Growth rate and condition of walleye, sauger, and dwarf walleye in a large Canadian lake

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Sheppard KT, Hann BJ, Davoren GK

Abstract

The second largest inland walleye (*Sander vitreus*, (Mitchill, 1818)) and sauger (*Sander canadensis* (Griffith and Smith, 1834)) fishery in Canada is found in Lake Winnipeg, Manitoba. To manage the fishery for a sustainable future, the growth and condition of these fish must be understood. Objectives were to 1) examine baseline growth and condition of walleye and sauger in Lake Winnipeg, 2) evaluate variation between the North and South basins, and 3) contribute observational findings on the distribution of dwarf walleye. Gill-nets were set to catch walleye, sauger and dwarf walleye throughout both basins at various locations and in all seasons. North Basin walleye and sauger had higher growth rates and condition relative to the South Basin. This may be due to differential exploitation rates or diets such as the consumption of invasive rainbow smelt in the North Basin and not in the South Basin. Dwarf walleye were observed more frequently in the South Basin than the North Basin. Overall, this study provides important baseline data on the growth and condition of walleye and sauger populations prior to invasion of the spiny water flea (*Bythotrephes longimanus* (Leydig, 1860)) and zebra mussels (*Dreissena polymorpha* (Pallas, 1771)).

Keywords: Condition, ecology, growth, population dynamics, walleye (*Sander vitreus* (Mitchill, 1818)), sauger (*Sander canadensis* (Griffith and Smith, 1834)).
Introduction
Lake Winnipeg, Manitoba is the tenth largest freshwater lake in the world by surface area (23,750 km$^2$) and it supports the second largest inland fishery in Canada, focusing on walleye (Sander vitreus (Mitchell, 1818)) and sauger (Sander canadensis (Griffith and Smith, 1834)) (Johnston et al. 2012). Estimates for the commercial harvest of walleye and sauger in 2010 are 5.7 million kg (round weight) of walleye and 239,000 kg (round weight) of sauger which translates to $16.8 million in walleye and $952,000 in sauger (Sustainable Development, Wildlife and Fisheries Branch 2017). Lake Winnipeg has two distinct basins that have different prey (for walleye and sauger) abundances and fish communities in the open water season. Prey abundance is higher in the South relative to the North Basin (Lumb et al. 2012) and the prey fish community in the North Basin is dominated by the recently-invaded rainbow smelt (Osmerus mordax (Mitchell, 1814)), whereas emerald shiner (Notropis atherinoides (Rafinesque, 1818)) is prevalent in the South Basin (Lumb et al. 2012). Walleye and sauger have been shown to feed heavily on invasive rainbow smelt in the North Basin of Lake Winnipeg (Sheppard et al. 2015) and this study will examine the potential effect of this predator-prey relationship on the condition and growth of walleye and sauger in the lake. With other invasions to the lake, such as zebra mussels and spiny water fleas (2013 and 2011 respectively; Jansen et al. 2017), this paper will provide baseline information to help predict the effects of these invasions on walleye and sauger and aid in their management. In addition to limnological differences between the two basins of the lake in mid-summer (e.g., temperature, turbidity; McCullough and Levesque 2011), exploitation rates of walleye and sauger also differ between the basins, with the South Basin supporting the vast majority of the commercial harvest due to accessibility (Franzin et al. 2003; Moles et al. 2010).

The exploitation rates, limnology and prey community of a water body can greatly influence important aspects of fish life history, such as growth rate, length, mass, 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). Condition and growth of piscivorous fishes are clearly linked to prey availability and prey type consumed (VanDeValk et al. 2008). Indeed, higher net energy should translate into higher energy reserves, which can be allocated to growth, maintenance or reproduction (Madenjian et al. 1996; Einfalt and Wahl 1997; Stewart and Watkinson 2004; VanDeValk et al. 2008; Kaufman et al. 2009). For instance, increased walleye growth has been associated with invasions of rainbow smelt (Jones et al. 1994), which walleye and sauger consume.
predominantly in the North Basin of Lake Winnipeg (Sheppard et al. 2015). Although the energy density of rainbow smelt does not appear to be greater per gram than other prey (e.g., cisco, freshwater drum and troutperch) in the North Basin (Sheppard et al. 2015), smelt is likely the most energetically profitable prey type owing to its larger body size (Sheppard et al. 2015), high abundance in the North Basin (Gamble et al. 2011; Lumb et al. 2012) and ease of capture (i.e. remain motionless in the water column to avoid predation; Mason et al. 1998). Natural and fishery-induced mortality can also influence growth and condition; for instance, heavily exploited walleye populations tend to be in better condition (i.e., have a higher body lipid content; Kaufman et al. 2007) due to lower population densities, effectively removing prey density as a limiting factor. Indeed, commercial exploitation rates of walleye and sauger are considered to be very high in Lake Winnipeg compared to other water bodies (Kaufman et al. 2007). There are minimum mesh size regulations to regulate the commercial harvest, which differ between the basins (76 mm minimum in the South Basin, 95 mm minimum in the North Basin in the open water season; Ayles et al. 2011). Interestingly, a growth morphotype of walleye, the dwarf walleye, which grows more slowly and matures at a later age, occurs in Lake Winnipeg and appears to be more abundant in the South Basin where it is subject to commercial fishing but is less susceptible to common fishing gear until it is much older (Johnston et al. 2012). Overall, quantifying life history traits is important for appropriate management of economically and ecologically important species.

The primary objective of this study was to quantify the growth and condition of walleye, sauger, and dwarf walleye in both basins of Lake Winnipeg. Because of sex-based differences in reproductive allocation, growth and condition (Scott and Crossman 1998; Purchase et al. 2005; Madenjian et al. 2009; Johnston et al. 2012), sex-specific growth rates and body condition were compared within each species/morphotype between basins. Basin variation in sex-specific growth rates and condition are hypothesized to have one of two possible patterns. If a diet composed of rainbow smelt is an important factor determining growth rates and condition, fish would likely have higher growth rates and condition in the North Basin relative to the South Basin. Alternatively, if higher commercial exploitation rates and higher prey abundance in the South Basin combine to minimize intraspecific competition, fish would likely have higher growth rates and condition in the South relative to the North Basin. Comparing the growth rates and condition of a species between basins is important for setting differential fishing regulations for each basin in order to manage each species effectively. Overall, this study provides a better understanding of the
growth and condition of walleye, dwarf walleye and sauger populations in Lake Winnipeg and the potential impact of non-indigenous rainbow smelt on their growth and condition which may contribute to management of and policy decisions for the commercial fishery.

Methods and Materials

Study Area

The invasive rainbow smelt (*Osmerus mordax*) was first documented in Lake Winnipeg in late 1990 (Franzin et al. 1994) and now, during the open water season, almost exclusively inhabits the North Basin (2.2 g wet weight/1,000 m$^3$; Lumb et al. 2012). In contrast, the native emerald shiner (*Notropis atherinoides*) dominates the South Basin (3.9 g wet weight/1,000 m$^3$; Lumb et al. 2012) of Lake Winnipeg. Overall, prey fish abundance is higher in the South Basin (~8 g wet weight/1,000 m$^3$) relative to the North Basin (~3.5 g wet weight/1,000 m$^3$; Lumb et al. 2012). In mid-summer, Lake Winnipeg experiences limnological differences in mean depth (North Basin 13.3 m; South Basin 9.7 m), surface and bottom temperature (respectively, North Basin 19.7 ± 1.7 °C and 17.9 ± 1.4 °C; South Basin 21.5 ± 1.1°C and 20.8 ± 1.1°C), and mean Secchi depth (North Basin 1.4 ± 0.4 m; South Basin 0.6 ± 0.2 m; McCullough and Levesque 2011).

Field Sampling

Walleye and sauger were collected using 12-hour gill-net sets of varying stretched mesh sizes (multiple panels; 25 – 127 mm) arranged horizontally and perpendicular to the shore overnight. Four locations in the South Basin and seven locations in the North Basin were sampled in spring (2010, 2011), summer (2010) and fall (2010, 2011; Fig. 1). Commercial fishers from Gimli, MB provided fish in the winter (March 2011; 76 mm stretched mesh gill-nets set near-shore through ice). Samples sizes were spatially supplemented by trawling in the North and South Basins of Lake Winnipeg during spring (2010, 2011), summer (2010) and fall (2010, 2011). Trawls were conducted at up to 65 stations (Fig. 1) from the M.V. *Namao* using a beam-trawl with 6 mm stretched mesh size at the cod-end. The trawl was deployed at varying depths (surface, mid or deep relative to station depth) for 30 minutes.

Up to 30 walleye and 30 sauger were randomly subsampled (the operator chose fish
without looking) from the available catch at each gill-net and trawl location. 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). Mesenteric fat was excised and preserved in 70 % ethanol and sagittae otoliths were removed, wiped clean, and stored dry.

**Laboratory Processing**

Age was estimated for each fish to calculate 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 (90% alcohol; Logsdon 2007; Graeb et al. 2010). 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). The method used for aging sagittae otoliths was validated by an expert (L. Heuring, Manitoba Conservation and Water Stewardship, Fisheries Branch, Winnipeg, MB) who later verified the accuracy of age determination for 28% of the fish (accuracy was 90 %).

Length and round weight of each fish was used to calculate the relative condition index ($K_r$; Hansen and Nate 2005). Additionally, as walleye, and likely sauger, are known to store their fat in the viscera (Henderson and Morgan 2002; Kaufman et al. 2007), condition was assessed using a bioenergetic method, i.e., mesenteric fat stores. Mesenteric fat levels in the body cavity were rated qualitatively from 0 – 2, with 0 indicating little to no mesenteric fat (0 – 25%), 1 indicating some (roughly 25 – 75%), and 2 indicating a large amount (75 – 100%).

**Data Analysis**

Data analysis was performed using the Statistix 10 software. Length data were normally distributed (verified using Shapiro-Wilk and Kolmogorov-Smirnov tests) and, thus, parametric statistics were used. To investigate differences in sex-specific growth rates between species/morphotype and basin, an analysis of covariance (ANCOVA) was used to compare mean
lengths adjusted to the average age. Significant differences indicated differences in growth rate. Using age as a covariate assumes a linear relationship; therefore, age² was used as a covariate as well to ensure that the ANCOVA also represented non-linearity in the shape of the growth curve. Sex, species, and basin were included as independent factors in the analysis and all two-way and three-way interactions were included in the model. As the ANCOVA assumes that all species/morphotypes and sexes of fish have the same growth curve, we additionally performed an analysis of variance (ANOVA) on the three most frequently observed age classes to determine whether length differed among fish at each age and whether age-specific length differed significantly between species or sex. There were sufficient data for ages 3-, 4- and 5-year-old normal walleye and sauger, and these ANOVAs addressed the issue of the rapidly changing shapes of the growth curves at these ages. Fish older than age 5 were nearing the growth plateau (Fig. 2a, b and c); therefore, it was reasonable to rely on ANCOVA with age and age² as the covariates for these older fish.

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 (Sheppard 2013); however, the Von Bertalanffy growth curve was selected because of its extensive use in fish growth studies and the opportunity to compare results with other studies (Kritzer et al. 2001; Lumb et al. 2007). The Von Bertalanffy growth curve (Fork Length = L∞*(1-e^(-kt0))) was constrained by defining the length at age zero as 0 cm and estimating the length at age infinity as the maximum length of fish caught for each sex and species/morphotype. Constraining the Von Bertalanffy growth curve in this manner does not result in a substantial bias in either freshwater or reef fish species (Kritzer et al. 2001; Beauchamp 2002) and is consistent with Manitoba monitoring programs for this species and other freshwater fish (Lumb et al. 2007).

Length and round weight were used to determine an allometric linear regression for condition and a relative condition index (Kₙ). Kₙ was calculated for each individual following Hansen and Nate (2005):

\[ K_n = W / (\alpha L^\beta) \]

where W is the round weight (g), L is the length (mm), and α and β are regression coefficients from the function \( \log(W) = \log(\alpha) + \beta \cdot \log(L) \) that was fit by a separate least squares regression for each
combination of sex and species/morphotype. \( K_n \) values were plotted in a histogram to identify outliers (i.e. points greater than three standard deviations outside the mean), which were eliminated before further testing (i.e. one or two outliers in each species/morphotype). \( K_n \) data were normally distributed (verified with Shapiro-Wilk and Kolmogorov-Smirnov tests) and, thus, an ANOVA was used to determine whether condition varied with maturity, sex (walleye only), basin, and season (along with interactions) within a species/morphotype. To examine their interaction, it was necessary to compute a separate ANOVA with a combined basin/season factor. Post hoc Scheffé’s tests were used to determine differences between factors including the interaction between basins and among seasons. Within seasons, we combined years (i.e. spring 2010 and 2011; fall 2010 and 2011) due to the lack of significant differences between years (Sheppard 2013).

An ANOVA was used to determine if the mesenteric fat index varied with maturity, sex, species, basin and season. Post hoc Scheffé’s tests were performed to determine if there were significant differences between the mesenteric fat levels. Additionally, an ANOVA determined if there were significantly different mesenteric fat levels for fish with different \( K_n \) values, and Pearson’s correlation was performed to determine whether these two condition indices were correlated. Mesenteric fat levels were transformed to the midpoint of their fat content (0 = 12.5%, 1 = 50% and 2 = 87.5%) for presentation (Fig. 5).

**Results**

In total, 616 walleye, 32 dwarf walleye and 462 sauger were sampled (15% of these samples were collected from trawls). 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 two dwarf walleye were obtained from the North Basin, suggesting that they may not be present in large numbers. Additionally, sauger appear to exist in lower densities in the North Basin compared to the South Basin (over 90% of sauger sampled were from the South Basin) which may be related to commercial exploitation rates and minimum mesh size regulations. Similarly, the numbers of each size and sex of fish varied among 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. A table of sample sizes can be found in the Appendix (Table A1).
**Growth Rate**

Normal walleye had significantly higher growth rates than sauger, and both had significantly higher growth rates than dwarf walleye (ANCOVA, Table 1, Fig. 2a). Walleye and sauger in the North Basin had higher growth rates than those in the South Basin (Fig. 2b, c), and female walleye had higher growth rates than males, shown by larger length-at-age (ANCOVA, Table 1, Fig. 3).

Walleye had consistently larger age-specific mean fork lengths than sauger, females of both species had significantly larger average fork lengths than males (ANCOVA, Table 1, Fig. 3) and these differences were significant in ages 3, 4 and 5 fish, for which we had sufficient sample sizes (Fig. 3). Both walleye and sauger in the North Basin generally had larger average fork lengths than conspecific fish from the South Basin for the majority of ages; however, this was only significant for age 5 walleye (Table 1, Fig. 3). Interactions in the model (basin*sex, species*sex, basin*species and basin*species*sex) were also not significant (Table 1). The covariates, age and age$^2$, were both statistically significant, illustrating that there was a curvilinear relationship between length and age (Table 1, Fig. 2).

The growth rates of dwarf walleye were analyzed separately from growth of normal walleye and the ages of dwarf walleye sampled were notably older than the majority of normal walleye sampled (Fig. 3). The age and age$^2$ covariates were statistically significant and there was no significant difference in growth between sexes (Table 1). An ANOVA examining differences in growth of dwarf walleye between basins was not performed due to low sample sizes from the North Basin.

**Condition**

Using allometric linear regressions, significant differences were not found between coefficients of male and female walleye (Sheppard 2013) and, thus, data for both sexes were combined in one linear regression for analysis of walleye condition. Unlike walleye, there were significant differences in the coefficients of male and female sauger (Sheppard 2013), thus separate equations were generated.

Relative condition ($K_n$) of walleye differed between basins (Fig. 4a) and among seasons (Fig. 4b). There was a significant interaction between season and basin (ANOVA; Table 2). Maturity, season, basin and season/basin were all found to be significant factors in the sauger model (Table 2). *Post hoc* tests revealed that North Basin walleye and sauger both had
significantly higher $K_n$ than those in the South Basin (Fig. 4a). $K_n$ of walleye and sauger differed among seasons and was significantly higher in winter relative to any other season for walleye (Fig. 4b). Sample sizes for dwarf walleye in the North Basin were too low to compare between basins.

Walleye and sauger from the North Basin had significantly higher mesenteric fat levels than those in the South Basin ($F_{1,691} = 68.06, p < 0.001$ and $F_{1,514} = 137.41, p < 0.001$ respectively; Fig. 5a). Mesenteric fat varied significantly among seasons for walleye ($F_{3,689} = 40.27, p < 0.001$), being highest in the summer, but did not differ among seasons for sauger ($F_{3,512} = 0.86, p = 0.488$; Fig. 5b). Female walleye had significantly higher levels of mesenteric fat than males ($F_{1,691} = 63.90, p < 0.001$; Fig. 5c), whereas male and female sauger did not differ ($F_{1,514} = 1.44, p = 0.231$; Fig. 5c). Mesenteric fat levels did not differ between mature and immature walleye ($F_{1,691} = 0.50, p = 0.479$; Fig. 5d), whereas mature sauger had higher mesenteric fat levels than immature sauger ($F_{1,514} = 12.45, p < 0.001$; Fig. 5d).

$K_n$ values were significantly different among mesenteric fat levels in walleye (ANOVA, $F_{2,690} = 14.93, p < 0.001$) and sauger ($F_{2,513} = 10.94, p < 0.001$). For walleye and sauger, mesenteric fat levels 1 and 2 (50% and 87.5% respectively when transformed to their midpoint) did not differ, but both were higher than fat level 0 (12.5% when transformed to their midpoint; Scheffé’s multiple comparison of means; Fig. 6). Additionally, $K_n$ and mesenteric fat level were significantly correlated for walleye ($r < 0.3198, p < 0.0001$) and sauger ($r < 0.2107, p < 0.001$).

For dwarf walleye, $K_n$ did not differ between maturity stages or sex; thus, the sexes were pooled in the allometric linear regression analysis (Table 2). Condition differed among seasons (Table 2), with higher condition in the fall than the spring but did not differ from the summer or winter (Fig. 4). There was no mesenteric fat in dwarf walleye, regardless of maturity, sex or season (Fig. 5).

Discussion

Walleye had higher growth rates than sauger, consistent with reports in the literature (Scott and Crossman 1998; Stewart and Watkinson 2004; Johnston et al. 2012), and age-specific female
Walleye were significantly longer than males, as is common in many fish species with divergent sex-based energy demands during spawning (Roff 1983). Additionally, condition was highest at the end of the growing season (late summer - winter) and lowest during and after spawning, as observed previously (Cren 1951; Hansen and Nate 2005; Kaufman et al. 2007; Vassilopoulou and Harabalabous 2008; McPherson et al. 2011). A correlation between morphometric and bioenergetic (i.e. mesenteric fat index) measures of condition were found, suggesting that both methods are useful measures of condition for walleye and sauger. Walleye and sauger showed spatial variation in growth and condition, with both species having higher growth and condition in the North Basin relative to the South Basin of Lake Winnipeg. Interestingly, despite these spatial and temporal differences, growth and condition of walleye in Lake Winnipeg is higher than many other locations throughout Canada (our study; Kaufman et al. 2007; Moles et al. 2008).

Growth and condition were higher in the North Basin despite the higher commercial exploitation of walleye (Johnston et al. 2012) and higher prey abundance in the South Basin (Lumb et al. 2012), likely interacting to minimize intraspecific competition. As rainbow smelt comprises a high percentage of walleye (84.5-87.2%) and sauger (34.5-56.3%) diets during the open water season in the North Basin of Lake Winnipeg (Sheppard et al. 2015), the prevalence of this non-indigenous prey fish may explain the higher growth and condition of walleye and sauger in the North Basin. Indeed, 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 other fish species, such as alewife (*Alosa pseudoharengus* (Wilson, 1811)) (Cade et al. 2008). Rainbow smelt have a fusiform body shape with no spines (Hoyle and Keast 1987), making them easy to ingest, similar to gizzard shad (*Dorosoma cepedianum* (Lesueur, 1818)), alewife and cisco (*Saccharomyces cerevisiae* (Hansen, 1883)) (Hoyle and Keast 1987; Einfalt and Wahl 1997). As the latter species are all profitable prey types in terms of their morphology, energy density and predator escape response (Einfalt and Wahl 1997; Kaufman et al. 2009), higher growth rates of walleye have also been associated with increases in abundance of these native prey species in other systems (Swenson and Smith 1976; Knight et al. 1984; Hartman and Margraf 1992; Madenjian et al. 1996; Porath and Peters 1997; Kaufman et al. 2009).

The substantial variation in growth and condition between populations in the North and South basins of Lake Winnipeg suggests that there may be limited or infrequent mixing of adults between basins. Differences in scale shape of walleye between basins of Lake Winnipeg have also
been found (Watkinson and Gillis 2005), supporting the hypothesis that there may be basin-specific stocks of walleye. One study showed that there is little genetic variation in walleye in Lake Winnipeg which may suggest that the differences in the walleye between basins may be due to differences in their environment (Backhouse-James and Docker 2012). Although variation in temperature and turbidity between basins would influence walleye and sauger growth and condition, differences in temperature between basins is minimal and the entire lake would be considered highly turbid, suggesting again that this variation in growth and condition may be primarily due to dietary differences.

Lake Winnipeg is unique, as it appears to be one of the only ecosystems that has walleye, sauger, and dwarf walleye living sympatrically (Johnston et al. 2012). All three groups occupy the waters of the South Basin, whereas it appears that normal growth walleye and sauger (at lower densities) may be the only groups occupying 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 population size of sauger in the North Basin is, in fact, smaller. In systems where walleye and sauger coexist, there is often competition for resources, as evidenced by declines in sauger abundance relative to walleye abundance (Swenson and Smith 1976; Johnston et al. 2012). Higher exploitation of walleye in the South Basin may decrease walleye abundance enough to allow both species to coexist and for sauger to be more abundant in the South Basin (Johnston et al. 2012). Additionally, as sauger is often found in more turbid environments than walleye, this species might have an advantage over walleye in the South Basin (Ali and Anctil 1977; Swenson 1977; Johnston et al. 2012). Indeed, 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. Johnston et al. (2012) also reported that dwarf walleye seemed restricted to the South Basin and that they likely were not recruited to the fishing gear until they were much older potentially creating an advantage for dwarf walleye in the South Basin. Additionally, the most abundant forage fish (rainbow smelt) in the North Basin is larger relative to the most abundant forage fish (emerald shiner) in the South Basin (Sheppard 2013), giving smaller predators a disadvantage in the North Basin, as they would not have large enough gapes to access these more profitable prey. This suggests that survival of dwarf walleye would be higher in the South Basin, where they seem to exist in higher densities.
In conclusion, the differences in growth and condition of walleye and sauger between basins may be attributed to inter-basin dietary differences (Sheppard 2013), mostly resulting from the invasion of rainbow smelt into Lake Winnipeg. Additionally, greater fishing effort in the South Basin, compared to the North Basin may allow sauger to coexist with walleye as well as increase the prevalence of dwarf walleye in the South Basin. Overall, this study contributes observations of dwarf walleye distribution and provides baseline data against which to assess the future growth and condition of these populations owing to recent invasions of zebra mussels and spiny water fleas into Lake Winnipeg.

Acknowledgments

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Table 1: Analysis of covariance (ANCOVA) and analysis of variance (ANOVA) of length for walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye. Species, sex and basin were the categorical variables, and in ANCOVA age and age² were the covariates. A superscript z indicates factors that were not applicable, either because they were covariates that did not apply to ANOVA, or due to low/no sample sizes.

<table>
<thead>
<tr>
<th>Model</th>
<th>All fish - ANCOVA</th>
<th>Walleye, Sauger Age 3,4,5 - ANCOVA</th>
<th>Walleye, Sauger Age 3 - ANOVA</th>
<th>Walleye, Sauger Age 4 - ANOVA</th>
<th>Walleye, Sauger Age 5 - ANOVA</th>
<th>Walleye, Sauger Age &gt;5 - ANCOVA</th>
<th>Dwarf Walleye - ANCOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>p</td>
<td>df</td>
<td>F</td>
<td>p</td>
<td>df</td>
</tr>
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<td>1</td>
<td>15.65</td>
<td>&lt;0.001</td>
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<td>&lt;0.001</td>
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<td>&lt;0.001</td>
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<td>1</td>
<td>13.98</td>
<td>&lt;0.001</td>
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<td>1.21</td>
<td>0.27</td>
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<td>0.46</td>
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<td>---</td>
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<td>0.00</td>
<td>0.99</td>
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<td>192</td>
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<td>264</td>
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<td>197</td>
<td>325</td>
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Table 2: Analysis of variance (ANOVA) for the relative condition ($K_n$) of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye. A superscript $y$ indicates basin and season were separate main factors, but were not a balanced factorial. 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 $z$ indicates 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Walleye</th>
<th></th>
<th></th>
<th>Sauger</th>
<th></th>
<th></th>
<th>Dwarf Walleye</th>
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<td>$p$</td>
<td>df</td>
<td>$F$</td>
<td>$p$</td>
<td>df</td>
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<td>21</td>
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Figure Captions

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.

Figure 2: Fork length-at-age of normal growth walleye (black, *Sander vitreus*), sauger (grey, *Sander canadensis*) and dwarf walleye (dotted) in Lake Winnipeg, Manitoba (a), fork length-at-age of age 3-5 walleye (b) and sauger (c) seperated into the North Basin (black) and South Basin (grey). All trend lines fitted using the Von Bertalanffy growth curve where $t_0$ was set to zero and $L_\infty$ was set to the maximum length of each group of fish sampled.

Figure 3: Age-specific mean (± SE) fork lengths (mm) of male (black) and female (grey) walleye (*Sander vitreus*) (a, b), sauger (*Sander canadensis*) (c, d), and dwarf walleye (e) in the South (a, c, e) and North (b, d) Basins of Lake Winnipeg. Dwarf walleye were not found in the North Basin, therefore only South Basin is shown.

Figure 4: Mean (± SE) relative condition ($K_n$) of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye categorized by North Basin (grey) and South Basin (white; a) and season (b; spring-white, summer-dark grey, fall-light grey, winter-black). Bars within a species/morphotype having the same letter are not significantly different ($p > 0.05$), while those with different letters are significantly different ($p < 0.05$) as determined by Scheffé’s post hoc tests. Basin/season for sauger were tested relative to a reference (South - Spring 2011; denoted with ‘ref’) because it had the lowest $K_n$ value and a high sample size.

Figure 5: Mean (± SE) mesenteric fat level of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye categorized by basin (a; North Basin grey, South Basin white), season (b; spring white, summer dark grey, fall light grey, winter black), sex (c; female grey, male white), and maturity (d; mature grey, immature white). Bars within a species/morphotype having the same letter are not significantly different ($p > 0.05$), while those with different letters are significantly different ($p < 0.05$) as determined by Scheffé’s post hoc tests. Mesenteric fat levels were transformed to the midpoint of their fat content (0 = 12.5%, 1 = 50% and 2 = 87.5%) for presentation.
Figure 6: Mean (± SE) relative condition ($K_r$) of walleye ($Sander vitreus$) (black; $n=693$) and sauger ($Sander canadensis$) (gray; $n=516$) with three different levels of mesenteric fat. Mesenteric fat levels were transformed to the midpoint of their fat content ($0 = 12.5\%, 1 = 50\%$ and $2 = 87.5\%$) for presentation.
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.

153x204mm (300 x 300 DPI)
Figure 2: Fork length-at-age of normal growth walleye (black, Sander vitreus), sauger (grey, Sander canadensis) and dwarf walleye (dotted) in Lake Winnipeg, Manitoba (a), fork length-at-age of age 3-5 walleye (b) and sauger (c) separated into the North Basin (black) and South Basin (grey). All trend lines fitted using the Von Bertalanffy growth curve where $t_0$ was set to zero and $L_\infty$ was set to the maximum length of each group of fish sampled.
Figure 3: Age-specific mean (± SE) fork lengths (mm) of male (black) and female (grey) walleye (Sander vitreus) (a, b), sauger (Sander canadensis) (c, d), and dwarf walleye (e) in the South (a, c, e) and North (b, d) Basins of Lake Winnipeg. Dwarf walleye were not found in the North Basin, therefore only South Basin is shown.

153x204mm (300 x 300 DPI)
Figure 4: Mean (± SE) relative condition (Kn) of walleye (Sander vitreus), sauger (Sander canadensis) and dwarf walleye categorized by North Basin (grey) and South Basin (white; a) and season (b; spring-white, summer-dark grey, fall-light grey, winter-black). Bars within a species/morphotype having the same letter are not significantly different (p > 0.05), while those with different letters are significantly different (p < 0.05) as determined by Scheffé’s post hoc tests. Basin/season for sauger were tested relative to a reference (South - Spring 2011; denoted with ‘ref’) because it had the lowest Kn value and a high sample size.
Figure 5: Mean (± SE) mesenteric fat level of walleye (Sander vitreus), sauger (Sander canadensis) and dwarf walleye categorized by basin (a; North Basin grey, South Basin white), season (b; spring white, summer dark grey, fall light grey, winter black), sex (c; female grey, male white), and maturity (d; mature grey, immature white). Bars within a species/morphotype having the same letter are not significantly different (p > 0.05), while those with different letters are significantly different (p < 0.05) as determined by Scheffé’s post hoc tests. Mesenteric fat levels were transformed to the midpoint of their fat content (0 = 12.5%, 1 = 50% and 2 = 87.5%) for presentation.
Figure 6: Mean (± SE) relative condition (Kn) of walleye (Sander vitreus) (black; n=693) and sauger (Sander canadensis) (gray; n=516) with three different levels of mesenteric fat. Mesenteric fat levels were transformed to the midpoint of their fat content (0 = 12.5%, 1 = 50% and 2 = 87.5%) for presentation.
Appendix:

Table A1: Sample sizes of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye by basin and age class.

<table>
<thead>
<tr>
<th>Age</th>
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<th>Sauger</th>
<th>Dwarf Walleye</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td>South Basin</td>
</tr>
<tr>
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</tr>
<tr>
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<tr>
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