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*), as well as lake whitefish (*Coregonus clupeaformis*; Scott and Crossman 1998). Walleye and sauger have been documented to feed on trout-perch (*Percopsis omiscomaycus*), young white bass (*Morone chrysops*), young freshwater drum (*Aplodinotus grunniens*), emerald shiner (*Notropis atherinoides*), young walleye, young sauger, young yellow perch, young burbot (*Lota lota*), sticklebacks (Gasterosteidae family) and other small fishes but they will also eat a number of invertebrates (Maloney and Johnson 1957; Priegel 1969; Parsons 1971; Forney 1974; Forney 1977a; Forney 1977b; Swenson 1977; Scott and Crossman 1998; Nielsen 1980; Frey 2003; Pierce et al. 2006; Madenjian et al. 2009). Seasonal dietary shifts have been documented for both walleye and sauger that generally show the consumption of mayfly larvae in spring and increased use of fish throughout the summer (emerald shiner particular-

ly in the summer) and fall (Parsons 1971; Hartman and Margraf 1992; Knight and Vondracek 1993; Quist et al. 2002; Frey 2003; Kaufman et al. 2009).

Cisco and rainbow smelt have been found to be important prey of walleye, particularly rainbow smelt, despite cisco providing a higher (2X) energetic gain (Jones et al. 1994; Kirn and LaBar 1996; Krueger and Hrabik 2005; Mercado-Silva et al. 2007; Bryan et al. 1996 ; Krueger and Hrabik 2005; Kaufman et al. 2009). The absence of cisco in walleye diets in some ecosystems (Jones et al. 1994; Kirn and LaBar 1996; Krueger and Hrabik 2005; Mercado-Silva et al. 2007) may be the result of walleye habitat overlapping more with smelt habitat than with cisco habitat during the summer months (Krueger and Hrabik 2005). In addition, walleye can ingest all length classes of smelt, whereas cisco quickly become too large for walleye to ingest (size refuge; Krueger and Hrabik 2005). Walleye can structure the composition of the prey community in their ecosystem by preying heavily on certain prey species, thus decreasing their abundance and potentially indirectly increasing the abundance of competing forage fish species. For example, increased predation pressure by walleye on rainbow smelt has caused declines in the overall abundance and size of smelt (Krueger and Hrabik 2005; Mercado-Silva et al. 2007; Walsh et al. 2008) as well as yellow perch in other ecosystems (Willms and Green 2007).

Gape-limitation determines the upper size range of prey that walleye and sauger can consume. The size of prey consumed by walleye ranges from 20-43% of its own body length (Parsons 1971; Knight et al. 1984; Einfalt and Wahl 1997; Porath and Peters 1997). Walleye swallow prey of a suitable size either caudally or laterally, unless the prey item has spines (Einfalt and Wahl 1997). If prey are ingested caudally, the predator may be using a pursuit foraging strategy. If prey are ingested laterally, the body depth and the

compressibility of the prey is likely more important than prey length in determining whether it is consumed (Einfalt and Wahl 1997). This means that deep-bodied prey types, such as cisco, reach a size that makes them difficult to ingest by walleye and sauger (Kaufman et al. 2009). Einfalt and Wahl (1997) found that walleye consumed prey with a body depth that was 5-9% of its own length. Fusiform (condensed) body shapes of some prey, such as emerald shiner and rainbow smelt, are easier for walleye and sauger to ingest (Hartman and Margraf 1992; Knight and Vondracek 1993); Einfalt and Wahl 1997).

The growth and condition of walleye and sauger vary with the productivity of the environment, prey availability and temperature (Stewart and Watkinson 2004). Condition of walleye also varies seasonally, as well as with the level of exploitation to which the population of fish are exposed (Quist et al. 2002; Kaufman et al. 2007; VanDeValk et al. 2008). Walleye and sauger are important species to the commercial and recreational fisheries throughout North America. The second largest inland commercial fishery in Canada is in Lake Winnipeg, Manitoba where walleye are the top species. The growth and condition of walleye in this lake is higher than in many other Canadian lakes (Kaufman et al. 2007; Moles et al. 2008).

Study Area

Lake Winnipeg is a north temperate lake that is eutrophic, turbid, rarely stratifies and has two distinct basins. The North Basin has a mean depth of 13.3 m, is less turbid (mean secchi depth: 1.2 ± 0.6 m), has lower nutrient inputs and is generally cooler (mean surface temperature: $15.22 \pm 3.54^{\circ}\text{C}$), whereas the South Basin has a mean depth of 9.7

m, is more turbid (mean secchi depth: $0.6 \pm 0.3\text{m}$) and is generally warmer (mean surface temperature: $17.03 \pm 4.50^\circ\text{C}$; Brunskill et al. 1980; Johnston et al. 2010; Table 1). There is also variation in the fish communities between basins. The major difference in the forage fish community is the presence of the invasive rainbow smelt in the North Basin and the native emerald shiner in the South Basin (Lumb et al. 2012). Rainbow smelt invaded the South basin of the lake in late 1990 and moved into the North basin. The introduction could be from one of two sources: direct introduction of live baitfish or via the English River System (Campbell et al. 1991; Franzin et al. 1994; Stuart et al. 2001). In terms of predator abundance, less is known. The dwarf morphotype of walleye seems to occur only in the South Basin and sauger seem to be more abundant in the South Basin (Johnston et al. 2010; Table 1). Differences in the commercial fishery also exist between basins. In the North Basin there is a larger minimum mesh size (108 mm) allowed for commercial harvest than in the South Basin (76 mm), where there is also higher fishing pressure and greater harvest (Johnston et al. 2010). The walleye in both basins of this lake are highly exploited compared to walleye in other systems (Kaufman et al. 2007). Overall, the second largest inland commercial fishery in Canada is based on this lake (Johnston et al. 2010), supporting high commercial landings ($\sim 4.5 \times 10^6$ kg of walleye and $\sim 2.5 \times 10^5$ kg of sauger in recent years; Brunskill et al. 1980; Kaufman et al. 2007; Moles et al. 2008; Johnston et al. 2010; Lumb et al. 2011). Additionally, the condition of walleye is among the highest reported (Kaufman et al. 2007; Moles et al. 2008).

There is relatively little known about Lake Winnipeg and the fishes that inhabit it. For example, only a few of the spawning grounds of walleye have been identified and to my knowledge sauger breeding grounds have yet to be identified (Johnston et al. 2010). It

is also unknown whether walleye move between basins (Backhouse-James and Docker 2012) or whether there are subpopulations that remain within certain parts of the lake (Watkinson and Gillis 2005). If individuals move between basins, this would potentially involve traveling large distances (Lake Winnipeg is 436 km in length; Brunskill 1980). This is possible, as sauger are reported to travel up to 161 km in the Mississippi River (Scott and Crossman 1998) and walleye are reported to travel 150 km or more between Lake Huron and Lake Erie (Todd and Haas 1993). Similarly, a tagging study in Lake Winnipeg revealed that walleye travel 200 km or more (half the length of the entire lake; Brunskill 1980; Walt Lysack, pers. comm. 2004 IN Watkinson and Gillis 2005).

In Lake Winnipeg, there are many native fish species that could constitute as prey for adult walleye and sauger. These species include yellow perch, shiner species, cisco, ninespine stickleback, burbot, sucker species, trout-perch, goldeye, walleye, sauger and lake whitefish (Scott and Crossman 1998; Olson et al. 2007). There are also invasive rainbow smelt and white bass that may provide important food sources for these top predators. Rainbow smelt invaded Lake Winnipeg in late 1990 and now almost exclusively inhabits the North Basin, possibly due to its preference for deep, cool, less turbid waters (Franzin et al. 1994). The potential prey in Lake Winnipeg all have various characteristics including size at maturity, morphology and behavior that will increase or decrease the search and/or handling time for walleye and sauger to (Table 2; Scott and Crossman 1998).

A few studies on walleye in Lake Winnipeg have provided evidence that the condition is high relative to walleye in other systems (Kaufman et al. 2007; Moles et al. 2008). One study documented the decline in sauger relative to walleye in the North Ba-

sin and the apparent exclusivity of dwarf walleye in the South Basin from 1979 to 2003 (Johnston et al. 2010). Johnston et al. (2010) determined that growth seemed to be higher in the North Basin; however, it was only significant for sauger not walleye. Johnson et al. (2010) also found increases in walleye and sauger condition from 1979 to 2003, which may be attributed to changes in nutrient loading, exploitation, temperature or prey type and availability (Johnston et al. 2010). Johnston et al. (2010) also noted that the influence of the rainbow smelt invasion on the growth and condition of walleye and sauger is unknown. The affect of rainbow smelt on these commercially important predators may be important for managing these species; therefore, the objective of this thesis is to provide more information that will help manage walleye, sauger and dwarf walleye in Lake Winnipeg, including the impact of rainbow smelt. Additionally it will provide a baseline for future invasions and other changes that the lake will likely experience.

Chapter Outline

The following chapter (Chapter 2) investigates predator-prey interactions of walleye and sauger in Lake Winnipeg. I investigated the dietary composition through gut content analysis of these piscivores in both basins of Lake Winnipeg. Owing to distinct ecological differences between the North and South Basins, I compared the dietary composition of both walleye and sauger between basins and among seasons in 2010-2011. In Chapter 3, I examined the variation in growth and condition of walleye and sauger between basins and among seasons (condition only) and theorized the potential role that dietary variations may be having. The possibility of differential growth and condition between basins

and among seasons being influenced by the dietary composition of walleye and sauger is of interest to the fishery for management purposes. In addition, differences in growth and condition of walleye and sauger between basins may suggest that basin-specific subpopulations of walleye and sauger exist in Lake Winnipeg. These topics and their influences on the fisheries management will be discussed in unison in the final chapter of this thesis (Chapter 4).

Table 1: Comparison of the South Basin and North Basin of Lake Winnipeg in regards to walleye and sauger abundance, along with their prey abundance and composition, turbidity, temperature, depth, surface area, volume and exploitation levels. Turbidity and temperature data were recorded as part of annual monitoring efforts by the Lake Winnipeg Research Consortium (LWRC) from late May to late October in 2010 and 2011. Walleye and sauger abundance from annual provincial monitoring is by catch per unit effort (number of fish per number of gill nets set) from 2009-2011. The asterisk (*) means that dwarf walleye were included in the estimate for walleye abundance.

Characteristic	South Basin	North Basin	References
Walleye abundance (CPUE)	50.4*	37.9	Manitoba Conservation and Water Stewardship, Fisheries Branch
Sauger abundance (CPUE)	94.1	6.87	Manitoba Conservation and Water Stewardship, Fisheries Branch
Dwarf Walleye abundance	Present	Absent	Johnston et al. 2010
Exploitation level	HIGHER	LOWER	Johnston et al. 2010
Forage fish abundance	~8 g/1000m ³	~3.5 g/1000m ³	Lumb et al. 2012
Most abundant forage fish	Emerald Shiner (3.9 g/1000m ³)	Rainbow Smelt (2.2 g/1000m ³)	Lumb et al. 2012
Mean turbidity (Secchi depth; m)	0.6 ± 0.3	1.2 ± 0.6	LWRC
Surface temperature range (°C)	6.62 - 25.13	8.73 - 22.56	LWRC
Mean (± SE) surface temperature (°C)	17.03 ± 4.50	15.22 ± 3.54	LWRC
Mean depth (m)	9.7	13.3	Brunskill 1980
Maximum depth (m)	19	14	Brunskill 1980
Surface area (km ²)	17,520	2,780	Brunskill 1980
Volume (km ³)	232.4	27.0	Brunskill 1980

Table 2: The potential prey species of walleye and sauger in Lake Winnipeg and their characteristics, including morphological traits (fin ray, body form), location in the water column, lake as well as schooling behaviour and maximum length.

Prey	Prey Latin Name	Fin Ray	Body Form	Water Column Location	Basin in L.Wpg.	Schooling or Solitary	Maximum Length (mm)
Cisco	<i>Coregonus artedi</i>	Soft	Broad	Mid-Deep Pelagic	Both	Schooling	353
Emerald Shiner	<i>Notropis atherinoides</i>	Soft	Fusiform	Surface Pelagic	South Basin	Schooling	103
Rainbow Smelt	<i>Osmerus mordax</i>	Soft	Fusiform	Mid-Deep Pelagic	North Basin	Schooling	203
Troutperch	<i>Percopsis omiscomaycus</i>	Soft	Broad	Demersal	Unknown	Unknown	102
Freshwater Drum	<i>Aplodinotus grunniens</i>	Spines	Broad	Demersal	Unknown	Unknown	508
Yellow Perch	<i>Perca flavescens</i>	Spines	Broad	Variable	Both	Both	254
White Bass	<i>Morone chrysops</i>	Spines	Broad	Variable	Both	Both	305
Walleye/Sauger	<i>Sander vitreus/ Sander canadensis</i>	Spines	Fusiform	Variable	Both	Both	508/406

Chapter 2: Diet of walleye and sauger and prey morphology

Introduction

In the context of foraging theory, an animal consumes prey in a way that maximizes its energy intake while minimizing its energy expenditure (i.e. net energy intake), resulting in enhanced fitness (Davies et al. 2012). This balance between energy consumed and energy expended determines the net profitability of a prey item (Davies et al. 2012). Energy expenditure includes energetic costs accrued while searching for and handling prey as well as digestibility (Estrabrook and Dunham 1976). Handling time is the amount of time required for a predator to pursue, capture and ingest a prey item before it can resume searching for its next food item (Estrabrook and Dunham 1976). Parameters such as prey morphology, size and behaviour influence handling time, whereas prey density primarily influences search time (Breck 1993). Many factors influence diet breadth, such as prey density (Kaiser and Hughes 1993), predator density (Partridge and Green 1985), competitor density (Partridge and Green 1985) and the probability of starvation (Caraco 1981; Magnhagen and Magurran 2008; Davies et al. 2012). For instance, when prey density is high, animals will often select one or two of the most energetically profitable prey types (specialist), but when prey density is low predators may incorporate many prey types into the diet (generalist), often in proportions similar to their abundance in the environment (Pulliam 1974). Often few species are incorporated into the diet (specialist) when the availability of a particular prey type is high (Knight et al. 1984).

For piscivorous fishes in north temperate areas, such as walleye (*Sander vitreus*) and sauger (*Sander canadensis*), search time may be more important than handling time in selecting prey items because they quite often consume only a few prey items per day (Breck 1993). Factors that can influence search time for these fishes include prey density (Pulliam 1974; Eggers 1978), abiotic environmental factors, as well as prey characteristics (Pulliam 1974; Eggers 1977; Eggers 1978; Eggers 1982; Breck 1993; Einfalt and Wahl 1997). Prey density will influence the rate at which the predator will encounter prey, with increased prey density resulting in less search time and more encounters with suitable prey (Werner 1974; Eggers 1977; Eggers 1978; Breck 1993). Although abiotic factors, such as turbidity and light levels, can influence the encounter rates of visually-feeding predators (Huh et al. 1976; Eggers 1977; Breck 1993; De Robertis et al. 2003), walleye and sauger have the capability of capturing prey in highly turbid waters because of the presence of *tapetum lucidum* in the retina of their eye (Ali and Ancil 1977; Swenson 1977; Vandenbyllaardt et al. 1991; Wahl 1994; Scott and Crossman 1998; Stewart and Watkinson 2004; Johnston et al. 2010). Additionally, certain characteristics of the prey may also influence search time, including size (length and body depth) as well as energy density (Pulliam 1974; Pulliam 1975; Eggers 1982; Breck 1993). For instance, predators can minimize the time spent searching by consuming fewer, more profitable prey (e.g. larger, high energy density) relative to many, less profitable prey (Breck 1993). Although it may be more energetically beneficial to consume larger prey, the prey size ingested ultimately will be constrained by gape limitations of the predator (Knight et al. 1984; Breck 1993; Einfalt and Wahl 1997; Porath and Peters 1997; Little et al. 1998; Bur et al. 2008).

Depending on the ecosystem investigated, walleye have been found to be both dietary generalists (MacLean and Magnuson 1977; Knight et al. 1984; Wahl 1994; Einfalt and Wahl 1997; Little et al. 1998; Hoxmeier et al. 2006; Madison and Wang 2006) and specialists (Krueger and Hrabik 2005; Mercado-Silva *et al.* 2007). In ecosystems where the planktivorous fish community includes high abundances of invasive rainbow smelt, as well as native cisco, bluegill, alewife or gizzard shad, walleye diets are primarily composed of these prey types (Swenson 1977; Hartman and Margraf 1992; Jones et al. 1994; Einfalt and Wahl 1997; Quist et al. 2002; Bur et al. 2008; Kaufman et al. 2009; Gamble et al. 2011). Alternately, when the planktivorous community is dominated by small forage fishes such as shiners (e.g. emerald shiners) with no larger prey, walleye tend to include many prey species in the diet (Parsons 1971; Knight et al. 1984; Einfalt and Wahl 1997). This varying dietary composition in turn influences the growth rates and condition of piscivore predators (Breck 1993; Einfalt and Wahl 1997; Hoxmeier et al. 2006). Bioenergetic models show that there is an increase in growth when predators eat small numbers of large prey (Breck 1993). In support, walleye that select large, energy dense prey, such as rainbow smelt and cisco, have been shown to have increased growth rates (Jones et al. 1994; Bryan et al. 1996; Kirn and LaBar 1996; Krueger and Hrabik 2005; Mercado-Silva et al. 2007; Kaufman et al. 2009).

Lake Winnipeg supports a large commercial fishery for walleye and sauger, bringing in roughly 48 million kilograms and roughly 142 million dollars to Manitoba every year (Johnston et al. 2010; Pers. Comm. Bill Galbraith). This lake is large by surface area (23,750 km²) but shallow (average 12 m), with two basins (Brunskill 1980). The North Basin is deeper (13.3 m), colder (surface: 15.22 ± 3.54 °C), with lower turbidity (secchi

depth: 1.2 ± 0.6 m) whereas the South Basin is shallower (9.7 m), warmer (surface: 17.03 ± 4.50 °C) and has higher turbidity (secchi depth: 0.6 ± 0.3 m; Brunskill 1980; see Table 1 in Chapter 1). Most of the walleye and sauger are landed in the South Basin and, thus, is more heavily exploited than the North Basin. The South Basin of the lake also has higher pelagic forage fish density than the North Basin (Lumb et al. 2012, see Table 1 in Chapter 1). There are six main forage fish species in the lake: emerald shiner, rainbow smelt, cisco, white bass, yellow perch and walleye (Lumb et al. 2012). Emerald shiner is the most abundant species in the lake and is almost exclusively found in the South Basin (emerald shiner: 3.9 g/1000 m³; all pelagic forage fishes: ~ 8 g/1000m³; Lumb et al. 2012; see Table 1 in Chapter 1). Rainbow smelt is the second most abundant species in the lake and almost exclusively found in the North Basin (rainbow smelt: 2.2 g/1000 m³; all pelagic forage fishes: ~ 3.5 g/1000m³), whereas the other four species can be found in both basins (Lumb et al. 2012; see Table 1 in Chapter 1). Because of sampling gear limitations, densities of species that are associated with bottom waters, such as troutperch and freshwater drum, are unknown (Lumb et al. 2012).

Objectives

The primary objective of this study was to compare the diet of walleye and sauger between the North and South Basins of Lake Winnipeg as well as across seasons to determine if diet may explain differences in the growth and condition of these fish, which was recently confirmed (see Chapter 3). The secondary goal was to provide the first baseline dietary information for these piscivorous species in Lake Winnipeg. First, I hypothesize that the dietary composition of walleye and sauger will differ between basins, be-

cause of the predominance of rainbow smelt in the North Basin and the predominance of emerald shiner in the South Basin (Lumb et al. 2012). Second, I hypothesize that the diet of walleye and sauger within each basin will be different, as these two species are known to occupy different habitats and dietary niches in other ecosystems (Swenson and Smith 1976; Swenson 1977). Finally, I hypothesize that the diet of each species will vary seasonally as a consequence of seasonal differences in the availability of prey items which has been observed in other lakes (Parsons 1971; Swenson 1977; Knight et al. 1984; Porath and Peters 1997; Little et al. 1998; Quist et al. 2002; Olson et al. 2007). To do this, I examined diets (using gut content analysis) separately for different species, sexes, sizes, ages and seasons. To understand dietary differences, prey species were collected to determine energy densities by bomb calorimetry and to develop otolith length – fork length and fork length-weight regressions. Using these regressions, I reconstructed the length, weight, and energy density of each prey item in the gut contents of walleye and sauger using otoliths. In addition, the first otolith catalogue was developed for prey species identification in Lake Winnipeg.

Methods and Materials

Field Sampling

Prey

Potential prey species of walleye and sauger (including cisco, rainbow smelt, yellow perch, freshwater drum, troutperch, young walleye and sauger, emerald shiner and white bass) were collected using the small-mesh size (25 mm) panel attached to the gill-

nets used to catch walleye and sauger and during trawling aboard the M.V. *Namao* in spring (late May-early June), summer (mid-July- early August) and fall (mid-September-early October). The number of fish captured in the small mesh gill-nets was usually small (< 30 of varying species) and, therefore, trawl samples were used to increase the sample size for each prey species. Trawls samples from a beam-trawl with 6mm mesh size at the cod-end was operated by Manitoba Conservation and Water Stewardship, Fisheries Branch for 30 minutes at varying depths (surface, mid or deep). The prey fish that were caught by trawl and gill-nets were immediately frozen on board ship and transported to the laboratory at the University of Manitoba where they remained frozen at -20°C until further analysis.

Predators

Walleye and sauger were collected by gill-netting and trawling in the North and South Basins of Lake Winnipeg during spring (May-June 2010 and 2011), summer (July-August 2010) and fall (September-October 2010 and 2011), whereas commercial fishers provided fish in the winter (March 2011) by gill-netting (76 mm mesh) through the ice. Trawls were conducted by Manitoba Conservation and Water Stewardship, Fisheries Branch at up to 65 stations (see Prey section for trawl details) on Lake Winnipeg from the M.V. *Namao*, owned and operated by the Lake Winnipeg Research Consortium (Figure 1). Up to 30 walleye and 30 sauger >200 mm fork length were sampled from individual trawls. Gill-netting was performed in up to four locations in the South Basin (Hecla Island, Victoria Beach, Gimli and Pine Dock) and up to seven locations in the North Basin (Berens River, George Island, Station 20, Warren's Landing, Eagle Island, Grand Rapids, and Station 43S), from a yawl deployed from the M.V. *Namao* (Figure 1). Multiple-panel

gill-nets of varying mesh sizes (25 – 127mm) were set perpendicular to the shore for 12 h overnight. Commercial fishers provided samples in the winter of 2010-2011 by using gill-nets deployed through the ice near Gimli, MB.

Up to 30 walleye and 30 sauger were randomly subsampled from the available catch at each location. The fork length (mm), round weight (wet weight or fresh weight; g; Kaufman et al. 2009), sex and maturity were measured immediately and recorded. The intestinal tract was excised and placed into a pre-labeled 250 mL plastic bottle, filled to one-third its volume with 70% ethanol. Samples were transported to the laboratory at the University of Manitoba for further analysis.

Laboratory Sampling

Prey – Baseline Information

Reference sets for whole prey fish, which were later used for the analysis of the prey from the gut contents of walleye, sauger and dwarf walleye, were identified to species and measured for fork length (mm) and weight (g). The sagittae otoliths were dissected from each fish, except for emerald shiner, and placed in a pre-labeled coin envelope to be catalogued. In the case of the emerald shiner, the lapilli and asterisci otoliths were used because the sagittae were difficult to find. Each pair of otoliths was photographed alongside a ruler using a camera attached to a dissecting microscope. Each otolith was measured from rostrum to post-rostrum using ImageJ (Version 1.4, National Institutes of Health, USA) to develop an otolith length-fork length regression for each prey species.

Whole prey fish were analyzed for energy density (also known as caloric content). Typically 5 fish were randomly selected per size class, per species, per season throughout

the lake. The size classes of each prey species were chosen based on the sizes available as well as the size at which they matured (Table 1). Individual fish were weighed, freeze-dried at -65°C for 48h and reweighed. The 5 fish per size class, species, and season were ground together in a new coffee grinder, carefully cleaned with ethanol after each sample was ground. Two 1 g pellets were combusted separately in a bomb calorimeter (Parr Instrument Company, 6300 Calorimeter model) to determine energy density. Two pellets per subsample were used as replicates for quality control. The samples were kept in desiccators throughout this process. The reference material was a 1 g pellet of benzoic acid that was 6318 cal/g dry weight. Sodium carbonate (0.0724N) and an indicator made from bromocresol green and methyl red were used for titrations (Parr Instrument Company 2005).

Predators – Stomach Content Analysis

Initially, each excised intestinal tract was rinsed over a 250 μm mesh sieve. The stomach was then separated from the rest of the gut and the stomach contents were washed into the sieve to remove gastric juices and digested materials. The larger prey items, such as bones and intact fish, were retained in the sieve. Otoliths were removed from intact fish and the remaining sieve contents were transferred to a petri dish where loose otoliths were picked out under 10X magnification using a dissecting microscope. Other non-fish items in the stomachs consisted of mayfly larvae which were identified to family and counted. All otoliths were identified to species using the otolith catalogue constructed by Sheppard (2010; 2012). The number of otoliths found per stomach from each species was enumerated to determine the number of each prey fish found in the gut contents. To do this, intact fish from the gut contents were dissected for their sagittae oto-

oliths (These were focused on because they are larger and species specific) which were then treated as a pair. Sagittae otoliths found loose in the gut contents were enumerated by species and divided by two (to account for potential pairs). The otoliths were then photographed under a dissecting microscope alongside a ruler. The length of each otolith was measured from the tip of the otolith (rostrum) to the base of the otolith (postrostrum) using ImageJ (Version 1.4, National Institutes of Health, USA). The lengths of paired otoliths (from intact prey items) were averaged. Pairs of otoliths and individual otoliths were stored dry in labeled coin envelopes (6 x 8 cm).

Data Analysis

Prey – Baseline Information

Representative photographs of the sagittae pair of otoliths for each fish prey species were used in the otolith catalogue to demonstrate how the otoliths were categorized by species (Appendix A). The relationship between fork length and otolith length was examined for all species and was pooled across spring, summer and fall. This relationship was not examined seasonally because the increase in otolith length is minute enough that my techniques could not detect them (Campana and Thorrold 2001). The relationship between fork length – weight was examined for all species in each season (spring, summer and fall) because the weight of a fish can change drastically throughout the season, especially before and after spawning (Porath and Peters 1997; Quist et al. 2002). Power curves were fitted to the fork length-weight data and lines were fitted to the fork length – otolith length data (see equations and r-squared for all relationships in Table 1, Appendix B). Outliers (three standard deviations outside the mean) were removed when detected.

This allowed for development of otolith length-weight regressions for all fish prey species, separated by season (spring, summer and fall).

Calories/g dry weight were transformed into joules/g wet weight using the wet weight/dry weight ratio which was calculated by dividing wet weight of the sample by the freeze-dried weight of the sample. By multiplying the values by 4.18 they are transformed from calories into Joules. The percentage differences between replicate analyses of a bomb calorimetry sample were calculated for quality control by taking the difference in the energy density (joules/g wet weight) of the replicates divided by the average of the two measurements, multiplied by 100. To determine if there were differences in prey energy densities, an analysis of variance was conducted with season, size and species as the factors in the model followed by multiple comparisons of the means (Scheffé's test).

Predators – Diet Analysis

All walleye and sauger were separated into 50 mm length classes (10 classes for walleye: 140 – 650 mm; 6 classes for sauger: 140 – 450mm) that approximately divided the fish by age class (Porath and Peters 1997). The normality of the data was examined for walleye and sauger but not for dwarf walleye due to small sample sizes in the South Basin and absence in the North Basin. The distribution of walleye and sauger were normal; therefore, parametric statistics were applicable.

The dietary composition of both walleye and sauger within each length class was summarized in a number of ways. The percentage of empty stomachs and the percentage of stomachs that were composed of only one prey type were determined in each season and in each basin. The percentage of empty stomachs was determined by dividing the

number of empty stomachs by the total number of stomachs sampled in each basin and each season. The percentage of stomachs with only one prey type was determined by dividing the number of stomachs that contained only one prey type by the total number of non-empty stomachs in each basin and each season.

I also determined the importance of each prey type in the diet. Prey importance was measured in four ways to give a complete description of the dietary composition of walleye and sauger gut contents. (1) Percentage frequency of occurrence of all prey types was measured as the number of non-empty stomachs in which each prey type was present. (2) Percentage by number was determined by dividing the total number of each prey type in all non-empty stomachs by the total number of prey items in all non-empty stomachs. (3) Percentage by weight was determined similarly using the weight of each prey item. (4) Percentage by joules was determined using the caloric content or energy density (Joules/gram wet weight) of each prey item, also based on its weight. To interpret differences in condition and growth of walleye and sauger (see Chapter 3), the focus was on the latter estimate, i.e. percentage caloric content when comparing diets within length classes between basins and among seasons.

To statistically compare the occurrence of the different prey types in the gut contents of walleye and sauger between basins and among seasons, the expected proportions of each prey type in the gut contents of both walleye and sauger were calculated and compared to the observed proportions (modified from O'Driscoll et al. 2001). The expected prey occurrence was calculated as:

$$E_{fsa} = p_{fi}n_{asi}$$

where $E_{f_{sa}}$ is the expected prey occurrence for a specific prey type (f), area (a) and season (s), with area referring to either the North or the South Basin; p_{fi} is the proportion of non-empty stomachs from a length class (i) that contain prey type f. For dietary comparison between basins, this value was calculated for all prey types in both basins combined within each length class of each predator species. For seasonal comparisons, p_{fi} was calculated using all prey types within each basin within each length class of each predator species and n_{asi} was the number of walleye or sauger in each length class in each basin (area) and season. For example, say that 50% of all non-empty stomachs from walleye (length 200 – 250 mm) in both basins in all seasons contained rainbow smelt. If there were 30 walleye (200 - 250mm) with non-empty stomachs in the North Basin from the fall, I would expect that 15 walleye (0.5×30) of the length category 200 – 250 mm in the North Basin in the fall would contain rainbow smelt. The observed values were the actual number of each prey type in the gut contents for each length class and predator species in each basin in each season. The expected and observed prey occurrence values were compared using Chi-square analyses. This test assumes that each stomach is an independent sample which may be incorrect if the fish were feeding in the same area at the same time that they were caught. These p values should, therefore, be taken conservatively.

To summarize the size of prey consumed by walleye and sauger in each basin, the range, mean, and standard error of the reconstructed fork length and weight were determined for each prey type consumed (see prey data analysis section). The reconstructed length and weight of each prey type were analysed for statistical difference between basins using an analysis of variance, controlling for predator length.

Results

Prey – Baseline Information

Fork length – otolith length linear relationships and fork length-weight power relationships varied among seasons and species (Table 1). Regression coefficients (r-squared values) were typically high (0.80 – 0.90); however, some were very low, likely attributable to small sample sizes for some prey species in some seasons (Table 3).

Replicates tested using bomb calorimetry varied by less than 4% for each sample that was run, which is within the acceptable range (Kelso 1972; Rand et al. 1994; Vondracek et al. 1996; Glover et al. 2010). Mean (\pm SE) energy densities (Joules / gram wet weight) of forage fish species in Lake Winnipeg did not vary significantly among species when pooled by size classes and seasons (Table 2). The energy densities of emerald shiner and troutperch differed significantly among seasons (emerald shiner: $F_{2,8} = 15.49$, $p < 0.005$; troutperch: $F_{2,3} = 17162.8$, $p = 0.005$). The mean energy density of emerald shiner was higher in summer and fall than in spring (Scheffé's: $p < 0.05$), and troutperch was highest in fall followed by summer and spring (Scheffé's: $p < 0.05$). Energy densities of all other prey species were not significantly different among size classes or seasons. The number of representatives for some size classes of each species in each season was small or absent, resulting in low statistical power (Table 3). Although energy densities did not differ among size classes, large fish tended to have higher energy densities than small and medium fish (Table 2).

Predators

In total, 693 walleye, 32 dwarf walleye and 516 sauger were sampled, of which most (85%) were captured by gill-netting (Table 3). Although every effort was made to obtain samples for all species/morphotypes and length classes from each basin in each season, there were inevitable gaps. For example, only 2 dwarf walleye were obtained from the North Basin, suggesting that they may not be present in large numbers or were not caught with the gear used. Because of the small sample sizes of dwarf walleye and their absence in the North Basin, these data were not analyzed, but are briefly presented after normal growth walleye, where possible.

The majority of walleye had prey in their stomachs (88%), and ranged in length from 250 - 450 mm (length classes 3-6; basins combined; Figure 2). The majority of sauger with non-empty stomachs (98%) ranged from 200–400 mm (length classes 2-5) in the South Basin, with only a few sampled from the North Basin (Figure 2). Because of their larger sample sizes, I focused statistical analyses on these length classes for each species.

Walleye

Basin Comparison

A significantly higher percentage of empty stomachs were found in walleye from the South Basin compared to the North Basin (Table 4, Appendix C). There were no statistically significant differences in the percentage of empty stomachs among seasons within basins (Table 4). There was a high percentage of walleye stomachs that consisted of entirely one prey type (78.5 – 95.5%; Table 4). The percentage of empty stomachs and stomachs with one prey type appeared higher for dwarf walleye than walleye; however, the sample size of dwarf walleye was low (Table 4).

In the North Basin, the frequency of occurrence of prey indicated that walleye stomachs almost always contained rainbow smelt (82.9%; Table 5). In contrast, the diet of walleye in the South Basin was not dominated by a single prey type (Table 5). The prey species with the highest frequency of occurrence was emerald shiner (32.2%), followed by mayfly larvae (15.9%) and yellow perch (12.8%) as well as other species (Table 5). Dwarf walleye had a high occurrence of mayfly larvae in their gut contents in the South Basin as well as some yellow perch and emerald shiner. Of the two dwarf walleye caught in the North Basin, one was non-empty and it contained a rainbow smelt.

The frequencies of occurrence of prey in the gut contents of walleye between 250-450 mm (length classes 3-6) were statistically compared between basins. Emerald shiner and yellow perch occurred in the gut contents significantly more in the South Basin than in the North Basin for all length classes of walleye (Appendix C). Rainbow smelt occurred in the gut contents significantly more in the North than in the South Basin for all length classes of walleye (Appendix C).

The gut contents of walleye in the North Basin were composed almost entirely of rainbow smelt regardless of how the data were summarized: by number (87.2%), by weight (84.5%) or by caloric content (85.7%; Table 5, Figure 3). The second most abundant prey type was cisco; however, this species occurred much less frequently (5.6% by number, 13.3% by weight, 12.1% by joules; Table 5, Figure 3). Unlike the North Basin, there was a much broader array of prey types found in the gut contents of walleye in the South Basin (Table 5, Figure 3), with a dominance of emerald shiner (63.2% by number, 33.7% by weight, 40% by joules; Table 5, Figure 3). The other prey species found in high abundance included troutperch, cisco, yellow perch, rainbow smelt, white bass and may-

fly larvae (Table 5, Figure 3). The non-empty stomachs that contained rainbow smelt were all from walleye caught in the most northern range of the South Basin. These dietary differences between basins remained consistent among all length classes (Figure 4).

Prey length was analyzed for differences between basins and found to be statistically significant ($F_{1,836} = 1207.71$, $p < 0.001$) when predator length was controlled for using an ANCOVA. Predator length was not a statistically significant factor in the analysis of prey length ($F_{1,836} = 0.38$, $p = 0.5383$); therefore, the length classes of walleye were grouped when performing further prey length analysis. The prey types consumed by walleye (all length classes combined) were larger (by species) in the North than in the South Basin (Table 5). Rainbow smelt, emerald shiner and cisco consumed in the North Basin were significantly longer and heavier than those consumed in the South Basin (cisco length: $F_{1,37} = 9.24$, $p = 0.0044$; cisco weight: $F_{1,37} = 4.52$, $p = 0.0405$; rainbow smelt length: $F_{1,262} = 65.80$, $p < 0.001$; rainbow smelt weight: $F_{1,262} = 30.14$, $p < 0.001$; emerald shiner length: $F_{1,398} = 30.75$, $p < 0.001$; emerald shiner weight: $F_{1,398} = 29.62$, $p < 0.001$). Walleye and sauger, as prey, were significantly longer when consumed by walleye in the North compared to the South Basin ($F_{1,10} = 6.81$, $p = 0.0283$).

Seasonal Comparison

The percentage of walleye stomachs that were found empty was consistent across seasons (24.6-47.3%) within each basin except for a near 2-fold increase (79.3 %) in the percentage of empty stomachs in the winter in the South Basin (Table 4). Low sample sizes precluded seasonal comparisons for dwarf walleye (Table 4). The percentage of walleye stomachs with only one prey type was consistent across seasons (78.5-95.5%)

within basins except for the summer in the South Basin (Table 4) when it was nearly half (31.4%) that of other seasons both within and between basins (Table 4).

Owing to the difference in dietary composition between basins, seasonal differences in the occurrence of prey types in non-empty walleye stomachs were examined within basins (Appendix C). In the North Basin, only mayfly larvae varied in occurrence seasonally, being significantly higher in the spring and summer than in the fall (in walleye 250 – 350 mm), possibly attributable to seasonal emergence patterns (Appendix C). In the South Basin, freshwater drum, mayfly larvae and yellow perch differed seasonally in occurrence (Appendix C). Freshwater drum occurred significantly more often in the gut contents of walleye (300-400 mm) in the summer relative to the spring, fall and winter (Appendix C). Mayfly larvae occurred significantly more often in the spring, fall and winter compared to the summer where they were not present in the gut contents of walleye in the South Basin (300-450 mm; Appendix C). Yellow perch were found significantly more often in the gut contents of walleye (350-400 mm) in the summer and fall than in the spring and winter where they were not present at all (Appendix C).

In the North Basin, the contribution of prey in terms of caloric content to the gut contents of walleye varied slightly with season for cisco and emerald shiner (Figure 5). Rainbow smelt remained consistently high throughout the seasons (87.9% in spring, 76.1% in summer and 88.4% in fall) while cisco contributed more to the diet in fall (6.4%) and emerald shiner contributed more to the diet in the summer (0.7%; Figure 5). All other prey types were low or absent in their caloric contribution to the diet throughout the seasons in this basin (Figure 5). Almost every prey type (except freshwater drum) varied seasonally in terms of its caloric contribution to the diet of walleye in the South Basin

(Figure 5). Mayfly larvae contributed in the spring (24.7%) and winter (27.9%) while cisco was higher in the spring (39.0%) summer (35.9%) and fall (19.8%) rather than the winter where they were absent (Figure 5). Troutperch, yellow perch and white bass had higher percent caloric contribution in the fall (16.7%, 13.4% and 15.1% respectively) than in all other seasons (Figure 5). Emerald shiner and walleye/sauger contributed to the diet more in the summer (27.7% and 9.7% respectively) than in any other season (Figure 5). Rainbow smelt contributed to the diet of walleye in the South Basin during the winter (68.7%) more than it had in any other season (Figure 5).

Sauger

Basin Comparison

There was no statistically significant difference in the percentage of empty stomachs between basins (Table 4) or among seasons in the North Basin; however, there was a difference among seasons in the South Basin (Appendix C). In the South Basin, there was a 2-fold increase in the percentage of empty stomachs in the winter (86.7%) than any other season (Table 4). There was a high percentage of sauger stomachs that consisted of only one prey type (67.2 – 100%) that was more common in the North Basin than in the South Basin (Table 4).

In the North Basin, the frequency of occurrence of prey indicates that in the gut contents, rainbow smelt were found in 41.2% of stomachs, followed by troutperch and freshwater drum (both 17.6%; Table 6). In contrast to North Basin walleye, other prey types were found in the gut contents including yellow perch, white bass, walleye/sauger and mayfly larvae (all 5.9%; Table 6). South Basin sauger contained many prey types

with troutperch having the highest occurrence (32.3%), mayfly larvae (24.1%), emerald shiner (16.3%) and freshwater drum (10.5%) followed by a few other species (Table 6).

The occurrence of prey in the gut contents of sauger between 200-450 mm (length classes 2-5) were statistically compared between basins. Rainbow smelt occurred in the gut contents significantly more often in the North than in the South Basin for all length classes of sauger examined (Appendix C). White bass also occurred significantly more often in the gut contents of sauger in the North Basin (350-400mm) than in the South Basin (Appendix C). For all other prey types there were no statistically significant differences between basins (Appendix C).

The gut contents of sauger in the North Basin were composed mostly of rainbow smelt regardless of how the data are summarized: by number (34.5%), by weight (55.8%) or by caloric content (56.3%; Table 6, Figure 6). The next most abundant prey types were freshwater drum (by number 27.6%) and troutperch (by weight 28.8%, by caloric content 29.7%; Table 6, Figure 6). In the South Basin, diets of sauger were composed of mostly troutperch (32.9% by number, 49.7% by weight and 48.2% by joules; Table 6, Figure 6). Emerald shiner (23.5% by number, 13.4% by weight and 17.8% by joules), freshwater drum (13.3% by number, 10.4% by weight and 9.8% by joules) and mayfly larvae (17.6% by number, 7.8% by weight and 6.8% by joules) were also abundant (Table 6, Figure 6).

In the North Basin, troutperch contributed the most calories (64%) to the diet of smaller sauger (140-250 mm) while the diet of larger sauger (250-450 mm) was predominantly rainbow smelt (90-100%; Figure 7a). Sample sizes of some length classes of North Basin sauger were small, so these trends should be observed cautiously. South Basin sau-

ger had a similar diet across length classes, consisting mainly of troutperch (29.1-76.7%; Figure 7b). Diet of large sauger (400-450 mm) contained more mayfly larvae (71.6%) than any other prey type; however, this could be a seasonal effect (Figure 7b).

Prey length increased significantly with sauger length ($F_{1,318} = 5.75$, $p = 0.0171$) and when sauger length was controlled using an ANCOVA, the sizes of the prey consumed in the North Basin were significantly longer than those consumed in the South Basin ($F_{1,318} = 14.86$, $p = 0.001$). Rainbow smelt in the gut contents of sauger were significantly longer in North Basin than in South Basin ($F_{1,10} = 5.45$, $p = 0.04$). Troutperch in the gut contents were heavier in the North than in the South Basin ($F_{1,120} = 5.42$, $p = 0.02$; Table 6).

Seasonal Comparison

The percentage of sauger stomachs that were found empty was consistent across seasons (18.2-49.7%) within each basin except for a near 2-fold increase in percentage of empty stomachs during the winter (86.7%) in the South Basin (Table 4). The percentage of sauger stomachs with only one prey type was consistent across seasons (74.7-100%) within basins except for the summer in the South Basin in which it was lower (67.2%) than in other seasons, both within and between basins (Table 4). In spring, summer and fall, the North Basin (91.7-100%) had a higher percentage of stomachs with only one prey type than the South Basin stomachs (67.2-81.4%; Table 4).

Owing to the different dietary composition of sauger between basins, seasonal differences in prey occurrence of non-empty stomachs within basins were examined (Appendix C). In the North Basin, there were no seasonal trends in the prey occurrence for any length classes of sauger (Appendix C). In the South Basin, freshwater drum, emerald

shiner, mayfly and troutperch differed seasonally in occurrence (Appendix C). Freshwater drum occurred significantly more often in the gut contents of sauger (200-350 mm in length) in the spring, summer and fall compared to the winter (Appendix C). Emerald shiner occurred significantly more often in the fall and spring gut contents of sauger (200-300 mm; Appendix C). Mayfly larvae occurred significantly more often in the spring and summer gut contents of sauger (250-300 mm; Appendix C) and in the spring, fall and winter for 300-350mm sauger (Appendix C). Troutperch were absent in the winter gut contents of 250-300 mm sauger, but present in all other seasons (Appendix C).

In the North Basin, the caloric contribution of prey to sauger varied slightly with season for rainbow smelt, troutperch, freshwater drum, walleye/sauger and mayfly larvae (Figure 8). Troutperch contributed in the summer (100%) and fall (12.4%) while freshwater drum, walleye/sauger, yellow perch and white bass contributed only in the spring (3.7%, 6.6%, 2% and 2.7%; Figure 8). Rainbow smelt contributed in the spring (88.6%) and fall (72.6%) while mayfly larvae contributed only in the spring (11.4%; Figure 8).

Almost every prey type (except yellow perch and freshwater drum) varied seasonally in caloric contribution to sauger diets in the South Basin (Figure 8). Troutperch contributed consistently throughout the spring, summer and fall with the peak contribution in the spring (69.7%; Figure 8). Cisco and walleye/sauger contributed more in the summer (19.8% and 44.3% respectively) than they did in other seasons, while freshwater drum and white bass contributed more in the fall than they did in other seasons (25.1% and 4.9% respectively; Figure 8). Emerald shiner contributed the most in the fall (20.7%) and winter (61.3%) while mayfly larvae contributed the most in the winter (38.7%) than they did in other seasons (Figure 8).

Discussion

The objective of this study was to determine the diet variations of walleye, sauger and dwarf walleye between basins and among seasons with intent to suggest the impact of the invasive rainbow smelt as well as to provide baseline information on walleye, sauger, dwarf walleye and their prey for future changes. Walleye and sauger were found to have different diets in the North Basin than in the South Basin of Lake Winnipeg. Although dietary differences were observed between these species, there were distinct similarities in their dietary variation between the basins. In the North Basin, walleye consumed almost entirely large rainbow smelt with few other prey types incorporated into the diet, despite the presence of other available prey types (Lumb et al. 2012). Similarly, sauger primarily consumed rainbow smelt and troutperch in the North Basin, with larger sauger consuming more rainbow smelt and smaller sauger consuming more troutperch. In contrast, diets of both species in the South Basin consisted of many prey types, with the largest caloric portion of gut contents consisting of emerald shiner for walleye and both emerald shiner and troutperch for sauger. The energy density (Joules/gram wet weight) of prey species in the North and South Basins did not differ significantly, but differences in the average length and weight of prey species between basins in the lake were pronounced. Specifically, walleye and sauger of each size class consumed longer and heavier prey in the North Basin compared to the South Basin.

Walleye diet in the North Basin was similar to other systems following rainbow smelt invasion, where rainbow smelt made up a high proportion (85.7%) of the diet (Lake Superior: Swenson 1977; Horsetooth Reservoir, Colorado: Jones et al. 1994). Although other prey types normally consumed by walleye and sauger were available (such as

cisco), the predominance of smelt in the guts suggests that these predators may be selecting this species (Pulliam 1974; Ricklefs and Miller 2000). There is lower handling time associated with rainbow smelt, as they are more easily captured relative to other species (e.g. cisco) likely related to their predator avoidance strategy (to remain motionless as opposed to constant swimming; Mason et al. 1998). Additionally, smelt are large compared to the most abundant prey in the South Basin (i.e. emerald shiner) and abundant in the North Basin, likely making them the most energetically profitable prey (Gamble et al. 2011; Lumb et al. 2012). Sauger of different lengths in the North Basin may select rainbow smelt and troutperch differently as a consequence of gape-limitation or differences in foraging habitat. Rainbow smelt tend to be larger than troutperch, suggesting perhaps smelt are too large for smaller sauger to ingest (Little et al. 1998). Troutperch are generally found near the bottom of lakes whereas rainbow smelt are a mid-water species (Swenson 1977; Jones et al. 1994; Lumb et al. 2012) and, thus, it is possible that smaller sauger may reside closer to the bottom where there is likely reduced visibility and more cover (e.g. vegetation or debris) protecting them from potential predators, such as large northern pike, and less competitive interactions with walleye, whereas larger sauger may forage higher in the water column.

In contrast, walleye and sauger in the South Basin consumed many prey types, with the largest caloric portion of gut contents consisting of emerald shiner for walleye and both emerald shiner and troutperch for sauger. This is similar to most other ecosystems in which walleye most frequently consume a wide variety of yellow perch, cisco and emerald shiner (Parsons 1971; Knight et al. 1984; Hartman and Margraf 1992; Knight and Vondracek 1993; Einfalt and Wahl 1997; Porath and Peters 1997; Quist et al. 2002). The

wider variety of prey in the diet of walleye and sauger in the South Basin of Lake Winnipeg may be related to the dominance of the smaller-bodied emerald shiner relative to other species in this basin, although troutperch densities are unknown (Lumb et al. 2012). In support, if the most abundant prey species in the ecosystem are small-bodied (e.g. emerald shiners), walleye tend to have a wider breadth of prey species in the diet (Parsons 1971; Knight et al. 1984; Einfalt and Wahl 1997).

Another possible explanation for greater diet breadth in the South Basin relative to the North Basin of Lake Winnipeg is the higher turbidity in the South Basin (Secchi depth: 0.6 ± 0.3 m; see Table 1 in Chapter 1) relative to the North Basin (Secchi depth: 1.2 ± 0.6 m; see Table 1 in Chapter 1). Higher turbidity can decrease the visual acuity and contrast of prey in the water and limit the assessment of prey availability when searching. In support, Little et al. (1998) found that walleye in the turbid (Secchi depth: 1.0 – 8.0 m from June – September; Rawson 1950) Slave River in the Northwest Territories consumed a wide breadth of prey types; high turbidity was the most likely reason for this feeding behaviour. The visual acuity of walleye and sauger; however, is less likely to be compromised in turbid conditions and in comparison to other systems, both basins could be characterized as highly turbid (Ali and Anctil 1977; Ryder 1977; Brunskill 1980; Braekevelt et al. 1989; De Robertis et al. 2003).

Walleye and sauger may use different habitats, with walleye in more pelagic off-shore waters and sauger in more benthic near-shore waters (Swenson and Smith 1976; Swenson 1977; Scott and Crossman 1998). Observations during sampling revealed that walleye were caught in the gill-net panels farther from shore, while sauger were caught closer to shore. As troutperch is a demersal species, it is also possible that sauger are more associ-

ated with the bottom while walleye are more pelagic; however, this is unknown (Swenson and Smith 1976; Swenson 1977; Scott and Crossman 1998). In support, walleye and sauger in the Lake of the Woods, Minnesota showed differences in vertical strata, where walleye tended to occupy the shallower strata and fed on pelagic forage fishes, while sauger tended to occupy the deeper strata and fed on more demersal forage fishes (i.e. trout-perch; Swenson and Smith 1976).

There was seasonal variation in the diet of walleye and sauger, particularly in the North Basin; however, there were no clear trends. The lack of clear trends may be due to the availability of large smelt year-round in the North Basin and high forage fish density year-round in the South Basin. In support, Porath and Peters (1997) found that with higher abundances of prey fishes in Lake Ogallala, there was little seasonal variation in diet. Observed dietary variation among seasons seemed to be associated with mayfly emergence and the presence of young-of-the-year fishes in pelagic waters later in the fall (Knight et al. 1984; Little et al. 1998). Mayfly larvae represented a higher proportion of the diet in the winter, spring and summer compared to the fall in both basins and predatory species. Walleye gut contents from a Nebraskan reservoir, also attributed seasonal differences to mayfly emergence (Olson et al. 2007). Seasonal increases in the abundance of some young-of-the-year forage fishes, such as freshwater drum, white bass, yellow perch, as well as adult emerald shiner and troutperch have been found to influence the diet of walleye and sauger in many other systems (Parsons 1971; Swenson and Smith 1976; Swenson 1977; Knight et al. 1984; Little et al. 1998).

Conclusion

Walleye and sauger diets in the North Basin were dominated by the abundant and large rainbow smelt. Alternately, walleye and sauger diets in the South Basin were composed of a variety of prey types with a higher proportion of the abundant, small-bodied emerald shiner. Modeling has revealed that piscivores grow larger when they consume fewer, larger prey (Breck 1993). Therefore, the predominant incorporation of the abundant and larger rainbow smelt in the diets of walleye and sauger in the North Basin may lead to increased growth and condition of fish in this basin.

Table 1: Fish species in the diet of walleye and sauger divided into size classes, showing equations and r^2 values for relationships of otolith length –fork length and fork length – weight. Superscript z indicated that the size range is likely too large for walleye and sauger to consume. Emerald shiner fork length – otolith length regressions were determined using the ascerisci otoliths.

Common Name	Prey Latin Name	Size Category (mm)			Fork Length – Otolith Length Regression			Fork Length – Weight Regression		
		Small	Medium	Large	Spring	Summer	Fall	Spring	Summer	Fall
Troutperch	<i>Percopsis omiscomaycus</i>	20-50	N/A	51-110	$y=26.824x - 23.496$ $r^2 = 0.72$	$y=20.687x - 4.9227$ $r^2 = 0.98$	$y=18.263x + 2.5229$ $r^2 = 0.82$	$y=0.0312x^{3.77}$ $r^2 = 0.98$	$y=0.0478x^{3.52}$ $r^2 = 0.58$	$y=0.0679x^{3.21}$ $r^2 = 0.87$
Cisco	<i>Coregonus artedi</i>	>100	N/A	≤100	$y=24.41x + 22.58$ $r^2 = 0.61$	$y=31.486x + 2.4446$ $r^2 = 0.92$	$y=39.344x - 26.38$ $r^2 = 0.95$	$y=0.7321x^{2.37}$ $r^2 = 0.64$	$y=0.3688x^{3.03}$ $r^2 = 0.86$	$y=0.1132x^{3.94}$ $r^2 = 0.93$
Yellow Perch	<i>Perca flavescens</i>	>100	N/A	≤100	$y=38.9x - 26.968$ $r^2 = 1.0$	$y=29x - 1.3069$ $r^2 = 0.86$	$y=30.004x - 8.019$ $r^2 = 0.99$	$y=0.0585x^{4.34}$ $r^2 = 0.99$	$y=0.2072x^{3.25}$ $r^2 = 0.75$	$y=0.106x^{3.76}$ $r^2 = 0.98$
FreshwaterDrum	<i>Aplodinotus grunniens</i>	30-70	71-129	130-600 ^z	N/A	$y = 26.547x - 16.563$ $r^2 = 1.0$	$y = 16.032x + 12.319$ $r^2 = 0.84$	N/A	$y=0.0334x^{3.74}$ $r^2 = 0.99$	$y=0.1169x^{2.71}$ $r^2 = 0.87$
Rainbow Smelt	<i>Osmerus mordax</i>	>100	N/A	≤100	$y=28.307x + 11.579$ $r^2 = 0.97$	$y=28.63x + 8.6942$ $r^2 = 0.96$	$y=25.733x + 16.177$ $r^2 = 0.97$	$y=0.3733x^{2.36}$ $r^2 = 0.97$	$y=0.291x^{2.71}$ $r^2 = 0.94$	$y=0.2654x^{2.69}$ $r^2 = 0.97$
Emerald Shiner	<i>Notropis atherinoides</i>	35-59	60-84	85-100	$y=57.418x + 5.463$ $r^2 = 0.91$	$y=48.418x + 17.234$ $r^2 = 0.86$	$y=52.067x + 12.677$ $r^2 = 0.82$	$y=2.1365x^{3.29}$ $r^2 = 0.92$	$y=2.4533x^{2.58}$ $r^2 = 0.87$	$y=2.5633x^{2.77}$ $r^2 = 0.91$
White Bass	<i>Morone chrysops</i>	25-80	N/A	N/A	N/A	$y=18.391x + 6.0448$ $r^2 = 0.94$	$y=23.577x - 4.0512$ $r^2 = 0.97$	N/A	$y=0.1728x^{2.70}$ $r^2 = 0.94$	$y=0.5503x^{1.83}$ $r^2 = 0.77$
Walleye/Sauger	<i>Sander vitreus/Sander canadensis</i>	40-200	N/A	N/A	$y=44.942x - 38.675$ $r^2 = 0.91$	N/A	$y=-0.9489x + 91.228$ $r^2 = 6x10^{-5}$	$y=0.0756x^{4.03}$ $r^2 = 0.93$	N/A	$y=2.3328x^{0.63}$ $r^2 = 0.05$
Walleye	<i>Sander vitreus</i>	40-200	N/A	N/A	N/A	$y=42.149x - 9.5681$ $r^2 = 0.78$	N/A	N/A	$y=0.3318x^{3.31}$ $r^2 = 0.79$	N/A
Sauger	<i>Sander canadensis</i>	40-200	N/A	N/A	N/A	$y=2.1928x + 62.893$ $r^2 = 0.0045$	N/A	N/A	$y=0.148x^{3.8921}$ $r^2 = 0.94$	N/A

Table 2: Mean energy density (Joules / gram wet weight) values of forage fish species in Lake Winnipeg, with the standard deviation, where applicable.

Prey	Spring			Mean	Summer			Mean	Fall			Mean	Mean for Season and Size
	Small	Medium	Large		Small	Medium	Large		Small	Medium	Large		
Cisco	4930	---	4700	4810	5410	---	5810	5610	4720	---	5250	4990	5140 ± 440
Drum	---	---	---	---	5290	4880	7700	5960	5000	---	---	5000	5720 ± 1340
E. Shiner	6060	5240	4770	5360	7440	7470	8400	7770	7020	7890	7100	7340	6820 ± 1220
R. Smelt	5300	---	4960	5130	6580	---	6490	6530	5660	---	6060	5860	5840 ± 650
Sauger	4400	---	---	4400	4470	---	---	4470	---	---	---	---	4440 ± 50
Troutperch	---	---	4860	4860	5770	---	5760	5760	---	---	6390	6390	5700 ± 630
Walleye	4300	---	---	4300	5070	---	---	5070	---	---	---	---	4690 ± 540
White Bass	---	---	---	---	4930	---	---	4930	5560	---	---	5560	5240 ± 450
Yellow Perch	4480	---	4520	4500	5380	---	---	5380	4850	---	5980	5410	5040 ± 640
Walleye/Sauger	4590	---	---	4590	---	---	---	---	5100	---	---	5100	4850 ± 360

Table 3: Sample sizes of walleye, sauger and dwarf walleye in all seasons and years and the samples sizes of 10 prey types caught in all seasons in the North and South basins of Lake Winnipeg.

	Spring		Summer		Fall		Winter		Total
	North	South	North	South	North	South	North	South	
Predator Species									
Walleye	19	112	116	69	108	240	N/A	29	693
Dwarf Walleye	1	12	0	3	1	14	N/A	1	32
Sauger	8	193	11	116	32	126	N/A	30	516
Prey Species									
Troutperch	1	12	8	83	0	12	N/A	N/A	116
Cisco	9	18	18	27	5	24	N/A	N/A	101
Yellow Perch	0	6	0	29	2	7	N/A	N/A	44
Freshwater Drum	0	0	0	104	10	3	N/A	N/A	117
Rainbow Smelt	15	5	16	14	40	17	N/A	N/A	107
Emerald Shiner	10	20	11	25	12	24	N/A	N/A	102
White Bass	0	0	0	28	0	7	N/A	N/A	35
Walleye/Sauger	0	12	0	0	0	12	N/A	N/A	24
Sauger	0	1	1	6	0	0	N/A	N/A	8
Walleye	0	1	4	15	0	0	N/A	N/A	20

Table 4: The percentage of empty stomachs and stomachs containing only one prey type from the gut contents of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye (*Sander vitreus*) in the North and South Basins of Lake Winnipeg, Manitoba.

Season	Sample Size	% Empty Stomachs	% Stomachs with one prey type
North Basin			
Walleye			
Spring 2010/2011	19	36.8	84.6
Summer 2010	116	42.2	94
Fall 2010/2011	108	39.4	95.5
Sauger			
Spring 2010/2011	8	62.5	100
Summer 2010	11	18.2	100
Fall 2010/2011	32	62.5	91.7
Dwarf Walleye			
Spring 2010/2011	1	100	0
Summer 2010	0	N/A	N/A
Fall 2010/2011	1	N/A	N/A
South Basin			
Walleye			
Spring 2010/2011	112	47.3	91.2
Summer 2010	69	24.6	31.4
Fall 2010/2011	240	41.5	78.5
Winter 2011	29	79.3	85.7
Sauger			
Spring 2010/2011	193	49.7	81.4
Summer 2010	116	47.4	67.2
Fall 2010/2011	126	37.3	74.7
Winter 2011	30	86.7	100
Dwarf Walleye			
Spring 2010/2011	12	41.7	85.7
Summer 2010	3	33.3	100
Fall 2010/2011	14	100	0
Winter 2011	1	100	0

Table 5: Percent frequency of occurrence of nine prey types from the gut contents of walleye (*Sander vitreus*) from Lake Winnipeg, Manitoba all seasons combined in 2010-2011, along with the mean (\pm SE) fork length and weight of each prey type.

Prey Item	Percent Occurrence	Length (mm)		Weight (g)		Number (%)	Weight (%)	Joules (%)	Rank by Joules
		Mean \pm SE	Range	Mean \pm SE	Range				
North Basin									
Troutperch	0	N/A	N/A	N/A	N/A	0	0	0	
Cisco	7.6	117.2 \pm 2.8	91.7-129.9	20.0 \pm 2.1	4.0-27.9	5.6	13.3	12.1	2
Yellow Perch	1.3	51.5 \pm 6.6	44.9-58.1	0.91 \pm 0.06	0.85-0.97	0.8	0.08	0.07	6
Freshwater Drum	0	N/A	N/A	N/A	N/A	0	0	0	
Rainbow Smelt	82.9	106.4 \pm 1.0	50.4-147.8	8.2 \pm 0.27	0.53-44.8	87.2	84.5	85.7	1
Emerald Shiner	2.5	78.7 \pm 1.3	73.8-82.2	4.7 \pm 0.25	4.2-6.0	2.6	1.5	1.6	3
White Bass	0	N/A	N/A	N/A	N/A	0	0	0	
Walleye/Sauger	0.6	132.7 \pm 3.0	129.7-135.7	4.3 \pm 0.01	4.3-4.3	0.8	0.39	0.32	4
Mayfly Larvae	5.1	N/A	N/A	0.58 \pm 0.15	0.31-1.2	3.0	0.2	0.16	5
South Basin									
Troutperch	5.0	66.9 \pm 5.4	15.2-122.5	5.5 \pm 1.2	0.03-26	3.4	9.1	9.5	3
Cisco	8.1	87.1 \pm 7.8	48.3-168.2	11.1 \pm 3.1	1.2-52.2	3.7	20.4	17.3	2
Yellow Perch	12.8	51.3 \pm 2.5	28.1-90.4	2.2 \pm 0.32	0.22-8.5	7.1	7.7	7	6
Freshwater Drum	5.0	18.6 \pm 2.9	3.8-73.8	0.23 \pm 0.16	0.01-4.2	4.2	0.48	0.43	9
Rainbow Smelt	9.3	79.3 \pm 28.0	28-126.0	4.0 \pm 0.63	0.17-15.0	5.0	9.8	9.2	4
Emerald Shiner	32.2	41.2 \pm 0.90	12-103.4	1.1 \pm 0.09	0.01-12.7	63.2	33.7	40	1
White Bass	8.9	60.7 \pm 2.8	35.6-102.9	3.6 \pm 0.56	0.55-16.7	5.3	9.4	8.8	5
Walleye/Sauger	2.7	75.0 \pm 10.0	28.5-111.1	4.5 \pm 0.04	4.4-4.7	1.5	3.2	2.8	8
Mayfly Larvae	15.9	N/A	N/A	1.9 \pm 0.55	0.31-16.6	6.6	6.2	4.9	7

Table 6: The percent frequency of occurrence of nine prey types from the gut contents of sauger (*Sander canadensis*) from Lake Winnipeg, Manitoba, along with the mean (\pm SE) fork length and weight of each prey type.

Prey Item	Percent Occurrence	Length (mm)		Weight (g)		Number (%)	Weight (%)	Joules (%)	Rank by Joules
		Mean \pm SE	Range	Mean \pm SE	Range				
North Basin									
Troutperch	17.6	78.2 \pm 5.8	60.8-94.1	7.9 \pm 1.9	3.1-14.2	17.2	28.8	29.7	2
Cisco	0	N/A	N/A	N/A	N/A	0	0	0	
Yellow Perch	5.9	50.6 \pm 2.0	48.5-52.6	1.5 \pm 0.20	1.3-1.7	6.9	2.1	2	5
Freshwater Drum	17.6	44.3 \pm 2.1	33.5-52.6	0.83 \pm 0.12	0.31-1.4	27.6	4.8	4.2	4
Rainbow Smelt	41.2	110.1 \pm 3.9	93.4-137.1	7.7 \pm 0.99	4.2-15.2	34.5	55.8	56.3	1
Emerald Shiner	0	N/A	N/A	N/A	N/A	0	0	0	
White Bass	5.9	53.6	N/A	1.8	N/A	3.4	1.3	1.3	6
Walleye/Sauger	5.9	66.4 \pm 3.6	62.7-70.0	4.5 \pm 0.01	4.5-4.5	6.9	6.6	5.9	3
Mayfly Larvae	5.9	N/A	N/A	0.92	N/A	3.4	0.67	0.56	7
South Basin									
Troutperch	32.3	67.0 \pm 1.9	26.6-154.5	4.4 \pm 0.3	0.18-25.3	32.9	49.7	48.2	1
Cisco	3.5	74.4 \pm 7.0	45.8-108.8	5.9 \pm 1.5	0.97-15.0	2.5	5.1	4.8	6
Yellow Perch	1.9	52.2 \pm 7.9	33.5-73.9	2.3 \pm 0.95	0.39-5.4	1.4	1.1	1.1	8
Freshwater Drum	10.5	35.7 \pm 4.3	7.5-161.2	2.3 \pm 1.2	0.02-53.4	13.3	10.4	9.8	3
Rainbow Smelt	0.4	79.6	N/A	6	N/A	0.3	0.58	0.56	9
Emerald Shiner	16.3	49.8 \pm 1.7	9.3-83.6	1.6 \pm 0.18	0.04-6.4	23.5	13.4	17.8	2
White Bass	2.3	64.0 \pm 8.4	38.7-102.7	3.1 \pm 0.82	0.68-5.98	2.0	2.1	2.2	7
Walleye/Sauger	8.6	80.2 \pm 5.5	37.3-139.3	4.3 \pm 0.71	0.90-18.5	6.5	9.7	8.7	4
Mayfly Larvae	24.1	N/A	N/A	1.3 \pm 0.36	0.31-16.9	17.6	7.8	6.8	5

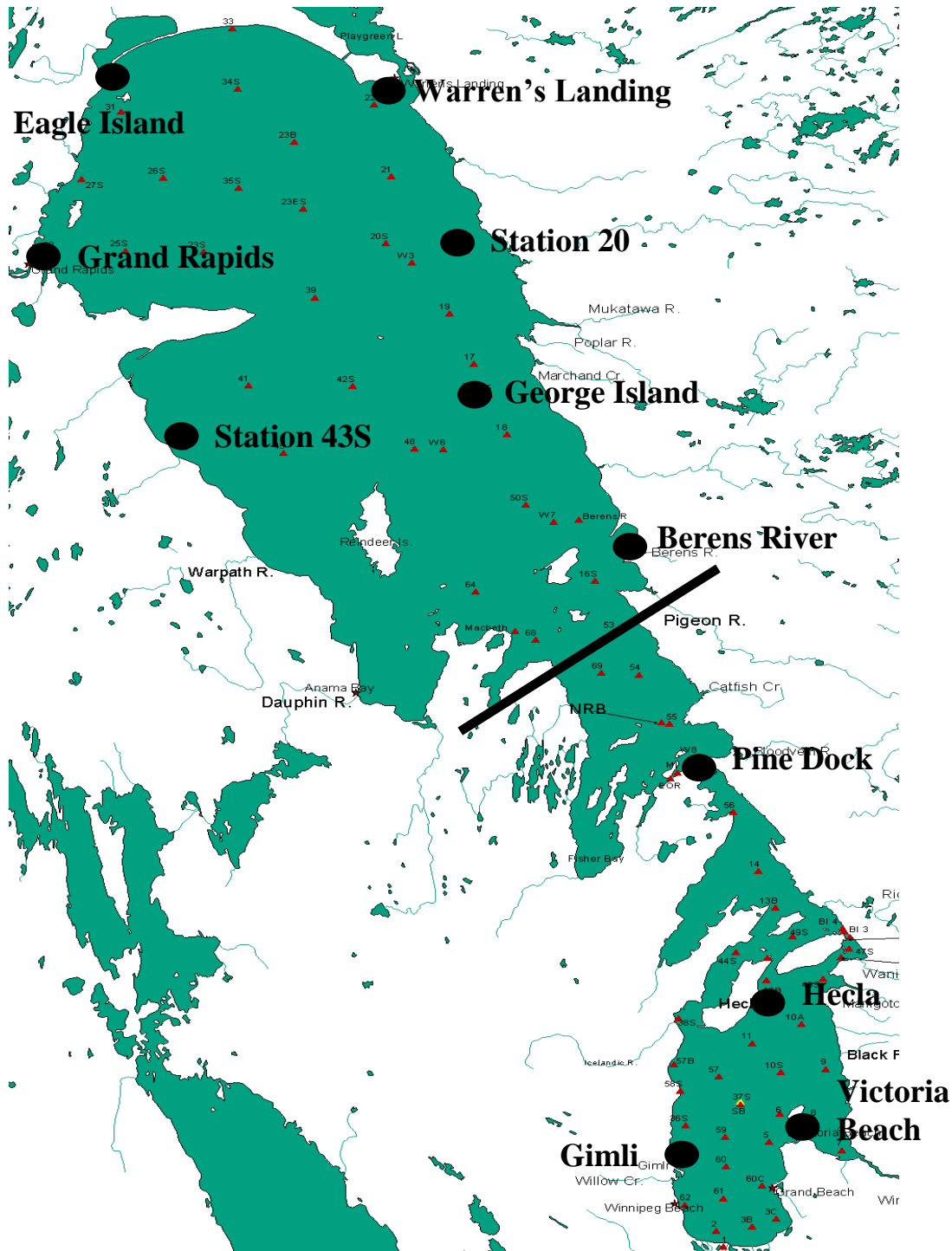
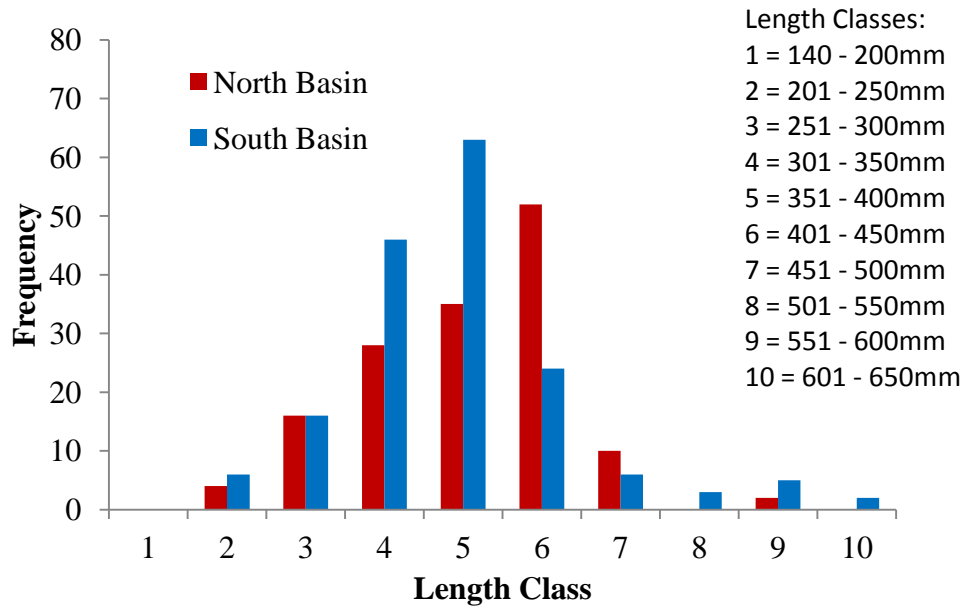
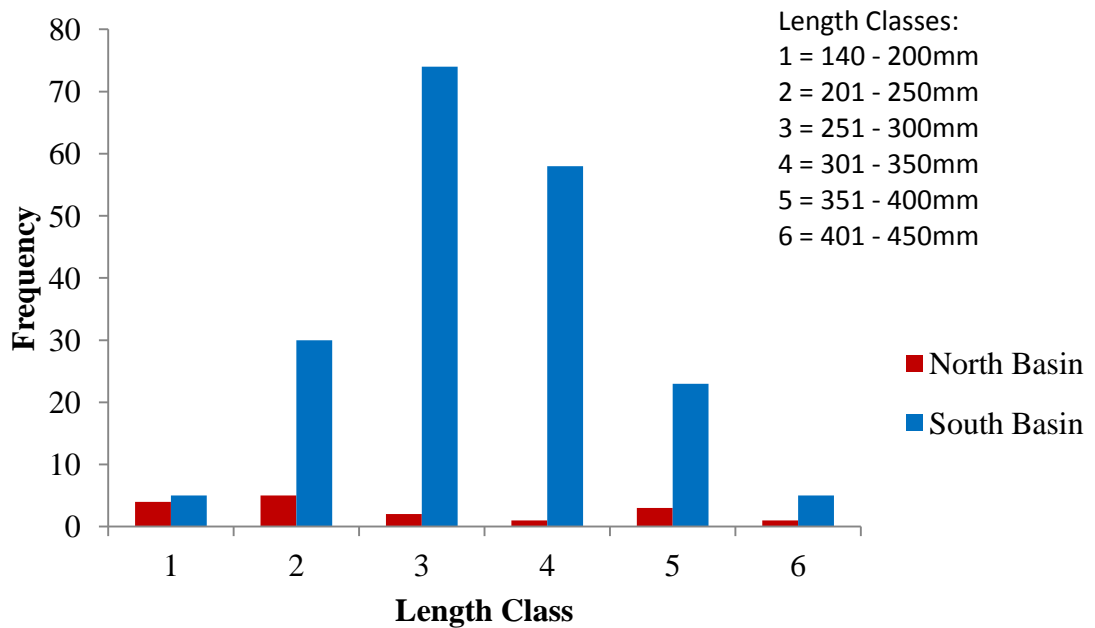


Figure 1: Map of Lake Winnipeg showing 11 gill-net locations (large black circles) and 65 trawl locations (small red triangles). The black line denotes the division between the South and North Basin.



(a)



(b)

Figure 2: Frequency of multiple length classes (fork length) of walleye (a) and sauger (b) caught with non-empty stomachs in the North and South Basins of Lake Winnipeg, Manitoba.

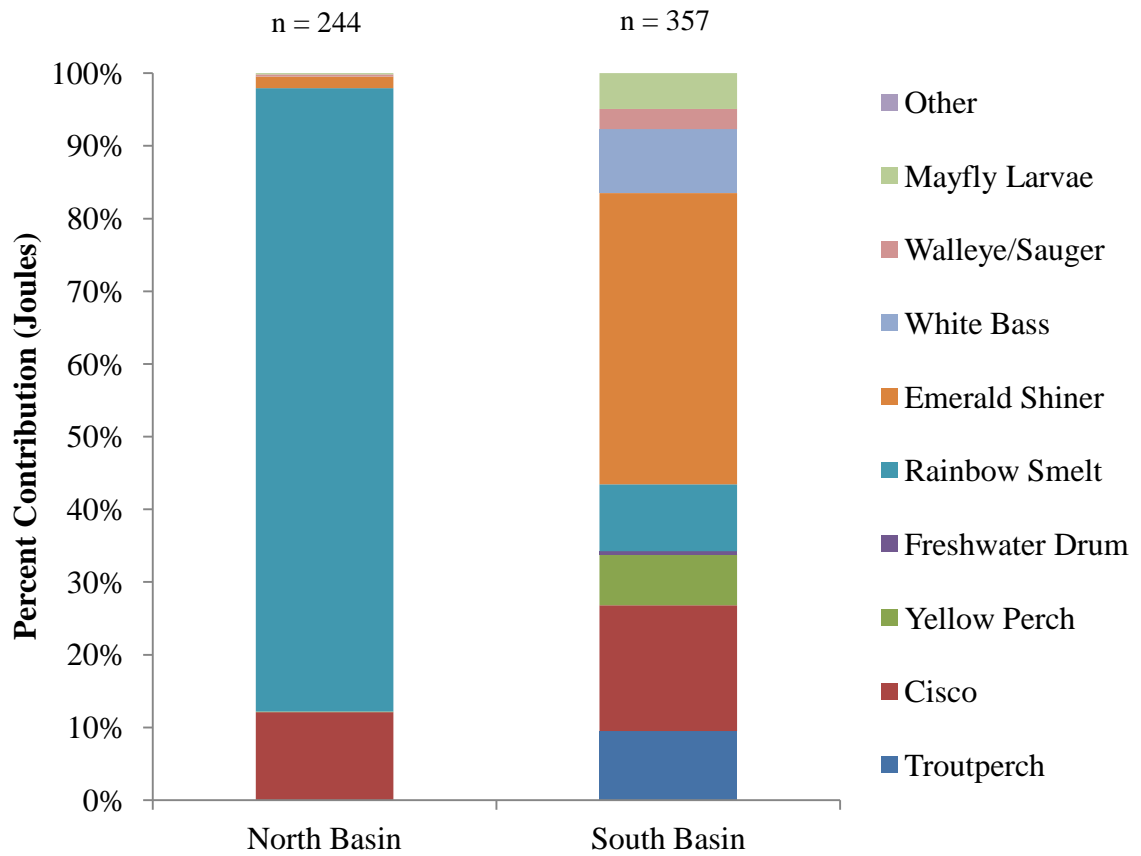
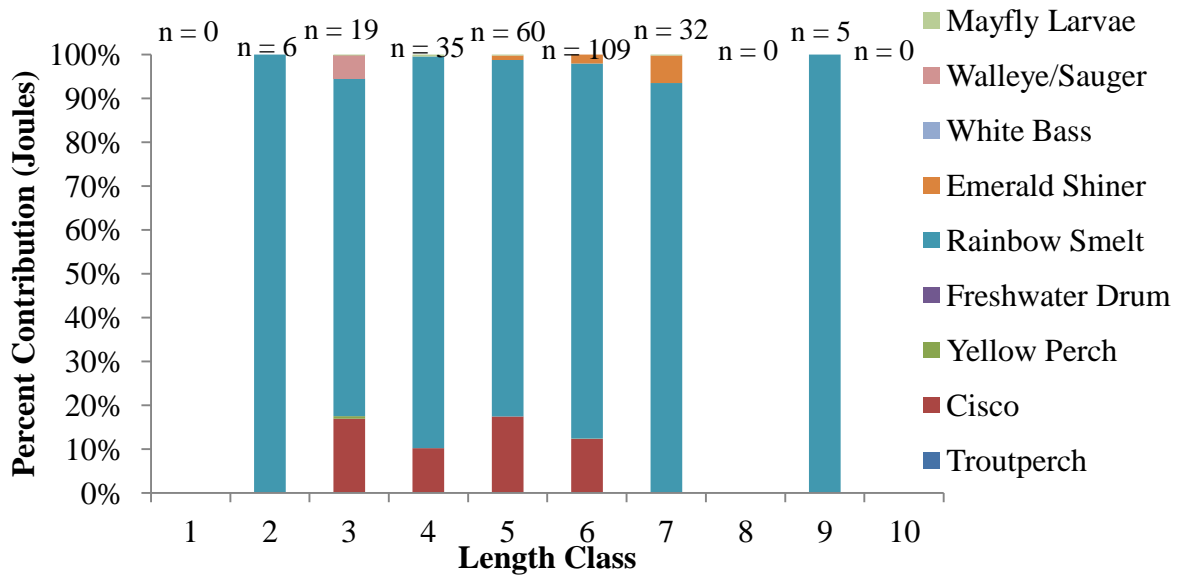
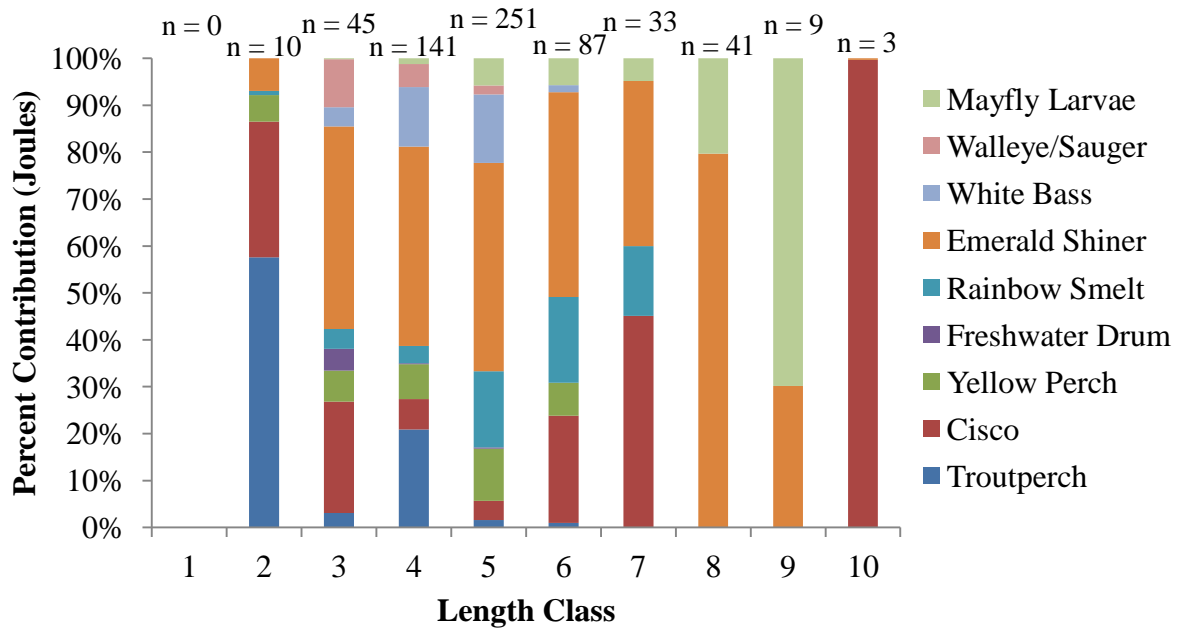


Figure 3: Percent composition by caloric content (Joules/g wet weight) of ten prey types ('other' consists of unknown fishes, burbot (*Lota lota*) and ninespine stickleback (*Pungitius pungitius*)) in the gut contents of walleye in the North and South Basins of Lake Winnipeg, Manitoba.

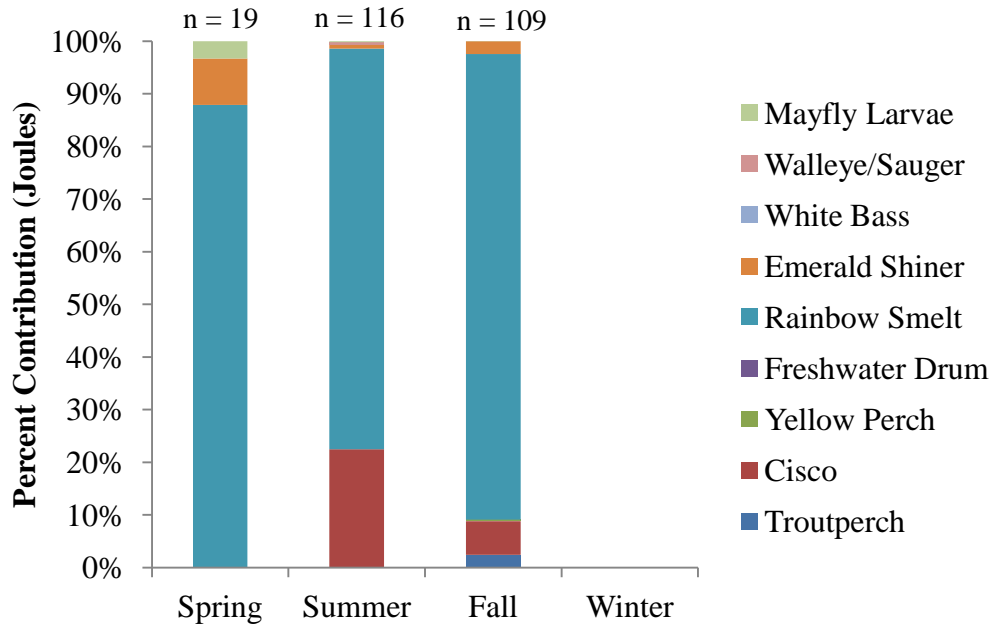


(a)

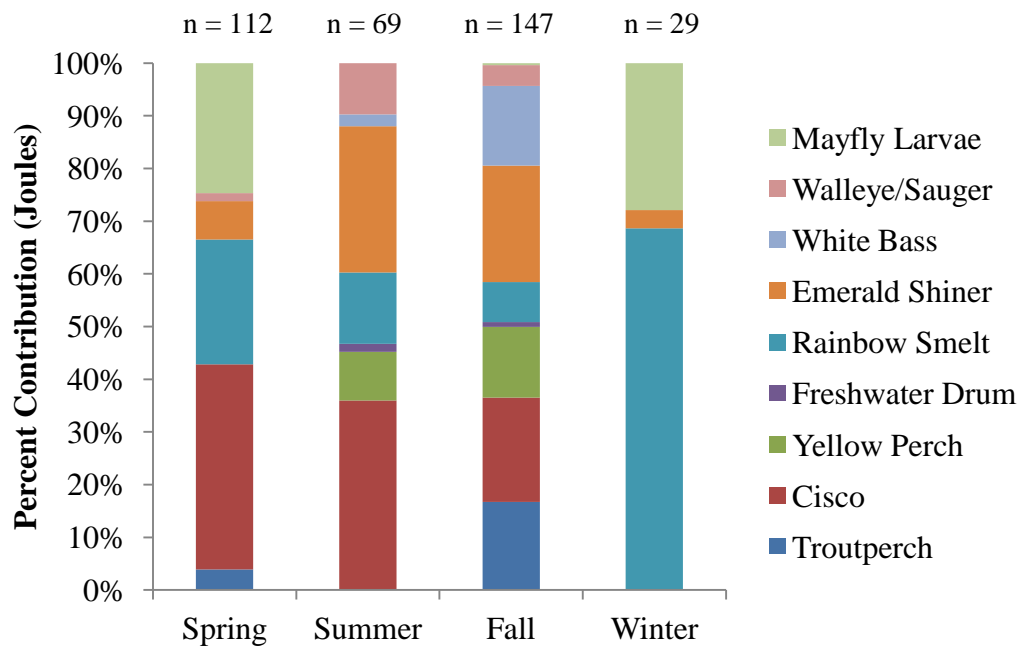


(b)

Figure 4: Percent composition by caloric content (Joules/g wet weight) of nine prey types in the gut contents of 50 mm length classes (range: 140 – 640 mm fork length) of walleye in the North (a) and South (b) Basins of Lake Winnipeg, Manitoba.



(a)



(b)

Figure 5: Percent caloric contribution of nine prey types to the gut contents of walleye in the North (a) and South (b) Basin of Lake Winnipeg during the spring, summer, fall and winter (South Basin only).

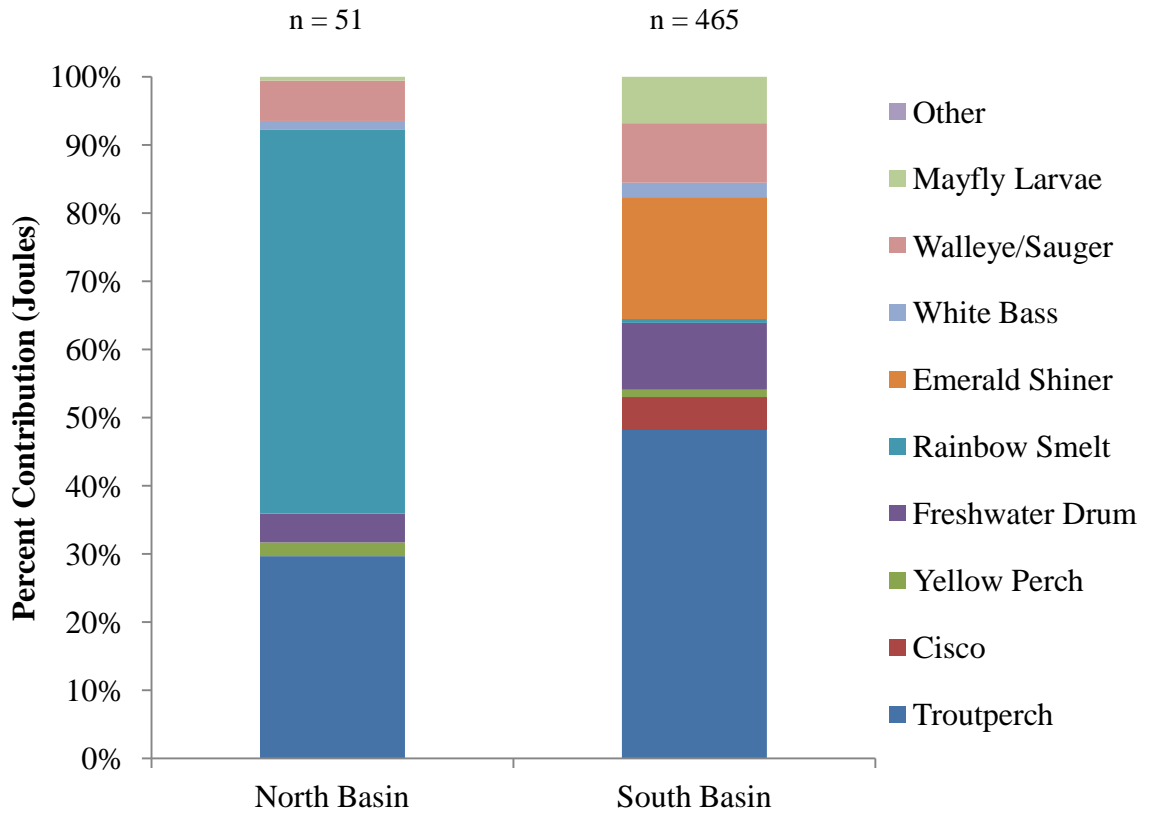
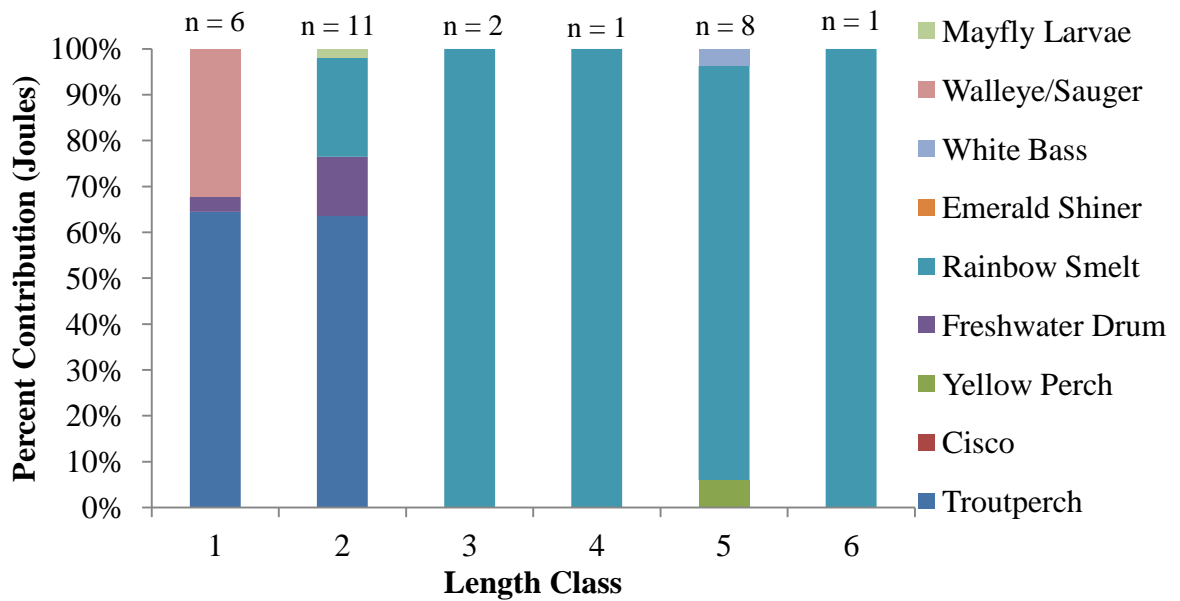
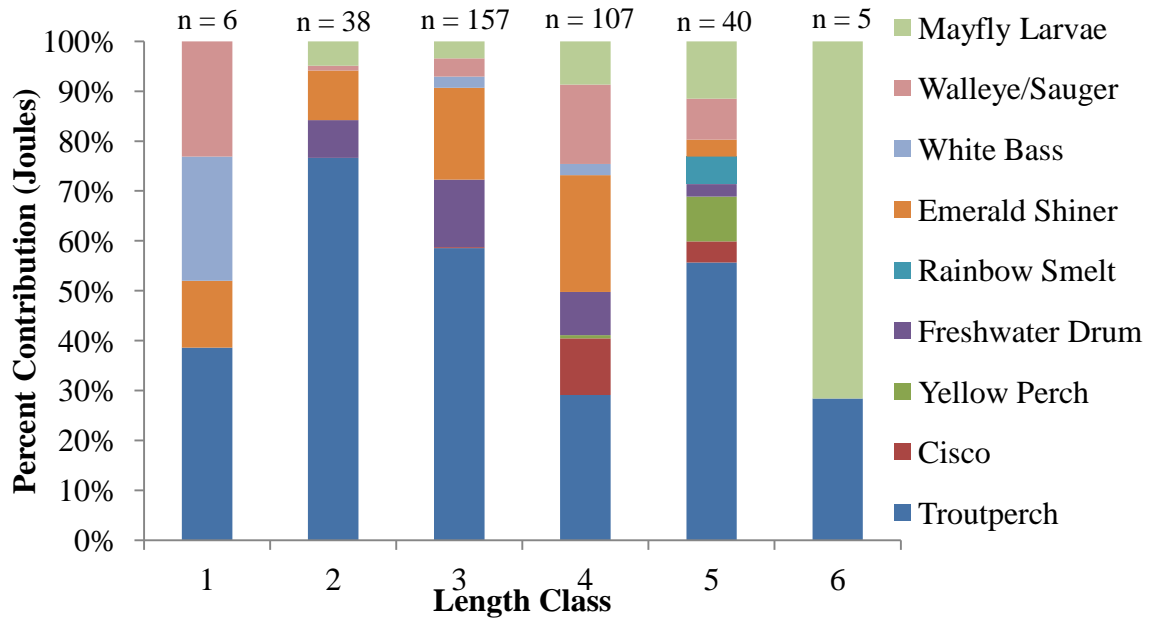


Figure 6: Percent composition by caloric content (Joules/g wet weight) of ten prey types ('other' consists of unknown fishes, burbot and ninespine stickleback) in the gut contents of sauger in the North and South Basins of Lake Winnipeg, Manitoba.

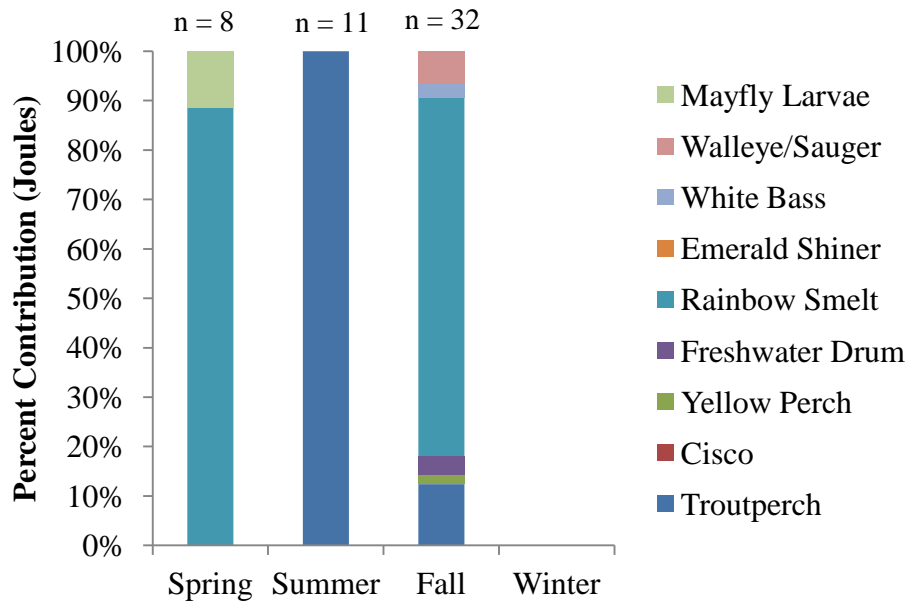


(a)

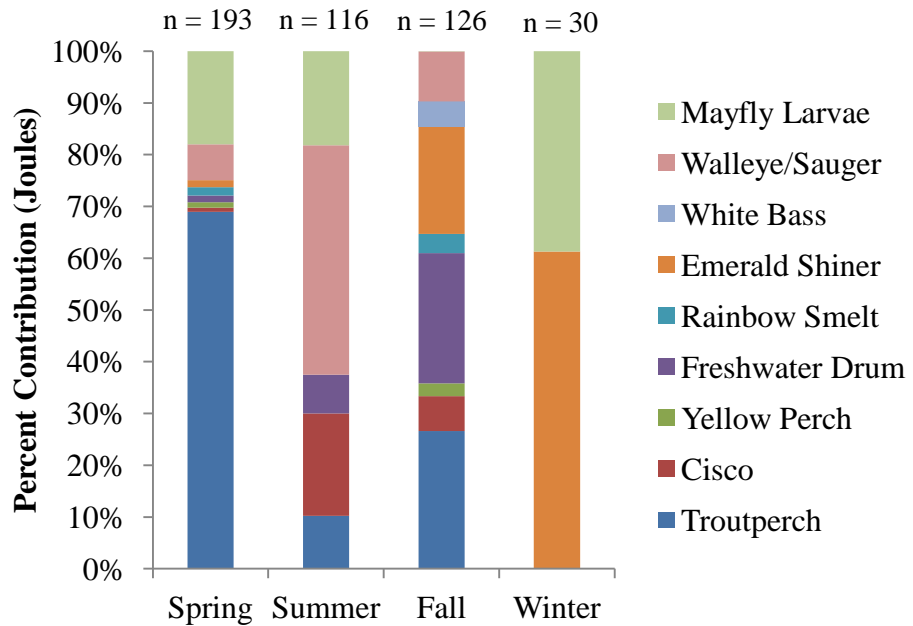


(b)

Figure 7: Percent composition by caloric content (Joules/g wet weight) of nine prey types in the gut contents of 50 mm length classes (range: 140-450 mm fork length) of sauger in the North (a) and South (b) Basins of Lake Winnipeg, Manitoba.



(a)



(b)

Figure 8: Percent caloric contribution of nine prey types to the gut contents of sauger in the North (a) and South (b) Basin of Lake Winnipeg during the spring, summer, fall and winter (South Basin only).

Appendix A: Photographs of representative otoliths from each prey type of walleye, sauger and dwarf walleye in Lake Winnipeg. Intervals on the scale bar in each photograph are 1 mm.



Yellow Perch (*Perca flavescens*)



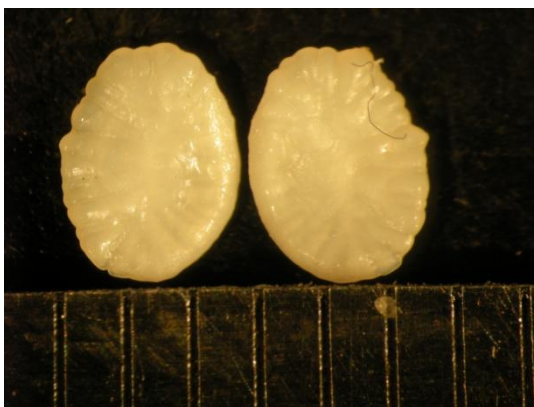
White Bass (*Morone chrysops*)



Emerald Shiner (*Notropis atherinoides*)



Cisco (*Coregonus artedii*)



Freshwater Drum (*Aplodinotus grunniens*)



Trout-perch (*Percopsis omiscomaycus*)



Rainbow Smelt (*Osmerus mordax*)

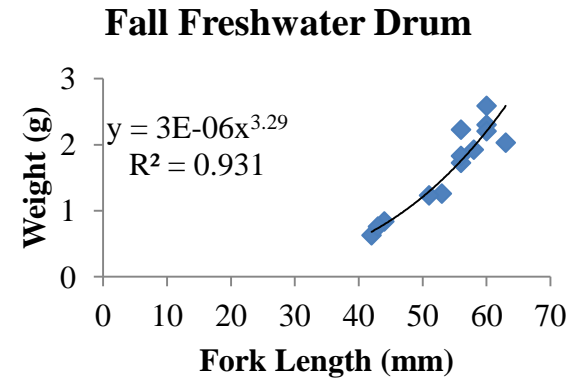
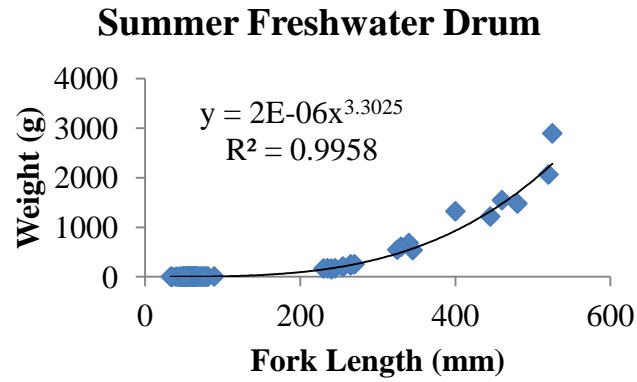
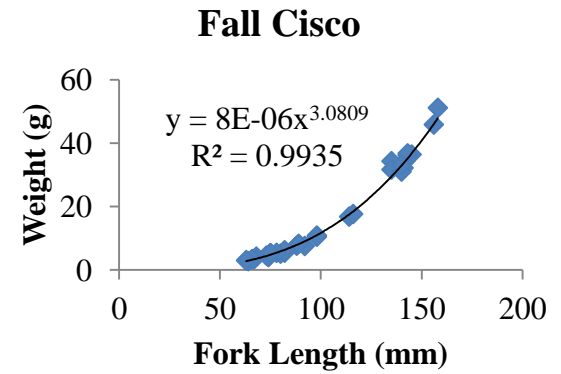
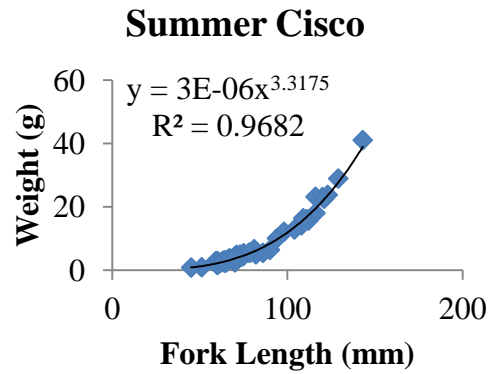
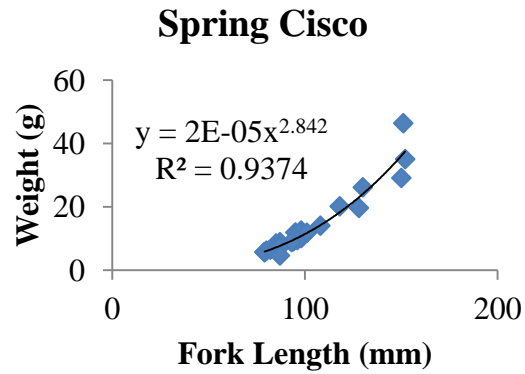


Sauger (*Sander canadensis*)

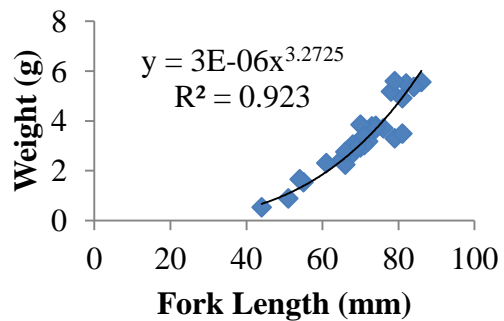


Walleye (*Sander vitreus*)

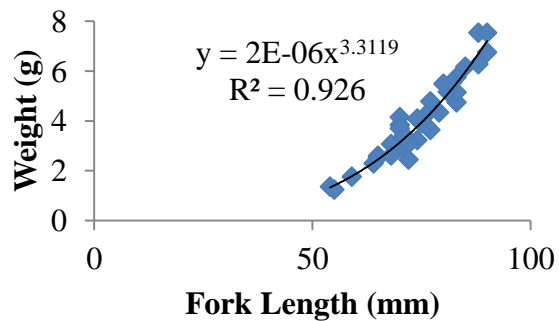
Appendix B: Fork length - weight and otolith length - fork length relationships for all prey type of walleye, sauger and dwarf walleye.



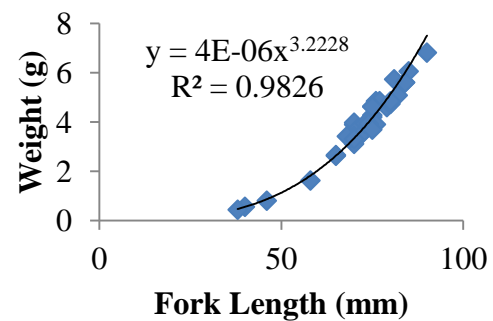
Spring Emerald Shiner



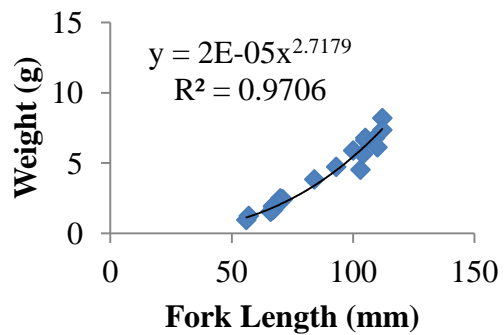
Summer Emerald Shiner



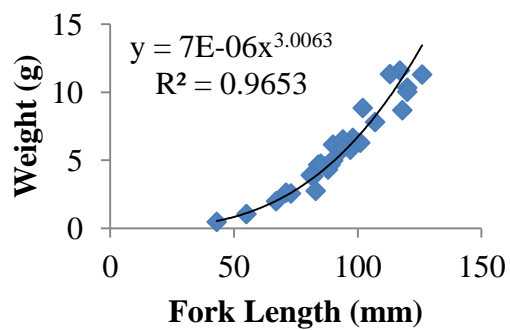
Fall Emerald Shiner



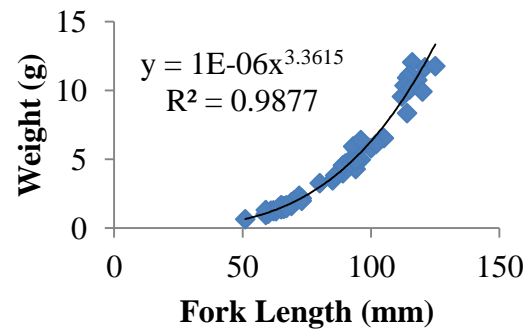
Spring Rainbow Smelt



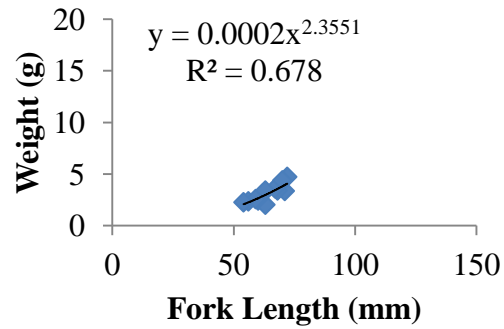
Summer Rainbow Smelt



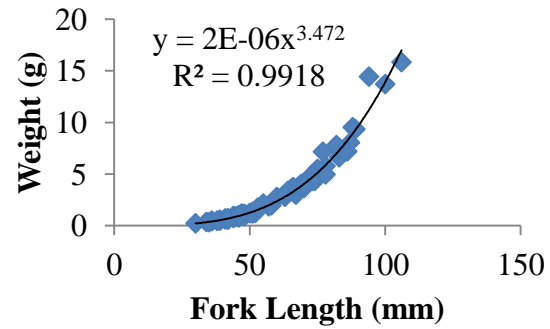
Fall Rainbow Smelt



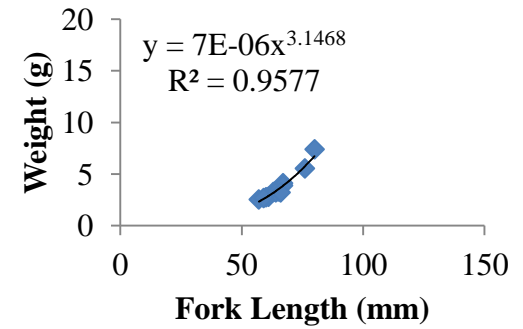
Spring Troutperch



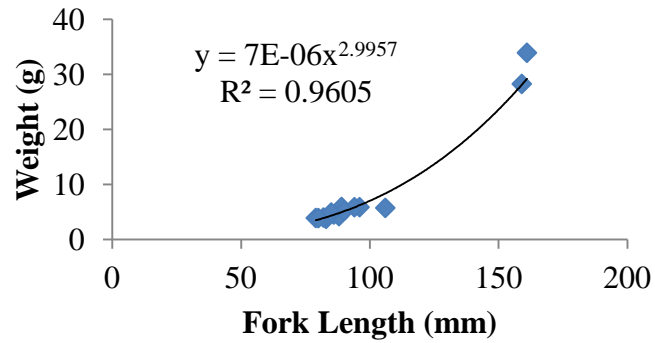
Summer Troutperch



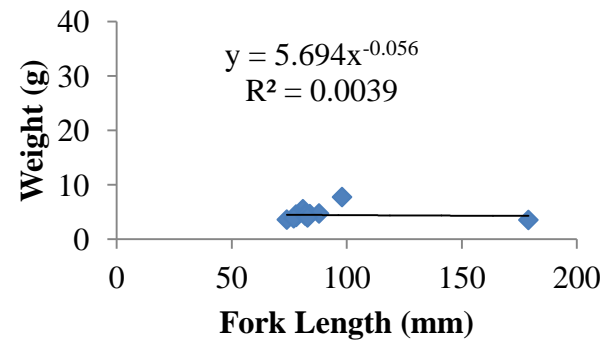
Fall Troutperch



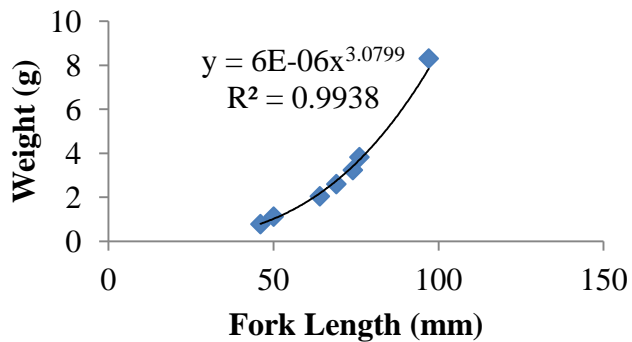
Spring Walleye/Sauger



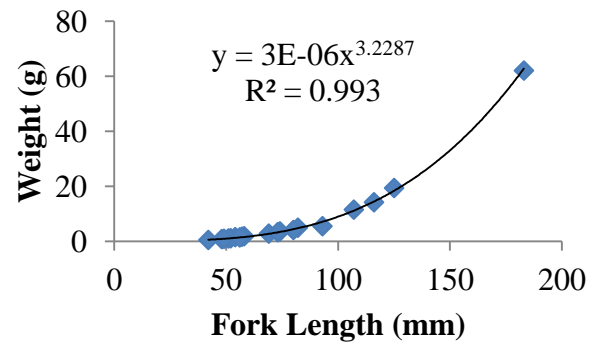
Fall Walleye/Sauger



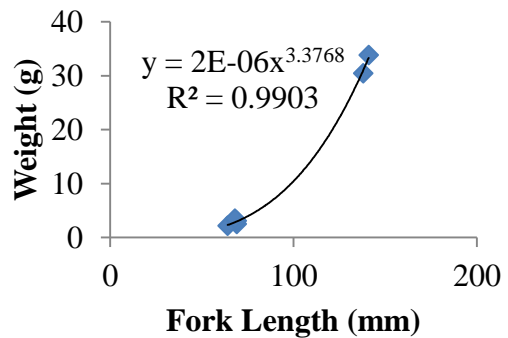
Summer Sauger



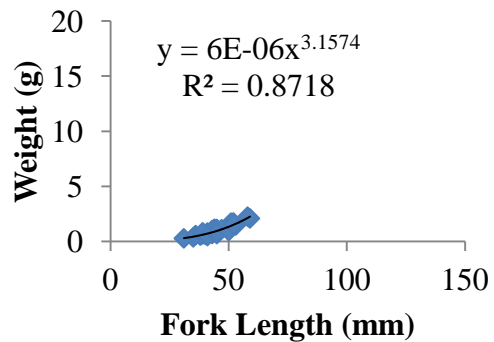
Summer Walleye



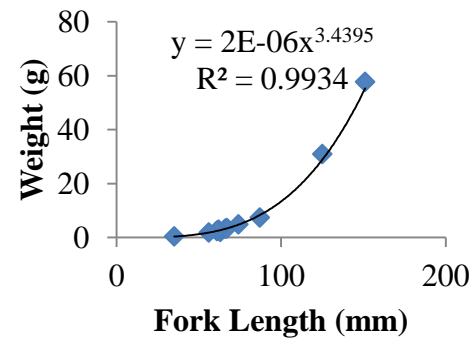
Spring Yellow Perch



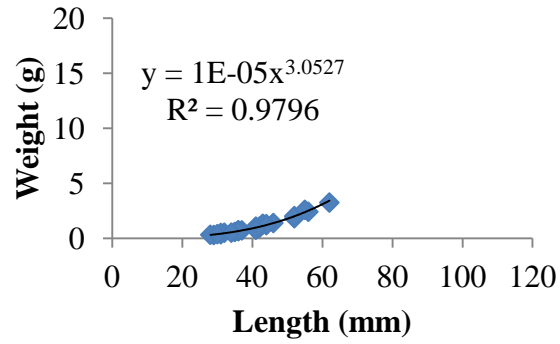
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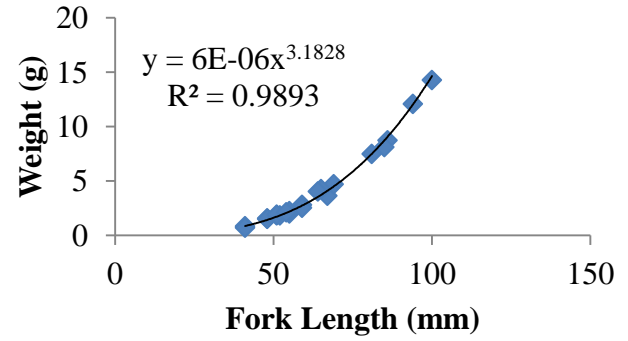
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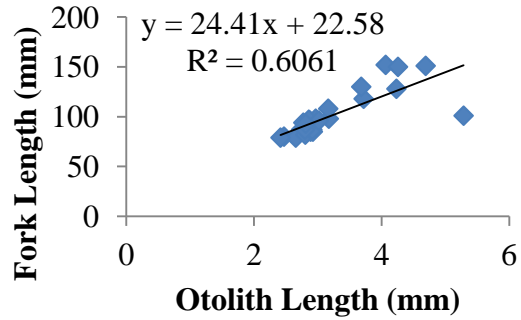
Summer White Bass



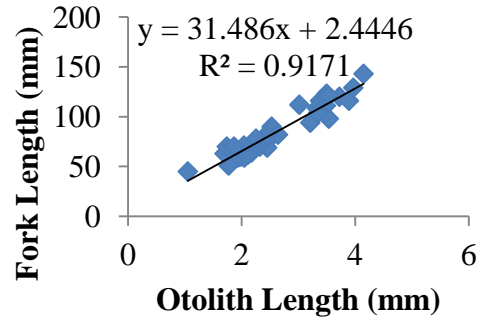
Fall White Bass



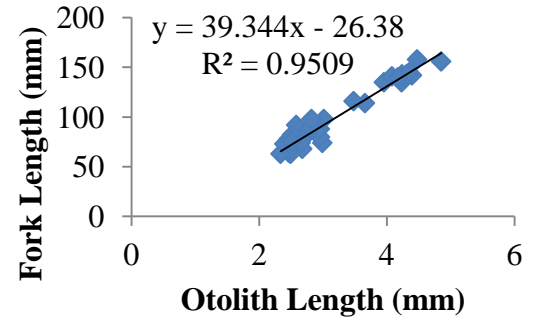
Spring Cisco



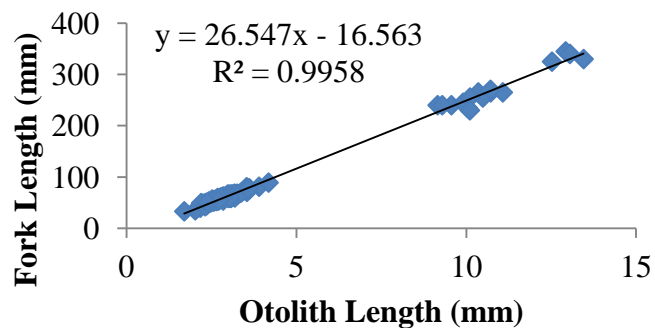
Summer Cisco



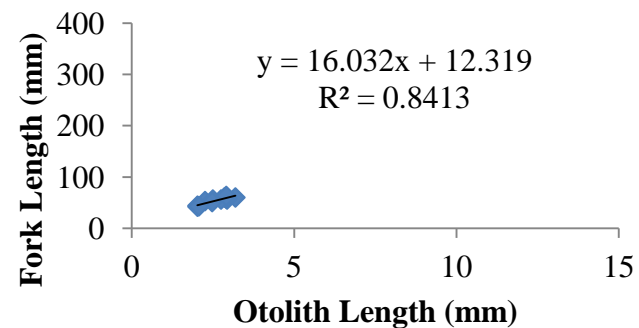
Fall Cisco



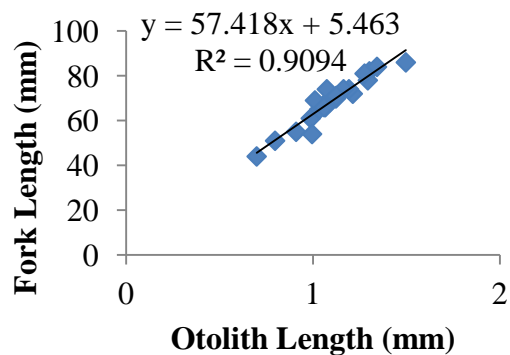
Summer Freshwater Drum



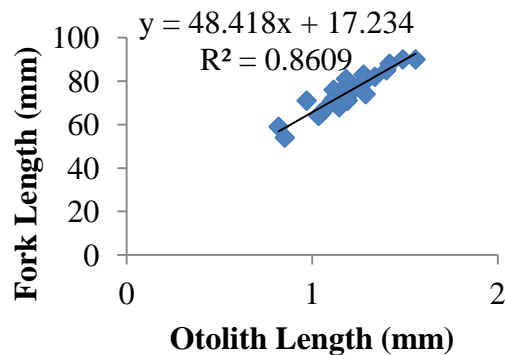
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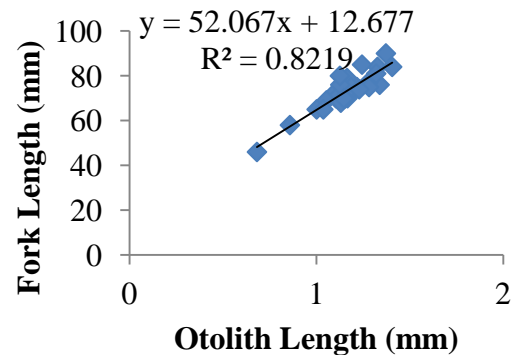
Spring Emerald Shiner



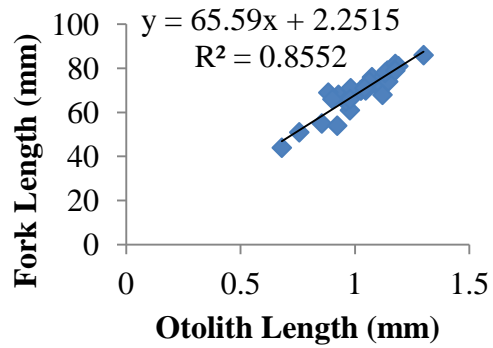
Summer Emerald Shiner



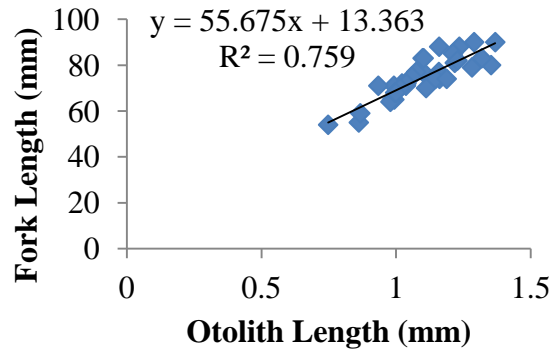
Fall Emerald Shiner



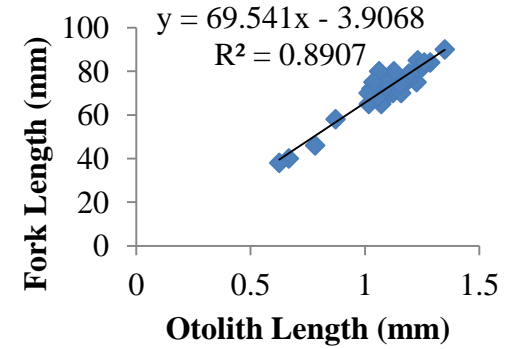
Spring Emerald Shiner



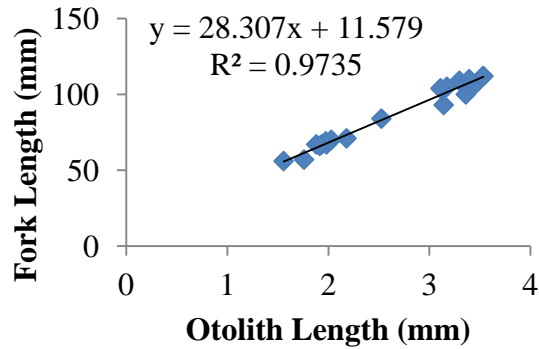
Summer Emerald Shiner



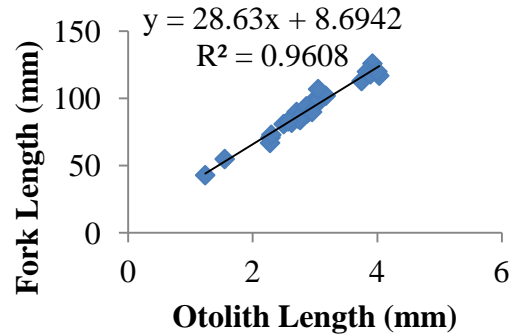
Fall Emerald Shiner



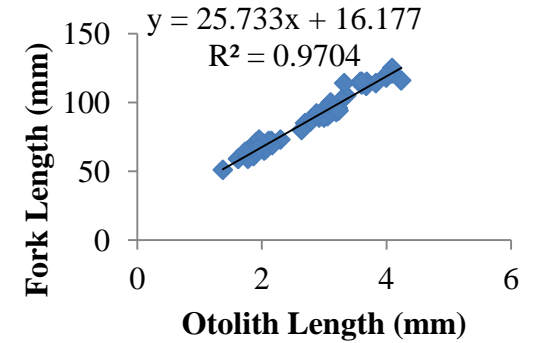
Spring Rainbow Smelt



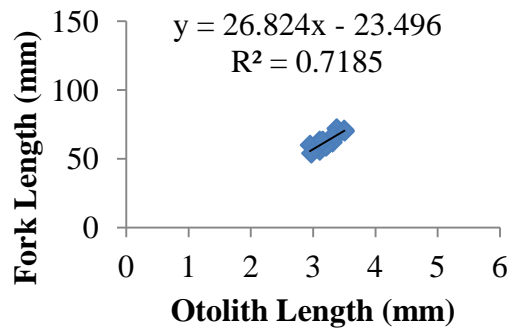
Summer Rainbow Smelt



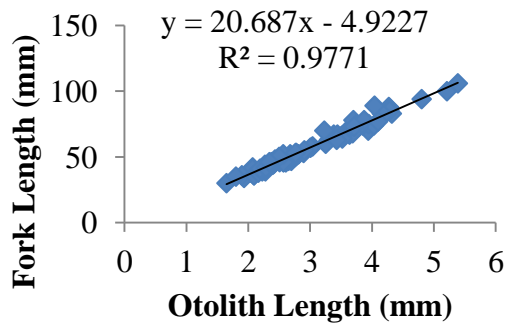
Fall Rainbow Smelt



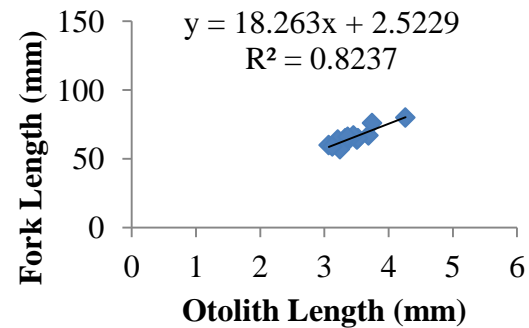
Spring Troutperch



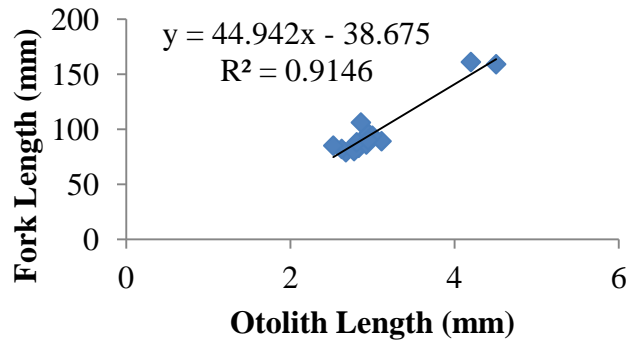
Summer Troutperch



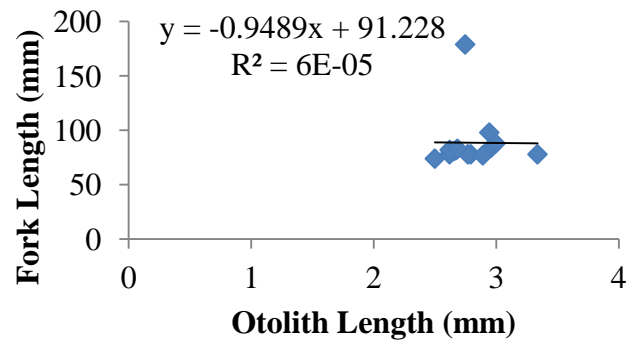
Fall Troutperch

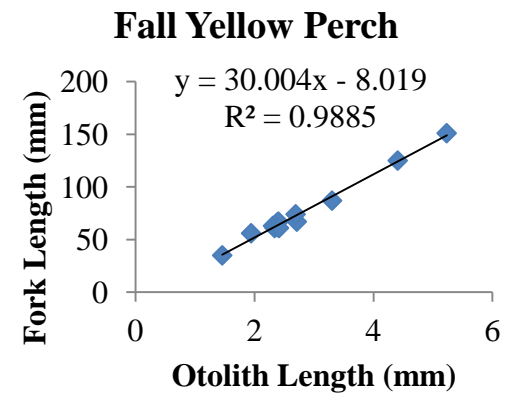
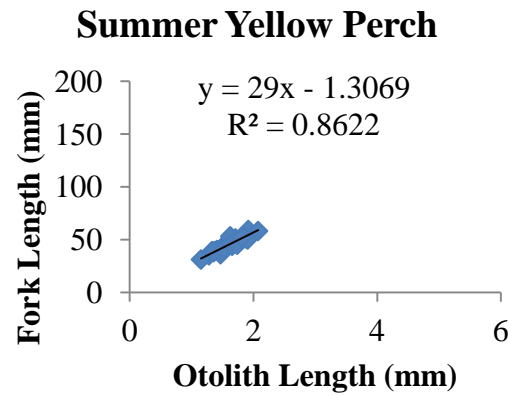
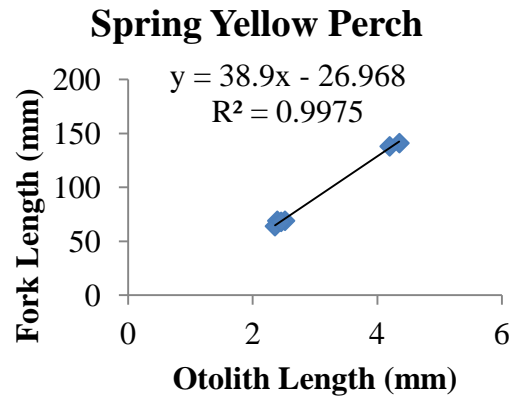
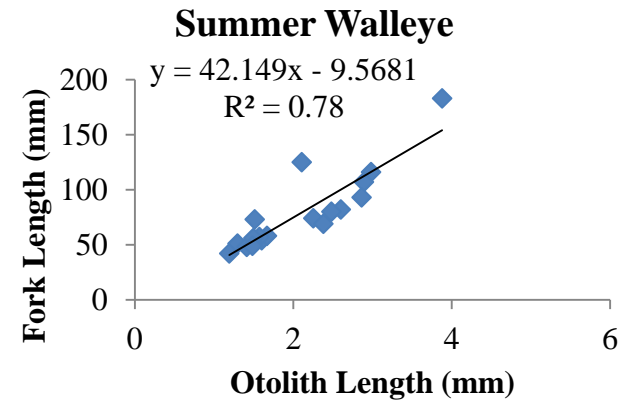
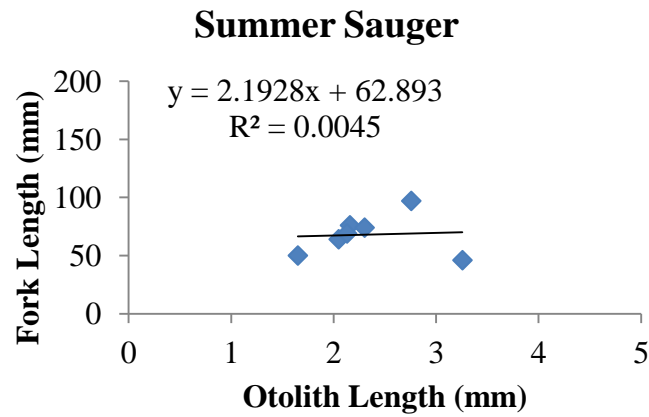


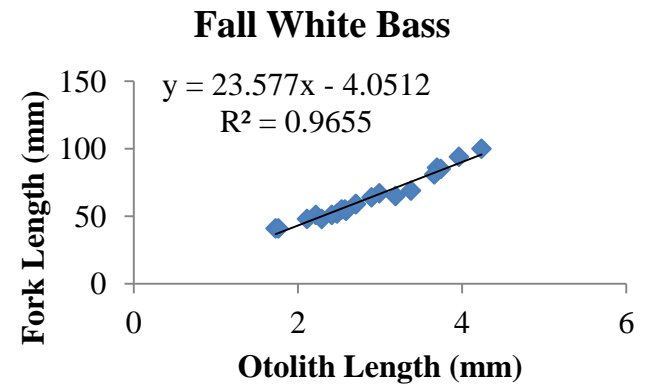
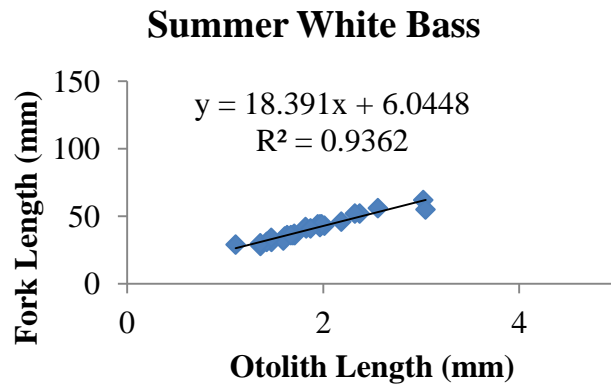
Spring Walleye/Sauger



Fall Walleye/Sauger







Appendix C: Chi Square Tables for statistical comparison of diet for walleye and sauger, spatially and seasonally. NS indicates that the p value was larger than 0.05 and; therefore, was not significant. Basin comparisons were done using one degree of freedom and seasonal comparisons were done using two degrees of freedom for North Basin and three degrees of freedom for the South Basin (because winter samples only exist in the South Basin).

Walleye

Basin Comparison

Prey	Length Classes																			
	1		2		3		4		5		6		7		8		9		10	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	2	NS	1	NS	0.26	NS	1.54	NS	0.41	NS	1.67	NS	0	NS	0	NS	0	NS
Drum	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
ES	0	NS	0.67	NS	12	< 0.001	13.09	< 0.001	10.95	< 0.001	16.9	< 0.001	2.4	NS	0	NS	0.4	NS	0	NS
Mayfly	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
RS	0	NS	3.33	NS	7.14	< 0.01	29.92	< 0.001	29.58	< 0.001	10.1	< 0.01	3.23	NS	0	NS	5	< 0.05	0	NS
TP	0	NS	0.67	NS	1	NS	3.65	NS	1.67	NS	4.33	< 0.05	0	NS	0	NS	0	NS	0	NS
WA/SG	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
WB	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
YP	0	NS	1.33	NS	7.36	< 0.01	4.26	< 0.05	6.67	< 0.01	1.71	NS	0	NS	0	NS	0	NS	0	NS

Season Comparison

North Basin

Prey	Length Classes																			
	1		2		3		4		5		6		7		8		9		10	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	0	NS	0.78	NS	0.08	NS	5.08	NS	0.75	NS	0	NS	0	NS	0	NS	0	NS
Drum	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
ES	0	NS	0	NS	0	NS	0	NS	1.92	NS	3.64	NS	1	NS	0	NS	0	NS	0	NS
Mayfly	0	NS	0	NS	15	< 0.001	9	< 0.05	0.75	NS	0.37	NS	9	< 0.05	0	NS	0	NS	0	NS
RS	0	NS	0	NS	0.81	NS	0.92	NS	0.09	NS	0.18	NS	1	NS	0	NS	0	NS	0	NS
TP	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
WA/SG	0	NS	0	NS	0.78	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
WB	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
YP	0	NS	0	NS	0.67	NS	0	NS	0	NS	0.86	NS	0	NS	0	NS	0	NS	0	NS

South Basin

Prey	Length Classes																			
	1		2		3		4		5		6		7		8		9		10	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	1.5	NS	1.8	NS	1.1	NS	5.69	NS	0.17	NS	0.5	NS	0	NS	0	NS	0	NS
Drum	0	NS	0	NS	0.2	NS	20.56	< 0.001	23.64	< 0.001	0	NS	0	NS	0	NS	0	NS	0	NS
ES	0	NS	0.5	NS	1.2	NS	6.86	NS	4.97	NS	2.13	NS	5.5	NS	0.3	NS	0.3	NS	1	NS
Mayfly	0	NS	0	NS	2.2	NS	8.43	< 0.05	19.66	< 0.001	9.11	< 0.05	0.88	NS	0.3	NS	0	NS	0	NS
RS	0	NS	0.5	NS	1.2	NS	1.32	NS	2.84	NS	0.57	NS	5	NS	0	NS	0	NS	0	NS
TP	0	NS	2	NS	2.2	NS	1.7	NS	5.55	NS	1.43	NS	0	NS	0	NS	0	NS	0	NS
WA/SG	0	NS	0	NS	1	NS	1.57	NS	0.58	NS	0	NS	0	NS	0	NS	0	NS	0	NS
WB	0	NS	0	NS	0.4	NS	5.28	NS	7.8	NS	1.43	NS	0	NS	0	NS	0	NS	0	NS
YP	0	NS	0.25	NS	4.32	NS	1.59	NS	8.65	< 0.05	1.43	NS	0	NS	0	NS	0	NS	0	NS

Sauger

Basin Comparison

Prey	Length Classes											
	1		2		3		4		5		6	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	0	NS	0.03	NS	0.1	NS	0.26	NS	0	NS
Drum	1.25	NS	1.17	NS	0.27	NS	0.14	NS	0.52	NS	0	NS
ES	0.8	NS	0.17	NS	0.57	NS	0.31	NS	0.13	NS	0	NS
Mayfly	0	NS	0.35	NS	0.7	NS	0.24	NS	0.91	NS	0.8	NS
RS	0	NS	6	< 0.05	74	< 0.001	58	< 0.001	8.93	< 0.01	5	< 0.05
TP	0.05	NS	0.71	NS	0.92	NS	0.34	NS	1.57	NS	0.2	NS
WA/SG	0.025	NS	0.17	NS	0.16	NS	0.21	NS	0.26	NS	0	NS
WB	0.8	NS	0	NS	0.08	NS	0.3	NS	7.67	< 0.01	0	NS
YP	0	NS	0	NS	0	NS	0.3	NS	0.71	NS	0	NS

Season Comparison

North Basin

Prey	Length Classes											
	1		2		3		4		5		6	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
Drum	0.33	NS	1.33	NS	0	NS	0	NS	0	NS	0	NS
ES	0	NS	0	NS	0	NS	0	NS	0	NS	0	NS
Mayfly	0	NS	4	NS	0	NS	0	NS	0	NS	0	NS
RS	0	NS	0.67	NS	0	NS	0	NS	0.25	NS	0	NS
TP	0.67	NS	4	NS	0	NS	0	NS	0	NS	0	NS
WA/SG	0.33	NS	0	NS	0	NS	0	NS	0	NS	0	NS
WB	0	NS	0	NS	0	NS	0	NS	0.5	NS	0	NS
YP	0	NS	0	NS	0	NS	0	NS	0.5	NS	0	NS

South Basin

Prey	Length Classes											
	1		2		3		4		5		6	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Cisco	0	NS	0	NS	7.07	NS	4.33	NS	0.2	NS	0	NS
Drum	0	NS	11.29	< 0.05	13.46	< 0.001	9.34	< 0.05	4.05	NS	0	NS
ES	0.67	NS	15.57	< 0.001	29.45	< 0.001	7.51	NS	1.09	NS	0	NS
Mayfly	0	NS	1.86	NS	11.73	< 0.001	19.49	< 0.001	7.64	NS	1	NS
RS	0	NS	0	NS	0	NS	0	NS	1.09	NS	0	NS
TP	3	NS	4.32	NS	10.27	< 0.05	3.22	NS	3.05	NS	4	NS
WA/SG	0.67	NS	0.49	NS	1.2	NS	1.83	NS	1.15	NS	0	NS
WB	0.67	NS	0	NS	5.41	NS	1.41	NS	0	NS	0	NS
YP	0	NS	0	NS	0	NS	1.41	NS	3.9	NS	0	NS

Chapter 3: Variation in growth rate and condition of walleye, dwarf walleye and sauger

Introduction

Fish population dynamics are an integrated response to a number of physical, chemical and biological factors. These factors influence important aspects of life history, such as growth rate, length, weight, mesenteric fat levels and overall body condition of fish (Huh et al. 1976; Quist et al. 2002; Hoxmeier et al. 2006; Kaufman et al. 2007; McPherson et al. 2011). Growth rate is commonly assessed as a change in length over time (age) and varies among individuals of a population (Kaufman et al. 2009). Body condition refers to the weight of individuals at a particular length, wherein a fish of the same length as another but weighing more, is in better condition (Hansen and Nate 2005; VanDeValk et al. 2008). A fish in better condition has higher energy reserves which can be put toward reproduction and growth than a fish in poor condition (Kaufman et al. 2007; VanDeValk et al. 2008; McPherson et al. 2011). Among many other factors, diet is an important determinant of growth rate and condition because higher energy consumption should translate into higher energy stores which can be allocated to growth, maintenance or reproduction (Madenjian et al. 1996; Einfalt and Wahl 1997; VanDeValk et al. 2008; Kaufman et al. 2009). It is important to study and integrate these factors to understand and manage fish populations, from both economic and ecological perspectives.

Walleye (*Sander vitreus*) and sauger (*Sander canadensis*) are large, piscivorous fish that are economically and ecologically important in North America, and whose

growth and condition have been examined in many ecosystems. Growth rates tend to vary with the productivity of the environment, with higher energy consumption translating into higher growth rates (Stewart and Watkinson 2004). Similarly, condition of piscivorous fishes is clearly linked to diet, prey availability and growth (VanDeValk et al. 2008). Other factors that influence growth and condition include prey type, water temperature, population density, as well as natural and fishery-induced mortality. Temperature is a key factor for north temperate piscivores, influencing foraging behaviour, metabolism (leading to growth), condition and survival, among other things (Quist et al. 2002). Optimum temperatures for walleye are below 22°C and optimum growth has been documented when water temperatures are 12-15°C (Quist et al. 2002). As water temperatures increase above 22°C, walleye reduce foraging activities and have lower consumption rates, growth and condition (Quist et al. 2002).

Seasonal variation in growth and condition is widely documented; these predatory fishes grow rapidly in the summer and fall after spawning, followed by slower growth in winter and spring to conserve energy for over-wintering and subsequent spawning (Quist et al. 2002; Kaufman et al. 2009). The condition of walleye also peaks during late summer and fall after maximizing prey consumption rates post-spawn (Quist et al. 2002). Condition then declines during the winter and particularly in spring as reserve energy is allocated to gonadal development and spawning (Quist et al. 2002). When determining growth rates of individuals in walleye populations, males and females must be examined separately because females typically attain a larger size than males (Scott and Crossman 1998; Purchase et al. 2005; Madenjian et al. 2009; Johnston et al. 2010). Similarly, condition often varies with sex of the fish, but trends vary among populations. For instance,

Kaufman et al. (2007) showed that roughly half the Canadian walleye populations examined pre-spawning and during spawning, showed higher condition in females and the other half higher condition in males.

Body condition in fish is assessed in several ways, all intended to evaluate the energy reserves of an individual. Condition in fish can be measured using morphometric, bioenergetic or biochemical techniques (McPherson et al. 2011). Some morphometric measures for fish include Fulton's Condition Factor (Kaufman et al. 2007), the relative weight index (Kaufman et al. 2007; VanDeValk et al. 2008), the adjusted relative weight index (Hansen and Nate 2005), and the relative condition index (Kaufman et al. 2007). Bioenergetic techniques are useful in categorizing condition based on deposits of fat in specific areas and organs of a fish, such as the liver (e.g. liver condition index) or mesentery (e.g. mesenteric fat level; McPherson et al. 2011). Biochemical techniques, including total muscle fatty acid and body lipid content analysis (Kaufman et al. 2007; McPherson et al. 2011), are most accurate but used less often because they are expensive and time consuming (McPherson et al. 2011). As walleye, and likely sauger, are known to store their fat in the viscera (Henderson and Morgan 2002; Kaufman et al. 2007), mesenteric fat stores, combined with morphometric measures of condition, can provide important information about body condition.

Lake Winnipeg, Manitoba is the tenth largest freshwater lake in the world by surface area and it supports the second largest inland fishery in Canada focusing on walleye and sauger (Johnston et al. 2010). Prey species in Lake Winnipeg that are potentially important in the diet of walleye, sauger and dwarf walleye (a growth morphotype) include the invasive rainbow smelt (*Osmerus mordax*) as well as native forage fishes, e.g., cisco

or lake herring (*Coregonus artedii*), troutperch (*Percopsisisomiscomaycus*) and emerald shiner (*Notropis atherinoides*). Lake Winnipeg has two distinct basins that have different prey fish communities and abundance. The most pronounced difference is the predominance of rainbow smelt in the North Basin and its near absence in the South Basin, compared with the reciprocal distribution of emerald shiner with its prevalence in the South Basin (Lumb et al. 2012). Prey abundance is higher in the South Basin relative to the North Basin (Lumb et al. 2012). Cisco, young white bass, young yellow perch and young walleye are the next most abundant prey species in the lake (Lumb et al. 2012). Prey associated with the bottom (i.e. troutperch and freshwater drum) have not been sampled for presence or abundance in this lake (Lumb et al. 2012).

A number of factors may lead to differences in growth and condition of walleye and sauger between basins in Lake Winnipeg. For instance, rainbow smelt invasions in other ecosystems have been linked to increased growth of walleye (e.g., Jones et al. 1994). Similarly, heavily exploited walleye populations tend to be in better condition (i.e., have a higher body lipid content; Kaufman et al. 2007). Exploitation of fish decreases the density of individuals in the population and effectively removes prey density as a limiting factor. Lake Winnipeg is considered to have a highly exploited walleye population compared to other known systems (Kaufman et al. 2007). The large commercial fishery for walleye and sauger on Lake Winnipeg brings in 48 million kilograms and roughly 142 million dollars to Manitoba every year (Manitoba Water Stewardship, Fisheries Branch 2008). There is higher fishing pressure in the South Basin of the lake owing to higher human population density around that basin and the comparative inaccessibility of the North Basin. Additionally, there are many other environmental differences between

basins, such as depth, temperature, turbidity, nutrient loading, as well as prey abundance and community composition differences outlined above (see Table 1 in Chapter 1).

Objectives

The first objective of this study was to determine if the growth and condition of walleye, sauger and dwarf walleye differed between the North and South Basin of Lake Winnipeg. Due to sex-based differences in reproductive allocation, sex-specific growth rates and body condition were compared for walleye, sauger and dwarf walleye. I hypothesized that female walleye and sauger have higher growth rates and condition than males in both basins. I also hypothesized that females and males of both species have different growth rates and condition between basins. If rainbow smelt presence and abundance is an important factor determining growth rates and condition, I predict that fish will have higher growth rates and condition in the North Basin relative to the South Basin. Alternately, if exploitation rates and prey abundance are more important in determining growth rates and condition, I predict that fish will have higher growth rates and condition in the South Basin relative to the North Basin. This study will lead to a better understanding of the potential impacts of the invasive rainbow smelt on walleye populations in Lake Winnipeg, and will provide baseline data to assess future threats.

Methods and Materials

Field Sampling

Walleye and sauger were collected by gill-netting and trawling in the North and South Basins of Lake Winnipeg during spring (2010 and 2011), summer (2010) and fall (2010 and 2011), whereas commercial fisherman provided fish in the winter (2010-2011). Trawls were conducted by Manitoba Conservation and Water Stewardship, Fisheries Branch, at up to 65 stations on Lake Winnipeg from the M.V. *Namao*, owned and operated by the Lake Winnipeg Research Consortium (Figure 1 in Chapter 2). A maximum of 30 walleye and 30 sauger > 200 mm fork length were sampled from these trawls. Gill-netting was performed in four locations (time and weather permitting) in the South Basin (Hecla Island, Victoria Beach, Gimli and Pine Dock) and seven locations (time and weather permitting) in the North Basin (Berens River, George Island, Station 20, Warren's Landing, Eagle Island, Grand Rapids and Station 43S), from a yawl deployed from the M.V. *Namao*, with the number of locations varying seasonally and annually (Figure 1 in Chapter 2). Multiple-panel gill-nets of varying mesh sizes (25 – 127mm) were set perpendicular to the shore for 12 h overnight. The commercial fishermen who provided samples in the winter of 2010-2011 used gill nets deployed through the ice near Gimli, MB.

Up to 30 walleye and 30 sauger were randomly subsampled from the available catch at each location. An identification (ID) number was assigned to each fish and the species/morphotype, fork length (mm), round weight (wet weight or fresh weight; g; Kaufman et al. 2009), sex and maturity were measured and recorded. Morphotypes of normal and

dwarf walleye were verified in the laboratory based on length-at-age data and categorized according to standards established by Moles et al. (2010). The intestinal tract, including any mesenteric fat, was excised and placed into a pre-labeled 250 mL plastic bottle, filled to one-third its volume with 70% ethanol. Sagittae otoliths were removed, wiped clean, and placed in pre-labeled coin envelopes.

Laboratory Processing

Age was estimated for each fish to allow computation of growth rates (Kaufman et al. 2009). Sagittae otoliths have been shown to provide the most accurate estimate of age in walleye, sauger, and many other species (Logsdon 2007; Walsh et al. 2008; Graeb et al. 2010). Otoliths were first cracked in half across the nucleus and then the cracked edge was lightly burned over an alcohol burner. They were then placed, burnt side up, in modeling clay in a petri dish filled with water. A dissecting microscope at 10X magnification was used to count the annuli of the otoliths to determine the age of each fish (Logsdon et al. 2007; Graeb et al. 2010). Accuracy of the age determination was assessed by an expert (Laura Heuring, Manitoba Department of Conservation and Water Stewardship) who verified the age of 312 of the fish (accuracy was 90%).

The recorded length and round weight of each walleye and sauger were used in the computation of the relative condition index (K_n ; Hansen and Nate 2005) of each individual fish. In addition to this morphometric method, condition was assessed using a bioenergetic method, i.e., mesenteric fat stores, because walleye, and probably sauger, carry energy stores in their viscera (Henderson and Morgan 2002; Kaufman et al. 2007). Mesenteric fat levels in the body cavity were examined and rated qualitatively from 0-2; 0 -no

mesenteric fat (0-25%), 1- some (roughly 25-75%), and 2 - a large amount (75-100%) of mesenteric fat. It is important to note that most individuals had either a lot of mesenteric fat or very little and therefore category 1 was rarely assigned.

Data Analysis

The distribution of the length data was examined using Shapiro-Wilk and Kolmogorov-Smirnov tests and was best described as normal; therefore, parametric statistics were used. To determine if there were significant differences in growth rate between sex, species/morphotype and basin, an analysis of covariance (ANCOVA) was used which compares mean lengths adjusted to the average age. Any significant differences found in mean lengths indicate significant differences in growth rate. Both age and age² were used as covariates to ensure that the ANCOVA also represented non-linearity in the shape of the growth curve. Age as a covariate assumes a linear shape for the data while age² accounts for some degree of non-linearity. Sex, species and basin were used as factors in the analysis and all two-way and three-way interactions were included in the model.

The ANCOVA assumes that all species/morphotypes and sexes of fish have the same growth curve. Because of this, another approach was used where an analysis of variance (ANOVA) was performed on fish of the three major age classes to determine whether differences existed in length among fish at each age and whether, at a specific age, a species or sex was significantly different from another. There were sufficient data for ages 3-, 4- and 5-year old normal walleye and sauger, and these ANOVAs helped alleviate the issue of the rapidly changing shapes of the growth curves at these ages. However, fish older than age 5 had low sample sizes and were nearing the growth plateau

(Figure 1a, b and c); therefore, for these older fish it was reasonable to rely on ANCOVA with age and age² as the covariates. Significant differences in length at a specific age, found with the ANOVA, indicate significant differences in growth rate.

The relationship between age and length was fitted to several standard functions, e.g., power, polynomial, logarithmic, exponential and linear, in addition to the Von Bertalanffy growth curve, and the fit of the curves was tested using the Akaike Information Criterion (AIC) test. Many models were competing and plausible; however, the Von Bertalanffy growth curve was selected for its extensive use in fish growth studies and the opportunity to compare results with other studies. The Von Bertalanffy growth curve (Fork Length = $L_{\infty} * (1 - e^{-k(\text{Age}-t_0)})$) was constrained by the assumptions needed to fit the curve. The growth curve was constrained by defining the length at age zero as 0 cm and an estimate of the length at age infinity, the maximum length of fish caught for each sex and species/morphotype. There is evidence that constraining the Von Bertalanffy growth curve, as was done in this study, does not result in a substantial bias in either freshwater or reef fish species (Krtizer et al. 2001; Beauchamp 2002). This method is consistent with those of the provincial monitoring programs for this species as well as many other freshwater fish growth studies (Lumb et al. 2007).

Condition, calculated from the length and round weight recorded in the field, was used to determine an allometric linear regression for condition and a relative condition index (K_n). The K_n values were used to test the significance of ecological factors such as season and basin in an analysis of variance with *posthoc* pairwise comparison using Scheffé tests. The formula for K_n , follows Hansen and Nate (2005):

$$K_n = W / (\alpha L^\beta)$$

where W is the round weight (wet weight or fresh weight; g; Kaufman et al. 2009) of the individual, L is the length of the individual (mm), and α and β are regression coefficients from the function $\log(W) = \log(\alpha) + \beta \cdot \log(L)$ that was fit by least squares regression to the fishes being considered (species/morphotypes and sexes). The K_n values were plotted in a histogram to identify outliers (i.e., values three standard deviations outside the mean). One or two outliers were present in each species/morphotype and were eliminated before further testing. The remaining K_n data were consistent with a normal distribution (Used both Shapiro-Wilk and Kolmogorov-Smirnov tests).

The K_n values were used to determine how condition varied with maturity, sex (walleye only), basin and season, and were factors in the model (ANOVA). Interactions were also examined; however, due to an imbalance in the data available (low/no sample sizes in some basins/seasons), the basin-season interaction could be examined only if they were combined as a single factor. The Scheffé's multiple comparison analysis was used to determine differences between factors including the interaction between basins and among seasons. T-tests of the K_n values for walleye and sauger were used to compare the regression coefficients, α and β , to examine whether one species was in better condition than the other.

Condition based on the mesenteric fat index was analyzed to determine if condition index values varied with maturity, sex, species, basin and season as factors in the ANOVA model. A Scheffé's multiple comparison of the means was performed in addition to the analysis of variance to determine if there were significant differences in mesenteric fat levels. Additionally, an analysis of variance determined if there were significantly different mesenteric fat levels for fish with different K_n values, and a Pearson's

correlation was performed to determine whether these two condition indices were correlated.

Results

In total, 616 walleye, 32 dwarf walleye and 462 sauger were sampled. Although every effort was made to obtain samples for all species/morphotypes from each basin in each season, there were inevitable gaps. For example, only 2 dwarf walleye were obtained from the North Basin, suggesting that they may not be present in large numbers. Similarly, the numbers of each size and sex of fish varied between catches, so that most of the data were for 3- to 5-year old walleye and 3- to 5- and 7-year old sauger. As well, walleye >8 years old were mostly female.

Growth Rate

The growth rates of walleye, dwarf walleye, and sauger were significantly different; normal walleye had significantly higher growth rates than sauger, and both had significantly higher growth rates than dwarf walleye (ANCOVA, Table 1, Figure 1a). Walleye and sauger in the North Basin had higher growth rates than those in the South Basin (Figure 1b, c), and female walleye had higher growth rates than males (ANCOVA, Tables 1 and 2).

Separate ANCOVAs on subsets of the data were useful to investigate these interactions further. There were significant differences in length between walleye and sauger aged 3-5 years, with walleye being larger than sauger. Among 3-5 year old walleye and sauger, sex was a significant factor, with females usually larger than males (ANCOVA,

Table 1, Table 2), and basin was not significant (Table 1). Interactions in the model (basin*sex, species*sex, basin*species and basin*species*sex) were also not significant (Table 1). The covariates, age and age², were both statistically significant, illustrating that there was a curvilinear relationship between length and age (Table 1).

Each age class of walleye and sauger (age 3, 4 and 5) showed significantly different lengths between the two species as well as between sexes (Table 1). Walleye had consistently larger average fork lengths than sauger and females of both species had significantly larger average fork lengths than males (Table 2).

Age 5 walleye had significantly larger average fork lengths in the North relative to the South Basin; however, age 3 and 4 walleye did not (Table 1). Walleye in the North Basin generally had larger average fork lengths than the fish from the South Basin for the majority of ages (Table 2).

Sauger showed the same trends as walleye with North Basin fish having larger average fork lengths than South Basin fish for the majority of ages (Table 2). Age 5 sauger from the North Basin showed significantly larger average fork lengths than age 5 sauger from the South Basin (Table 1). Age 3 and 4 sauger showed no significant differences between basins (Table 1).

The growth of dwarf walleye was analyzed separately from normal growth walleye and the ages sampled were notably older than the majority of normal walleye samples (Table 2). The age and age² covariates were not statistically significant and there was no significant difference in growth between sexes (Table 1). An analysis of variation in growth between basins was not performed because dwarf walleye were not caught in the North Basin.

Condition

Walleye

The pattern of variation in condition of male and female walleye was examined by comparing allometric linear regressions (Table 3). No significant differences were found between coefficients of male and female walleye (t-test). Therefore, data for both sexes were combined in one linear regression for further analysis of the condition of walleye (Table 3).

Relative condition did not differ significantly for maturity and sex (ANOVA; Table 4). Season, basin and the combined season/basin factor were all found to be significant (Table 4). Scheffé's multiple comparison test of the mean K_n values revealed that the North Basin fish had significantly higher K_n than those in the South Basin (Table 5). Also, fish had significantly higher K_n in winter (2011) than any other season (Table 5). Fish in fall (2011) and spring (2010 and 2011) did not have a significant difference in K_n from each other (Table 5). Fall (2011) fish had a significantly higher K_n than fish in summer (2010) (Table 5). Fish from spring (2010 and 2011) and summer did not differ in K_n values (Table 5).

Walleye from different basins in Lake Winnipeg had significantly different mesenteric fat levels (ANOVA, $df = 1$, $F = 68.06$, $p < 0.001$), with walleye in the North Basin having a higher level of mesenteric fat than in the South Basin (Table 6, Figure 2c). Season was also statistically significant when looking at the differences in mesenteric fat in walleye (ANOVA, $df = 4$, $F = 40.27$, $p < 0.001$). In 2011, the mesenteric fat levels in walleye were different in spring, summer, fall and winter and their order from lowest to highest fat levels were: summer, fall, spring and winter (Table 6, Figure 2d). In 2010, the

fall fish had a higher level of mesenteric fat than fish from the fall in 2011 (Table 6, Figure 2d). Additionally, mesenteric fat levels were not significantly different between mature and immature walleye (ANOVA, $df = 1$, $F = 0.50$, $p = 0.479$; Table 6, Figure 2a). Sex was a statistically significant factor in the model (ANOVA, $df = 1$, $F = 63.90$, $p < 0.001$) with female walleye having a higher level of mesenteric fat than males (Table 6, Figure 2b).

When analyzing the two methods used for examining condition, the K_n values were significantly different for different levels of mesenteric fat in walleye (ANOVA, $df = 2$, $F = 14.93$, $p < 0.001$) when tested with mesenteric fat level as the main factor. Mesenteric fat levels 1 and 2 were not significantly different from each other; however, they were both significantly higher than fat level 0 (Scheffé's multiple comparison of means; Figure 3). Additionally, K_n and mesenteric fat level were significantly correlated ($r = 0.3198$, $p < 0.0001$).

Sauger

The pattern of variation in condition of male and female sauger was examined by comparing allometric linear regressions (Table 3). There were significant differences in the coefficients of male and female sauger (t-test, Table 3), thus the equations were left separate. As a result of this, sex was no longer an appropriate factor in the ANOVA for K_n of sauger data.

The K_n values for all sauger were used to test the effects of maturity, season and basin in an ANOVA. Maturity, season, and basin were all found to be significant factors in the model (Table 4). Similar to the walleye analysis, a combined season/basin factor

was conducted to examine their interaction using Scheffé's multiple comparison tests of the means. The season/basin factor was found to be significant, with North Basin sauger having significantly higher K_n than sauger in the South Basin (Table 5). Also, mature fish had significantly higher K_n than immature fish (Table 5). Fish in winter (2011) had a significantly higher K_n than fish in spring (2010 and 2011) and summer (2011); however, they had similar K_n to the fish in the fall (2011; Table 5). Condition of fish in fall (2011) was not significantly different from that in summer (2010) but was significantly higher than in spring (2010 and 2011). Spring (2010 and 2011) fish had the lowest K_n compared to fish in all other seasons (Table 5).

The mesenteric fat levels in sauger were significantly higher in mature fish than in immature fish (ANOVA, $df = 1$, $F = 12.45$, $p < 0.001$; Table 6, Figure 2a). Sex was not a statistically significant factor in the model (ANOVA, $df = 1$, $F = 1.44$, $p = 0.231$; Table 6, Figure 2b). Sauger from the North Basin in Lake Winnipeg had significantly higher mesenteric fat levels (ANOVA, $df = 1$, $F = 137.41$, $p < 0.001$) than the sauger in the South Basin (Table 6, Figure 2c). Season was not statistically significant when looking at the differences in mesenteric fat in sauger (ANOVA, $df = 4$, $F = 0.86$, $p = 0.488$); however, there were some subtle differences in spring, summer, fall and winter mesenteric fat trends (Table 6, Figure 2d).

The K_n value was significantly different for different levels of mesenteric fat in sauger (ANOVA, $df = 2$, $F = 10.94$, $p < 0.001$) when tested with mesenteric fat level as the main factor. Mesenteric fat levels 1 and 2 were not significantly different from each other; however, they were both significantly higher than fat level 0 (Scheffé's multiple

comparison of means; Figure 3). Additionally, K_n and mesenteric fat levels were significantly correlated ($r = 0.2107$, $p < 0.001$).

Dwarf Walleye

The pattern of variation in condition of dwarf walleye was examined using allometric linear regressions (Table 3) with coefficients and their standard errors in parentheses. Sexes were not separated because sample sizes were too small.

The relative condition (K_n) values for all dwarf walleye were used to test the effects of maturity, sex, season and basin in an ANOVA. Maturity and sex were not significant factors; thus, pooling the sexes in the allometric linear regression step of the analysis was appropriate (Table 4). Season was found to be significant (Table 4). Scheffé's multiple comparison test of the means of the K_n values showed that the dwarf walleye in the fall (2011) had significantly higher K_n than those in the spring (2010 and 2011); however, there was no significant difference in K_n when compared to the dwarf walleye in the summer (2010) or winter (2011; Table 5). The result of the comparison using winter (2011) fish is not necessarily representative due to a very low sample size ($n=1$) and so, these fish will not be included in the interpretation of these results.

The mesenteric fat levels in all dwarf walleye caught were zero, meaning there was no mesenteric fat regardless of the maturity, sex or season (Table 6). All dwarf walleye were from the South Basin; therefore, there was no comparison between basins (Table 6).

Discussion

The objective of this study was to examine the differences in growth and condition between basins and among seasons for walleye, sauger and dwarf walleye. The potential impact of the invasive rainbow smelt on the growth and condition of these fishes will also be discussed. Growth rates of walleye and sauger were higher and fish at age 5 were larger in the North Basin than in the South Basin of Lake Winnipeg. The condition of walleye and sauger also were significantly higher in the North than in the South Basin. Morphometric methods of measuring condition were correlated with bioenergetic methods, i.e., the mesenteric fat index, providing validation that both methods are useful measures of condition for walleye and sauger. Seasonal variation in condition was observed, as found in many north temperate ecosystems and many fish species, it was highest at the end of the growing season (late summer – winter) and lowest during and after spawning (Cren 1951; Hansen and Nate 2005; Kaufman et al. 2007; Vassilopoulou and Harabalabous 2008; McPherson et al. 2011). Overall, walleye had higher growth rates than sauger, consistent with reports in the literature (Scott and Crossman 1998; Stewart and Watkinson 2004; Johnston et al. 2010) and female walleye were significantly longer than males, as is common in many fish species with divergent sex-specific energy demands during spawning (Roff 1983).

Growth and condition were higher in the North Basin while the South Basin has higher commercial exploitation of walleye (Johnston et al. 2010) as well as higher prey abundance compared to the North Basin (Lumb et al. 2012). This suggests that the higher growth and condition in the North Basin may be influenced more by the presence of non-indigenous rainbow smelt that is almost exclusively in that basin of Lake Winnipeg. The

invasion of rainbow smelt into other systems has been associated with similarly higher growth of walleye (e.g., Jones et al. 1994), an effect that is also reported with invasions of alewife (Cade et al. 2008). Higher growth rate of walleye has also been associated with increases in abundance of native prey species in other systems such as cisco, gizzard shad and bluegill sunfish, which are all profitable prey types in terms of their morphology, energy density and behavioural differences (ie. predator escape response; Swenson and Smith 1976; Knight et al. 1984; Hartman and Margraf 1992; Madenjian et al. 1996; Einfalt and Wahl 1997; Porath and Peters 1997; Kaufman et al. 2009). Rainbow smelt have a fusiform body shape with no spines (Hoyle and Keast 1987), and gizzard shad, alewife and cisco are similarly soft-rayed with deep compressible bodies, features making them easy to ingest (Hoyle and Keast 1987; Einfalt and Wahl 1997). In contrast, bluegill have spines on their anal fins making ingestion more difficult. Einfalt and Wahl (1997) showed that the time and energy required to pursue, capture and ingest bluegill were higher than for other species such as gizzard shad; however, their abundance may be much greater in their relative systems.

Abiotic factors, such as temperature, light and turbidity, can also affect the growth and condition of fish. Temperature for poikilotherms, which cannot regulate their body temperature, influences everything from food consumption, reproduction and metabolism to growth, condition, survival and behavior (Huh et al. 1976; Beamish and MacMahon 1988; Quist et al. 2002). One would expect higher growth and condition in warmer waters (summer through fall in north temperate regions), recognizing that there is an upper tolerance level for walleye of 22°C (Quist et al. 2002). For the most part, the temperature of Lake Winnipeg is within the limits for walleye and sauger and the North Basin is

slightly cooler on average than the South Basin (see Table 1 in Chapter 1). Light and turbidity are important for the foraging behavior of a fish (Huh et al. 1976; De Robertis et al. 2003); however, this seems to affect piscivores less than planktivores (De Robertis et al. 2003). Walleye and sauger, in particular, have advantages over other species in highly turbid waters because of the presence of the *tapetum lucidum* in the retina of their eye (Ali and Anctil 1977; Ryder 1977; Braekevelt et al. 1989). Waters with low turbidity and high light have been reported to reduce the activity level of adult walleye (Ryder 1977). Additionally, this retinal structure is not fully developed in young walleye and sauger, coinciding with their zooplanktivore feeding stage, and its development coincides with walleye switching to piscivory (Braekevelt et al. 1989). In Lake Winnipeg, the turbidity is high in both basins but higher in the South Basin than the North Basin (see Table 1 in Chapter 1).

There was a general trend toward longer fish in the North Basin relative to the South Basin. In particular, 5-year-old walleye and sauger in the North basin were longer than the same age class in the South basin. Although this trend was observed in the age 3 and 4 walleye and sauger, the differences were not statistically significant. This may be explained by the shape of the growth curves of walleye and sauger. The growth curves of fish under different conditions diverge with age, and so differences become more apparent in older fish. There is an exponential increase in length in the first few years followed by a slowing in the growth around the age of sexual maturity (2-5 years). Young walleye and sauger allocate energy to growth to reduce their vulnerability to predation; once beyond a certain body size they are less susceptible to piscivory (Werner and Gilliam 1984). During this phase of fast growth there may be less variation in size at age if prey abun-

dance is high (Post and Parkinson 2001). Once they have reached this less vulnerable size, usually when they become sexually mature, they can begin to allocate energy to other things such as reproduction (Post and Parkinson 2001; Biro et al. 2005). Reproduction, especially for female fish, is energetically costly (Roff 1983). After fish reach reproductive maturity, their growth rate approaches an asymptote as they allocate energy reserves toward gonadal development in addition to maintenance and growth (Beamish and MacMahon 1988). Mature fish allocate different amounts of energy to both growth and reproduction, which could vary among individuals (Roff 1983; Post and Parkinson 2001). Additionally, as fish increase in size they are able to consume larger prey which are more energetically profitable compared to what a smaller fish could consume. Consuming a more energetically profitable diet and being able to allocate that energy to growth as well as reproduction may emphasize the variation in length at age in older fish.

The differences in growth and condition between basins suggest that the fish do not move regularly between basins. Substantial variation between populations suggests that there may be different metapopulations that do not mix as adults very often. However, no conclusive evidence to support different stocks of walleye was found on the basis of Fourier and Wavelet Analysis on scales from three known spawning grounds in Lake Winnipeg (Watkinson and Gillis 2005). Microsatellite and mitochondrial DNA markers have also been used to examine population structure of Lake Winnipeg walleye spawning in rivers (for the most part), and no conclusive evidence of metapopulations of walleye in Lake Winnipeg were found (Backhouse-James and Docker 2012). Therefore, spatial variation in population characteristics of walleye in Lake Winnipeg may be phenotypic rather than genotypic, and results of my study indicate that such variation could

be influenced by environmental factors such as prey type and abundance (Colby and Nepszy 1981).

Lake Winnipeg is unique, as it appears to be one of the only ecosystems that have walleye, sauger and dwarf walleye living sympatrically (Johnston et al. 2010). All three occupy the waters of the South Basin, while only normal growth walleye and sauger (at lower densities) occur in the North Basin. The seemingly lower densities of sauger in the North Basin could be attributed to the difficulty of sampling close to shore but might also suggest that there are fewer sauger in the North Basin. In systems where walleye and sauger coexist, there is often competition for resources resulting in declines in sauger abundance relative to walleye abundance (Swenson and Smith 1976; Johnston et al. 2010). Higher exploitation of walleye in the South Basin may increase walleye mortality enough to allow both species to coexist and for sauger to be more abundant in the South Basin (Johnston et al. 2010). Additionally, as sauger are often found in more turbid environments than walleye, this suggests that sauger might have an advantage over walleye in the South Basin (Ali and Ancil 1977; Swenson 1977; Johnston et al. 2010). Differential habitat use by percids has been documented in other systems (MacLean and Magnuson 1977).

There were low sample sizes of dwarf walleye in general, only two were caught in the North Basin relative to 30 in the South Basin throughout this study. In support, Johnston et al. (2010) reported that dwarf walleye were almost exclusively found in the South Basin. The exclusivity of dwarf walleye to the South Basin may be due to the minimum mesh size of commercial gill-nets being smaller in the South Basin (76 mm) relative to the North Basin (108 mm; Johnston et al. 2010). The South Basin mesh regulations may

create an advantage for dwarf walleye in terms of net avoidance (Johnston et al. 2010). Additionally, prey in the North Basin were larger relative to the South Basin (Chapter 2), giving larger predators an advantage, as they have large enough gapes to access these more profitable prey. Alternatively, dwarf walleye may not be large enough to access this profitable prey source and paired with the larger mesh regulations of the fishery in the North Basin, they would be at a disadvantage to normal growth walleye when inhabiting the North Basin. The morphology of dwarf walleye suggests that it inhabits and forages in more benthic regions which perhaps means that it can also tolerate high turbidity and low light for foraging. If this is the case, it again would be beneficial for dwarf walleye to live in the South Basin where turbidity is two-fold higher than the North Basin. Our diet analysis of dwarf walleye does not support a benthic or near-bottom feeding regime; however, low samples sizes make this inconclusive. Overall, these findings support low movement of individuals of the same species or morphotype between basins and it appears that dwarf walleye are best suited for the South Basin.

Conclusion

The variation in growth and condition of walleye and sauger between basins appears to be attributable to the presence of the invasive rainbow smelt in the North Basin. Physical factors, such as turbidity and temperature may also play a role; however, the presence of rainbow smelt seems to be more important for a couple of reasons. Turbidity is higher in the South Basin but that is relative to a still highly turbid North Basin and the surface temperature range in the two basins is not substantially different. While these physical parameters may be less influential, the most likely reason for differences in growth and

condition between basins may be the dominance of the large-bodied rainbow smelt in the North Basin and the dominance of small-bodied emerald shiner among prey in the South Basin (Lumb et al. 2012). While these differences are important, the growth and condition of walleye in this lake is still high relative to other systems (Kaufman et al. 2007; Moles et al. 2008). There were two studies on the growth and condition of walleye in various locations throughout Canada including Trout Lake, Winefred Lake, Lake Winnipeg, Lake of the Woods, Lac Beauchêne, Lake Nipissing, Lake Ontario, Tathlina Lake and Orange Lake (Kaufman et al. 2007; Moles et al. 2008). In both studies, Lake Winnipeg walleye had the highest growth and condition compared to walleye in all other lakes, which is important for both ecological and economic reasons (Kaufman et al. 2007; Moles et al. 2008).

Table 1: Differences in growth rates of walleye, sauger and dwarf walleye using analysis of covariance (ANCOVA) and analysis of variance (ANOVA) for length categories. Species, sex and basin were the categorical variables, and in ANCOVA age and age² were the covariates. A superscript z shows factors that were not applicable, either because they were covariates that did not apply to ANOVA, or because there was an imbalance in the data available.

Model	All fish - ANCOVA			Walleye, Sauger Age 3,4,5 - ANCOVA			Walleye, Sauger Age 3 - ANOVA			Walleye, Sauger Age 4 - ANOVA			Walleye, Sauger Age 5 - ANOVA			Walleye, Sauger Age >5 - ANCOVA			Dwarf Walleye - ANCOVA		
	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value
Age ²	1	82.13	<0.001	1	15.65	<0.001	---	---	---	---	---	---	---	---	1	6.25	<0.05	1	4.77	0.039	
Age	1	422.07	<0.001	1	31.46	<0.001	---	---	---	---	---	---	---	---	1	11.73	<0.005	1	6.06	0.021	
Species	2	1216.34	<0.001	1	333.64	<0.001	1	56.66	<0.001	1	221.60	<0.001	1	116.92	<0.001	1	142.54	<0.001	---	---	---
Basin	1	12.92	<0.001	1	2.88	0.090	1	1.81	0.18	1	1.63	0.20	1	6.69	<0.05	1	3.57	0.060	---	---	---
Sex	1	8.85	<0.005	1	13.98	<0.001	1	12.36	<0.005	1	9.31	<0.005	1	78.78	<0.001	1	16.90	<0.001	1	0.71	0.41
Basin*Sex	1	3.75	0.053	1	1.21	0.27	---	---	---	---	---	---	---	---	1	0.78	0.38	---	---	---	
Species*Sex	2	5.87	<0.005	1	0.25	0.62	1	1.64	0.20	1	17.19	<0.001	1	1.97	0.16	1	4.08	0.045	---	---	---
Basin*Species	---	---	---	1	0.55	0.46	1	1.32	0.25	1	10.14	<0.005	1	0.71	0.40	1	1.56	0.21	---	---	---
Basin*Species*Sex	---	---	---	1	0.00	0.99	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Error	1092			784			192			320			264		205			25			
Total	1101			793			197			325			269		213			28			

Table 2: Mean fork length (\pm SE) at specific ages of normal walleye, dwarf walleye and sauger in both basins and for both sexes. Sample sizes used in calculating all mean values were ten or greater unless otherwise indicated by italicizing numbers. A superscript z means that no samples were available.

Basin	Walleye		Dwarf Walleye		Sauger	
	M	F	M	F	M	F
Age 2						
North	274 \pm 8.2	--- ^z	---	---	199 \pm 9.9	---
South	258 \pm 11.3	244 \pm N/A	---	---	206 \pm 5.3	208 \pm 18.1
Age 3						
North	329 \pm 3.6	---	---	---	263 \pm 10.5	---
South	327 \pm 3.9	365 \pm 9.7	---	---	241 \pm 4.1	257 \pm 6.9
Age 4						
North	401 \pm 3.7	383 \pm 9.5	---	---	263 \pm 21.2	259 \pm N/A
South	368 \pm 2.7	370 \pm 6.1	222 \pm N/A	---	270 \pm 3.4	300 \pm 4.3
Age 5						
North	411 \pm 4.6	437 \pm 5.6	---	---	338 \pm N/A	335 \pm 5.0
South	386 \pm 3.9	439 \pm 7.4	218 \pm N/A	---	282 \pm 3.5	314 \pm 4.0
Age 6						
North	465 \pm 21.0	---	---	---	324 \pm N/A	340 \pm N/A
South	394 \pm 10.4	454 \pm 13.6	334 \pm N/A	---	307 \pm 8.7	326 \pm 4.9
Age 7						
North	---	416 \pm N/A	---	---	363 \pm 8.3	399 \pm 5.6
South	470 \pm 7.9	468 \pm 10.6	278 \pm 20.0	---	346 \pm 5.0	375 \pm 6.6
Age 8						
North	---	---	---	---	---	384 \pm 18.2
South	456 \pm 15.8	523 \pm 7.7	293 \pm 24.9	293 \pm N/A	351 \pm 5.3	394 \pm 8.2
Age 9						
North	442 \pm N/A	547 \pm 9.5	---	---	---	---
South	488 \pm 19.3	544 \pm 12.4	292 \pm 20.0	318 \pm 7.5	356 \pm 10.5	304 \pm N/A
Age 10						
North	---	---	---	---	---	---
South	494 \pm N/A	550 \pm 15.4	300 \pm 25.0	---	---	---
Age 11						
North	---	---	---	---	382 \pm N/A	---
South	---	611 \pm 19.5	305 \pm 1.5	---	---	---
Age 12						
North	---	---	---	---	380 \pm N/A	---
South	---	---	314 \pm 20.0	298 \pm N/A	---	---
Age 13						
North	---	---	---	---	---	---
South	---	638 \pm 26.0	---	311 \pm N/A	---	---
Age 14						
North	---	---	---	---	---	---
South	---	---	269 \pm N/A	---	---	---

Table 3: Allometric linear regression equations for the growth of walleye, dwarf walleye and sauger in Lake Winnipeg, Manitoba.

Species	Sex	Allometric Linear Regression
Walleye	Female	$\log_{10} W = -5.618[0.166] + 3.260[0.0637](\log_{10} L)$
	Male	$\log_{10} W = -5.341[0.171] + 3.148[0.0669](\log_{10} L)$
	Combined	$\log_{10} W = -5.513[0.118] + 3.217[0.0458](\log_{10} L)$
Sauger	Female	$\log_{10} W = -5.422[0.140] + 3.165[0.0564](\log_{10} L)$
	Male	$\log_{10} W = -5.0327[0.176] + 2.997[0.0725](\log_{10} L)$
Dwarf Walleye	Combined	$\log_{10} W = -6.747[0.623] + 3.719[0.254](\log_{10} L)$

Table 4: Analysis of variance (ANOVA) for the relative condition (K_n) of walleye, sauger and dwarf walleye. A superscript y shows basin and season were separate main factors, but were not a balanced factorial. Thus to examine their interaction, it was necessary to compute a separate ANOVA with a combined basin/season factor and do Scheffé's multiple means tests within that factor. A superscript z shows factors that were not applicable, either because they were covariates that did not apply to ANOVA, or because there was an imbalance in the data available.

Model	Walleye			Sauger			Dwarf Walleye		
	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value
Sex	1	0.03	0.86	--- ^z	---	---	1	2.41	0.14
Maturity	1	1.59	0.21	1	4.08	0.044	1	0.07	0.79
Basin	1	161.23	0.000	1	30.37	0.000	----	---	----
Season	4	23.46	0.000	4	19.30	0.000	4	6.92	0.002
Basin/season ^y	7	35.32	0.000	7	14.55	0.000	----	---	----
Error	398			372			15		
Total	412			385			21		

Table 5: Scheffé’s multiple comparison test on the mean (\pm SE) relative condition (K_n) of walleye, sauger and dwarf walleye. Means within a factor followed by the same letter were not significantly different. An asterisk (*) means it is a significant result ($p < 0.05$) while ns means it is not significant. Scheffé’s test was presented relative to a reference case. South - Spring 2011 was chosen as the reference case because it had the lowest K_n value and had a high sample size. Ref delineates this reference value which other means were compared to for the Scheffé’s test. Superscript z shows factors that were not applicable, either because they were covariates that did not apply to ANOVA, or because there was an imbalance in the data available. A superscript y shows an imbalanced design (low/no samples sizes in some basins/seasons).

Model	Walleye		Sauger		Dwarf Walleye	
	K_n	Scheffé Groups	K_n	Scheffé Groups	K_n	Scheffé Groups
Sex						
Female	1.016 \pm 0.010	A	1.005 \pm 0.010	A	1.010 \pm 0.079	A
Male	0.992 \pm 0.008	A	1.000 \pm 0.010	A	0.982 \pm 0.030	A
Maturity						
Mature	1.004 \pm 0.009	A	1.029 \pm 0.009	A	0.978 \pm 0.028	A
Immature	0.995 \pm 0.009	A	0.968 \pm 0.011	B	1.048 \pm 0.109	A
Basin						
North	1.076 \pm 0.010	A	1.145 \pm 0.028	A	0.951	--- ^z
South	0.956 \pm 0.007	B	0.994 \pm 0.007	B	0.989 \pm 0.029	---
Season						
Spring 2010	0.956 \pm 0.021	BC	0.958 \pm 0.017	C	0.909 \pm 0.072	A
Spring 2011	0.964 \pm 0.014	BC	0.955 \pm 0.012	C	0.895 \pm 0.019	A
Summer 2010	1.017 \pm 0.009	C	1.020 \pm 0.012	B	1.123 \pm 0.137	AB
Fall 2011	0.970 \pm 0.011	B	1.080 \pm 0.015	AB	1.101 \pm 0.021	B
Winter 2011	1.123 \pm 0.020	A	1.146 \pm 0.020	A	0.972 \pm N/A	AB
Basin/season						
North – Spring 2010	1.201 \pm 0.016	A	1.158 \pm 0.037	ns ^y	---	---
North – Spring 2011	1.112 \pm 0.025	A	1.125 \pm 0.073	ns	---	---
South – Winter 2011	1.123 \pm 0.020	A	1.146 \pm 0.020	*	---	---
North – Summer 2010	1.064 \pm 0.011	A	1.151 \pm 0.038	*	---	---
South – Fall 2011	0.970 \pm 0.011	B	1.080 \pm 0.015	*	---	---
South - Spring 2011	0.929 \pm 0.012	B	0.946 \pm 0.011	ref	---	---
South – Summer 2010	0.914 \pm 0.008	B	1.008 \pm 0.012	*	---	---
South – Spring 2010	0.913 \pm 0.018	B	0.948 \pm 0.017	ns	---	---

Table 6: Scheffé's multiple comparison test of the mean (\pm SE) mesenteric fat level of walleye, sauger and dwarf walleye. Means within a factor followed by the same letter were not significantly different. A superscript z shows factors that were not applicable, either because they were covariates that did not apply to ANOVA, or because there was an imbalance in the data available.

Model	Walleye		Sauger		Dwarf Walleye	
	Mean	Scheffé Groups	Mean	Scheffé Groups	Mean	Scheffé Groups
Sex						
Female	1.257 \pm 0.076	A	0.413 \pm 0.042	A	0	A
Male	0.624 \pm 0.050	B	0.366 \pm 0.039	A	0	A
Maturity						
Mature	0.965 \pm 0.056	A	0.461 \pm 0.037	A	0	A
Immature	0.916 \pm 0.066	A	0.318 \pm 0.045	B	0	A
Basin						
North	1.263 \pm 0.074	A	0.754 \pm 0.062	A	---	--- ^z
South	0.618 \pm 0.052	B	0.025 \pm 0.023	B	0	---
Season						
Winter 2011	1.576 \pm 0.149	A	0.418 \pm 0.079	A	0	A
Spring 2011	0.948 \pm 0.095	B	0.433 \pm 0.045	A	0	A
Summer 2010	0.238 \pm 0.080	C	0.348 \pm 0.044	A	0	A
Fall 2010	1.291 \pm 0.052	A	0.400 \pm 0.039	A	0	
Fall 2011	0.649 \pm 0.104	BC	0.347 \pm 0.070	A	0	a

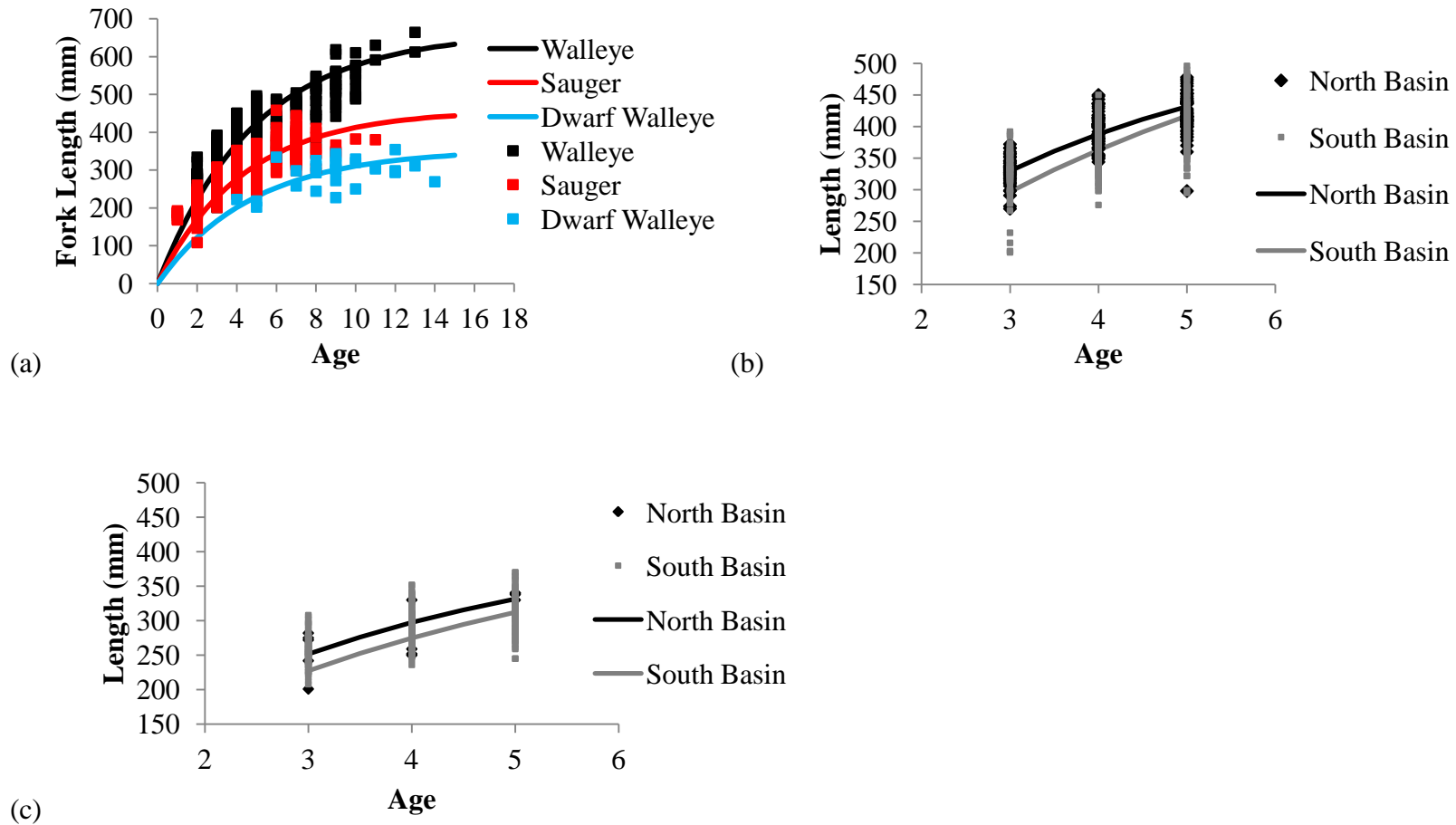


Figure 1: (a) Fork length-at-age of normal growth walleye, dwarf walleye and sauger in Lake Winnipeg, Manitoba. The trend lines were fitted using the Von Bertalanffy growth curve where t_0 was set to zero and L_∞ was set to the maximum length of each group of fish sampled. Fork length-at-age of age 3-5 (b) walleye and (c) sauger separated by basin.

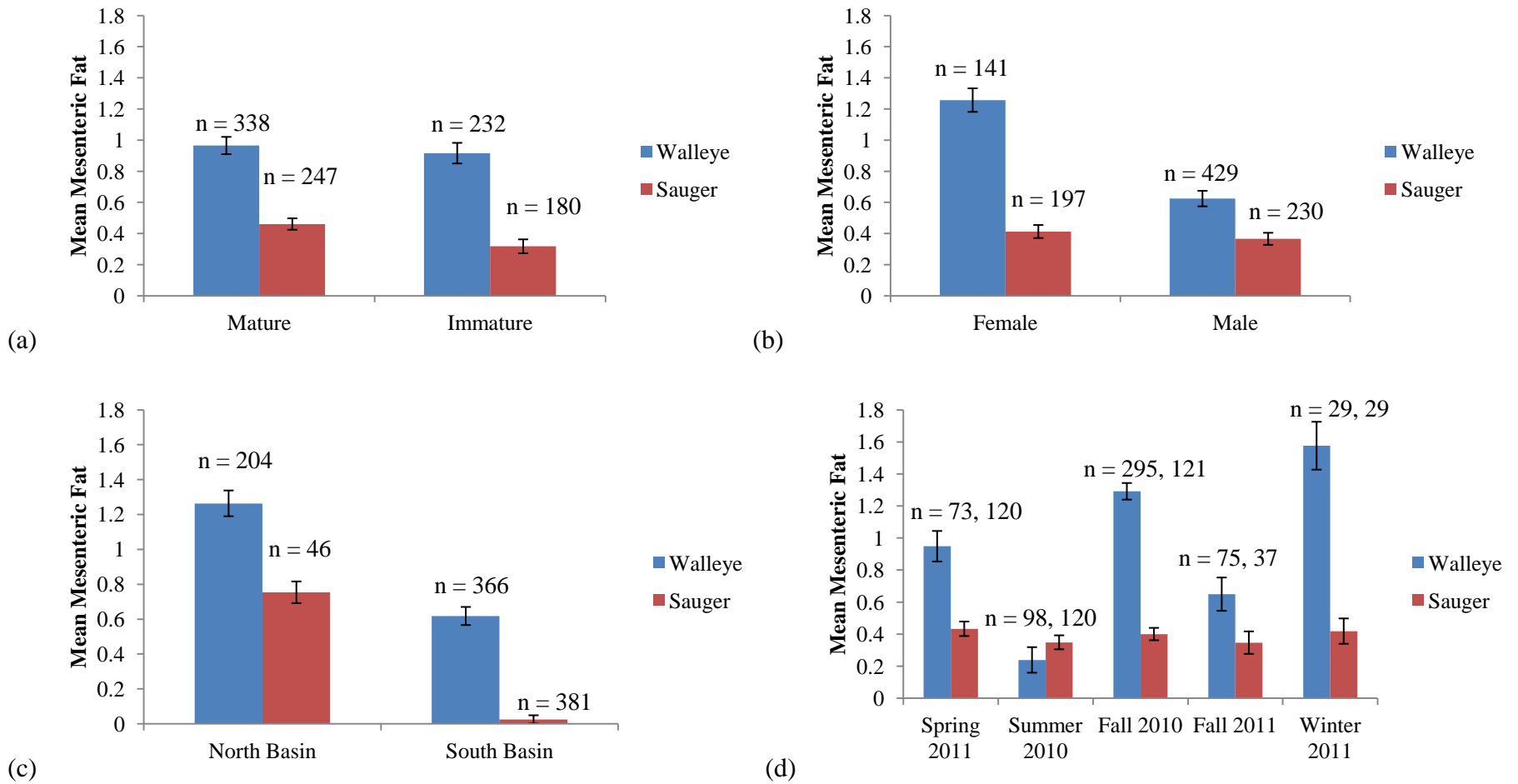


Figure 2: Mean (\pm SE) mesenteric fat levels of walleye and sauger in Lake Winnipeg using maturity (a), sex (b), basin (c) and season (d) to examine variation.

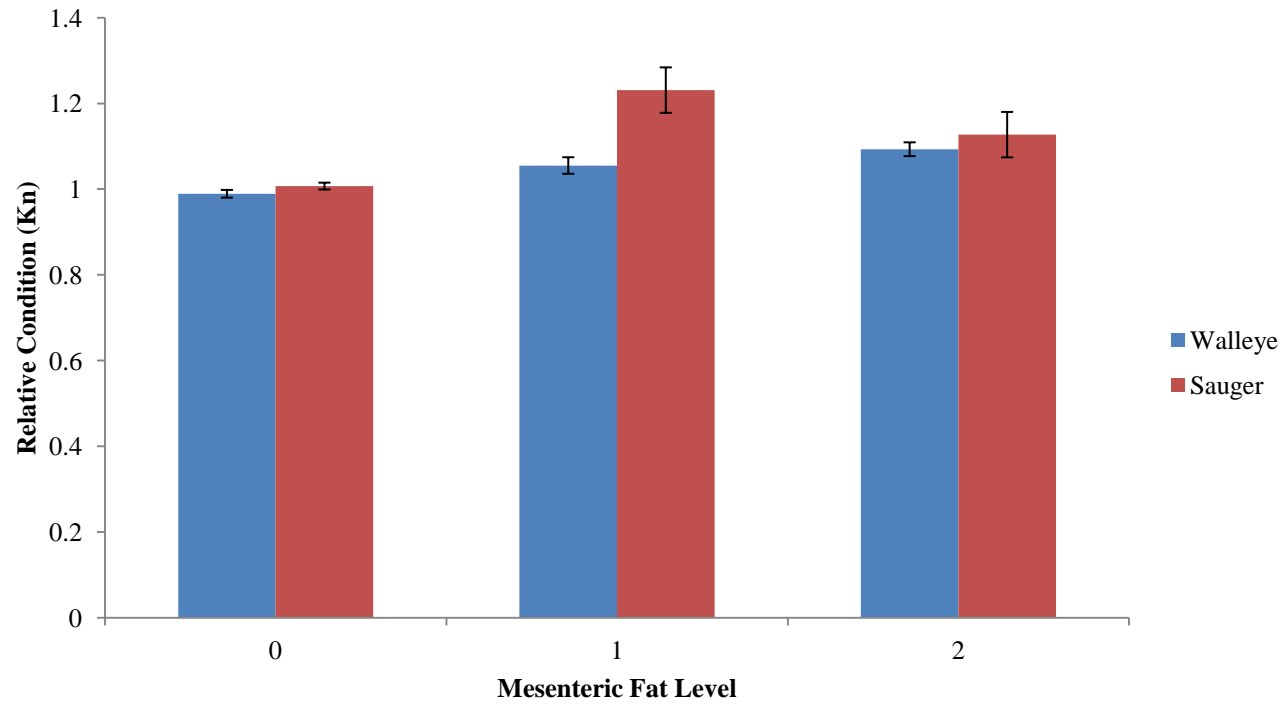


Figure 3: Mean (\pm SE) relative condition (K_n) of walleye and sauger with three different levels of mesenteric fat.

Chapter 4: General Discussion

The primary goal of my thesis was to examine basin and seasonal differences in the diet, growth and condition of walleye and sauger in Lake Winnipeg and secondarily to examine the influence of invasive rainbow smelt on species interactions and food web dynamics of Lake Winnipeg. I found a clear difference in the dietary composition of walleye and sauger between basins: a high proportion of larger rainbow smelt in the gut contents in the North Basin and a wide breadth of smaller prey species in the South Basin. Additionally, walleye and sauger growth and condition were found to be higher in the North Basin relative to the South Basin. Jones et al. (1994) showed that walleye growth increased in Horsetooth Reservoir, Colorado, after rainbow smelt invaded and became dominant in the diet. In other systems, a similar conclusion was reached where increased growth and condition were likely due to an abundant source of ideal prey like rainbow smelt (Porath and Peters 1997; Quist et al. 2002). Although temperature, turbidity, prey abundance and exploitation levels are factors that may influence walleye and sauger growth and condition in Lake Winnipeg, the presence of the invasive rainbow smelt in the North Basin and its absence in the South Basin seems to be the primary and most influential cause.

Anecdotal reports have suggested that the invasion of rainbow smelt into Lake Winnipeg was associated with increased abundance and size of walleye and, thus, this new, abundant prey item has had a positive influence on this important walleye and sauger fishery. The reports of larger size of walleye and sauger are consistent with the findings

of my study. Because walleye and sauger have high commercial value in Lake Winnipeg and many other systems, increased growth and condition associated with diets primarily composed of the invasive rainbow smelt is economically important. Although there is a concern that increased mesenteric fat in walleye in the North Basin may decrease the quality of flesh for sale in the fishery, this is unlikely because fat is primarily stored in the body cavity rather than in the muscle.

The gut contents of walleye and sauger also provided some insight into where in the water column these predatory piscivores feed in Lake Winnipeg. The prey found in the gut contents of walleye were almost exclusively pelagic forage fishes, suggesting that walleye primarily feed in pelagic zones of the lake. Sauger guts had a substantial amount of troutperch which are demersal forage fishes, suggesting that sauger feed more often in association with the bottom and perhaps this species occupies a different habitat than walleye. This is supported by previous research in which sauger have been found in more demersal and more turbid environments than walleye (Swenson and Smith 1976; Swenson 1977). Differences in habitat location may also be the reason fewer sauger are caught in the trawls. Habitat and foraging differences between walleye and sauger documented in other systems is thought to result from competition between species (Swenson and Smith 1976; Swenson 1977), which may also be the case in Lake Winnipeg. Future research should include a more comprehensive sampling program focused on prey species composition and abundance using bottom trawls to determine the abundance of benthic species, such as troutperch, in both basins of the lake, as well as other species in the deeper waters of the North Basin.

Although my sample size of dwarf walleye was low, some preliminary observations are offered here. The literature suggests that dwarf walleye inhabit more demersal environments (Moles et al. 2010); however, the results from the gut contents (South Basin fish only) showed a variety of pelagic forage fishes (i.e., cisco, yellow perch, emerald shiner) and some mayfly larvae. Only two dwarf walleye were caught in the North Basin which is consistent with abundance trends in a previous study on this lake (Johnston et al. 2010), suggesting that dwarf walleye are almost exclusively found in the South Basin. The relative condition (K_n) of dwarf walleye was within the range observed for normal walleye and sauger but no mesenteric fat was found on any of the individuals caught. This may be related to their exclusivity to the South Basin and the very low occurrence of rainbow smelt in their diet. Further research should include more extensive sampling of dwarf walleye to document their range extension in the lake as well as the types of prey that they are consuming. Determining whether dwarf walleye eat pelagic prey, as my study suggests, or benthic prey, as suggested by their morphology, would be interesting for understanding foraging niches of these predators.

Whether walleye and sauger regularly move between the basins of Lake Winnipeg is still unknown. There is evidence that supports walleye being one population, with individuals moving to some degree between basins (Backhouse-James and Docker 2012), whereas other evidence supports separate stocks within the lake (Watkinson and Gillis 2005). The presence of a walleye morphotype (dwarf walleye) in the South Basin but not in the North Basin may support that there is little to no movement between basins, as do the distinct differences in growth and condition of walleye and sauger between the North and South Basins. Further study of the movement patterns of individual walleye and sau-

ger within the lake could be addressed through tagging and/or an otolith micro-chemistry study, as both would indicate whether the fish remain within the same basin throughout their lifespan, as this study suggests.

Currently, walleye and sauger are commercially fished throughout the lake using gill-nets. Fishing efforts are more concentrated in the South Basin because of its smaller size, higher human population density and greater accessibility compared to the North Basin. A total allowable catch is set by the province of Manitoba to control the total biomass of walleye and sauger that can be landed in a given year; however, this total catch is not separated by species (walleye and sauger) or by basin. The fishery is opened in the spring after the majority of walleye have spawned, regardless of the fact that sauger spawn after walleye. Therefore, sauger caught by commercial gill-nets in the early spring are likely mature individuals that have not yet had the chance to spawn, thus decreasing the recruitment potential of sauger. In addition, the mesh size minima are different for the two basins because smaller walleye and sauger are more profitable (hence the small mesh size minima in the South Basin) and in the North Basin, lake whitefish are an important commercial species fished for in addition to walleye and sauger and they are caught with larger mesh (hence the larger mesh size minima). This is a start for managing these fishes by basin; however, more could be done by separating the timing of the fishery and the total allowable catch by species and by basin.

One of the underlying objectives of this project was to try to determine what impact the invasive rainbow smelt has had on the commercially important species of Lake Winnipeg, namely walleye and sauger. My study suggests that rainbow smelt are a positive influence on the walleye and sauger in this system. Rainbow smelt are continuing to in-

vade the upper reaches of this ecosystem by traveling through the Nelson River which bypasses reservoirs with varying ecosystem characteristics. Rainbow smelt seem to be a profitable prey for large walleye and sauger and perhaps they will provide the same resource to other piscivores, such as northern pike, which are prevalent in some of the Nelson River reservoirs.

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