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Nanayakkara, L., Leavitt, P., & Wissel, B. (2020). Resource-use, body condition and parasite load metrics indicate contrasting health of stocked and native game fishes in Canadian prairie lakes. *Fisheries Management and Ecology*. <https://doi.org/10.1111/fme.12447>

Published in:
Fisheries Management and Ecology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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Resource-use, body condition and parasite load metrics indicate contrasting health of stocked
and native game fishes in Canadian prairie lakes.

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14 **Abstract**

15 This study evaluated the status of native and stocked fish species in 13 prairie lakes in central
16 Canada over eight years (2007-14) using three metrics; resource-use (benthic vs. pelagic carbon
17 via stable isotopes), body condition (relative weight index W_r) and parasite load (cestode gut
18 enumerations). Analyses included game and non-game fishes, like naturally-occurring northern
19 pike (*Esox lucius*) and yellow perch (*Perca flavescens*), but focused on stocked walleye (*Sander*
20 *vitreus*) because of a robust recreational fishery. Walleye and northern pike were significantly
21 more reliant on benthic carbon than yellow perch or forage fishes ($P < 0.05$), but this reliance was
22 not associated statistically with any measured environmental variables for any species. In lakes
23 with game fishes, forage fishes exhibited higher reliance on benthic energy, possibly due to
24 predator avoidance strategy, particularly yellow perch. Walleye body condition index was
25 consistently lower (<95-105) than values exhibited by the other two game fishes (81-139), and
26 parasites were only common in walleye and associated with lake water salinity ($r^2 = 0.93$,
27 $P < 0.05$) and sex ($P < 0.05$). Based on results, the most desirable game fish, walleye, appears less
28 resilient to environmental variability than northern pike and yellow perch, making this species
29 more susceptible to impacts of future climate change.

Introduction

Inland waters provide numerous ecosystem goods and services, including water supply, regulatory services, food production and recreation (Costanza et al. 1997). In developed countries, recreational fishing is the most significant use of fish stocks, as well as an important social and economic driver of recreational use of inland waters (Post et al. 2002, Arlinghaus and Cooke 2009). In Canada, recreational fishing contributes \$8.8 billion annually to the economy with most of the fishing taking place in inland waters (Brownscombe et al. 2014). Currently, recreational fisheries appear to be more resilient to environmental change than commercial fisheries (Post 2013); however, evidence is mounting that the synergistic effects of climate change, intensive land-use and invasive species may interact with enhanced fishing pressure (Post et al. 2002) to threaten the adaptive capacity of lake ecosystems (McMeans et al. 2016).

Game fishes feed at higher trophic levels and are less resilient to environmental change than non-game (forage) fishes, because their higher metabolic costs make them physiologically susceptible to environmental stresses (Whitney et al. 2016). Furthermore, increasing lake temperatures are expected to exert a disproportionate negative impact on cool- and cold-water species, such as walleye (*Sander vitreus*), which are more susceptible to sub-lethal effects of temperature on physiology, growth, and reproduction (Lynch et al. 2016). Lake warming decreases the amount of dissolved oxygen (DO) in the water column, increasing the probability of either winter- or summerkill (Wetzel 2001). Elevated temperatures will also increase lakewater evaporation, potentially resulting in higher solute concentrations and osmotic stress (Starks et al. 2014, Whitney et al. 2016). Finally, as conditions shift away from the optimal range for cool-water species, elevated stress can alter immune system function and increase vulnerability to diseases and parasites (Wegner et al. 2008, Whitney et al. 2016).

Game fishes in hardwater prairie lakes may be especially vulnerable to cumulative and synergistic effects of environmental change (Starks et al. 2014). Such lakes are common on the Northern Great Plains, and are typically shallow, polymictic, and eutrophic with somewhat elevated salinities (Wissel et al. 2011). These lakes experience substantial seasonal and inter-annual variation in physical and chemical water parameters due to high climate variability (Pham et al. 2009) and anthropogenic activities, including intensive agriculture and irrigation (Starks et al. 2014). The Prairie Ecozone of Canada is predicted to experience more extreme climate events (i.e., droughts, deluges), higher than average rates of warming (Barrow 2009) and likely increased aridity, so it is essential to assess the current status of prairie fish populations. To evaluate the importance of these trends, it is important to identify potential sub-lethal impacts of changing environmental conditions on key population measures such as resource-use, growth and condition, and physiological vulnerability to disease and parasites (Murphy et al. 1991, Marcogliese et al. 2005, Vander Zanden et al. 2011).

The objectives of this study were to quantify temporal and spatial variation in the status of prairie lake fish populations in the Northern Great Plains of Canada. By utilizing a diverse set of lakes spanning more than an order-of-magnitude in most limnological, physical and chemical features (Appendix Table 1), we used these lakes as a model system (Wissel et al. 2011) to evaluate how indicators of fish-population health (as resource-use, body condition, parasite loads) respond to changing environmental conditions among years. The focal species for this study was walleye because it is the most desired species in these waters (Nanayakkara and Wissel 2017), yet is a stocked taxon which lacks natural genetic diversity across the study region (E. Starks, U. Regina, unpublished data). This study also assessed the same set of parameters for two common native game fishes, Northern Pike (*Esox lucius*) and Yellow Perch (*Perca*

flavescens), to evaluate if stocked and native species respond differentially to environmental change. Even though the study focused on game fishes, lakes with game fishes and forage fishes (n=8, high complexity), as well as lakes with only forage fishes (n=5, low complexity) were also included. This enabled us to test if presence of game fishes or more detrimental environmental conditions (elevated salinity, poor water quality) would impact population health of forage fishes. This study hypothesized that: 1) game fishes will exhibit variable resource-use, reflecting differences in lake productivity and physical extent of littoral areas; 2) walleye will have poorer body condition index than northern pike and yellow perch because they are not native to these lakes; 3) all three game fishes will exhibit higher parasite loads in years of elevated salinity and poor water quality and; 4) forage fishes will exhibit similar resource-use in both high and low complexity lakes due to their increased ability to withstand stress.

Methods

Study site

13 fish-bearing lakes were sampled in June and August from 2007 to 2014 to evaluate temporal and spatial variation of fishes among lakes within the Prairie Ecoregion of southern Saskatchewan (SK) in central Canada (Appendix Figure 1). These lakes are part of a 21-lake Long-Term-Ecological-Research program that has been conducted in most basins since 2002 (Pham et al. 2009). Study lakes comprised five sites of low fish complexity (only forage fishes) and eight basins with high complexity (forage fishes, benthivores, and game fishes). The term ‘forage fishes’ herein collectively refers to both potential prey of game fishes in high complexity lakes and any fishes found in low complexity lakes (Essington et al. 2015). Common game fishes and bottom-feeding benthivorous species include northern pike, walleye, yellow perch, whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and common sucker (*Catostomus*

commersonii). Seven of eight high-complexity lakes are regularly stocked with walleye fry to compensate for a lack of sufficient spawning habitat and natural reproduction (Saskatchewan Stocked Waters Guide (SSWG) 2017). All lakes are located in endorheic (hydrologically-closed) basins that lack channelized surface inflow or outflow, are mainly sustained through winter precipitation, and exhibit high rates of evaporation (Pham et al. 2009). Limnological measures (e.g., solute concentrations), morphometric features (e.g., depth), and trophic status vary considerably across survey lakes (Starks et al. 2014) and through time (Pham et al. 2009).

Sampling and analyses

Lakes were sampled in June and August annually from 2007 to 2014 using standard methods (Cooper and Wissel 2012a, 2012b, Starks et al. 2014). Water temperature (°C), total dissolved solids (g TDS L⁻¹), dissolved oxygen (mg O L⁻¹) and pH were all measured at 1-m intervals at the location of the deepest point in the lake using a YSI model 556 multi probe instrument. Depth values were obtained with a Laylin SM-5 electronic depth meter, and water transparency was measured using a 20-cm diameter Secchi disk. A 7-m tygon tube (5 cm internal diameter) was used to collect a depth-integrated water sample of these polymictic lakes. The tube was lowered to 0.5 m above the bottom for lakes with depth <7 m and only the upper 7 m were sampled for deeper lakes.

The integrated water sample was filtered through pre-washed GF/C filters (nominal pore size 1.2 µm) and stored at -15°C until analysis of chlorophyll (Chl *a*, Chl *b*, Chl *c*, total chlorophyll [TC]) Chl *a* extractions were performed with an acetone-methanol-water (80:15:5 by volume) solution and analyzed using standard spectrophotometric methods (Wellburn 1994).

Pelagic zooplankton were sampled using small (80- μ m mesh, 30-cm diameter) and large nets (500- μ m mesh, 50-cm diameter) for small and large species, respectively. Plankton nets were towed vertically from 0.5 m above the bottom to the surface at the sampling station. Collected samples were preserved in a 50% ethanol-sucrose solution for taxonomic identification and enumeration. Samples were identified to species and enumerated at the University of Regina using a SZX12 Olympus microscope. Bulk zooplankton samples from both nets types were also collected for stable isotope analysis. In addition, littoral macroinvertebrates were collected using a large sweep net (500- μ m mesh size) in near-shore habitats. Both sets of isotope samples were contained in filtered lake water and stored at -15°C prior to analyses.

Near-shore forage fishes were sampled using a beach seine net (2 m x 30 m, 10-mm mesh size) at mid-day following Cooper and Wissel (2012a). Fish were identified to species and stored at -15°C prior to further analyses. Game fishes and benthivores in high complexity lakes were sampled overnight using a gill net (1.5 m x 30 m, 55-mm mesh) placed perpendicular to shore. Fish were stored at -15°C until dissections and stable isotope analyses. Total length (cm), fork length (cm) (supplementary file), standard length (cm), weight (g) and sex were recorded for all samples. Stomach contents were identified to family and enumerated when possible. Stomachs and digestive tracts of individuals from all three game fish species exceeding 10 cm total length were opened longitudinally with a scalpel and directly examined (Justine et al. 2010) for internal parasites (Cestoda).

Following identification and dissections, a small amount (~1 g) of lateral muscle tissue was removed from each of 5-10 individuals per species and lake for stable isotope analysis (Pinnegar and Polunin 1999). Fish muscle samples, abundant taxa from large-bodied littoral macroinvertebrates (~1 individual sample⁻¹) and zooplankton (~30-150 individuals sample⁻¹)

were rinsed with deionized water, dried to constant mass at 50°C, and packed into tin capsules. Capsules were combusted in a Costech elemental analyzer connected to a Thermo Finnigan Delta V isotope ratio mass spectrometer (IRMS) at IECS. Internal laboratory standards of bovine liver and wheat flour were used as reference materials. Carbon and nitrogen isotopes were reported in the conventional δ notation (‰) relative to the international standards Vienna Pee Dee Belemnite (for carbon) and atmospheric N₂ (for nitrogen) (Peterson and Fry 1987). Due to the potential impacts of chemical lipid extraction on carbon and nitrogen isotope values (Logan et al. 2008), we used C:N based mathematical lipid-corrections outlined in (Braun et al. 2014) to normalize $\delta^{13}\text{C}$ values prior to analyses, to account for depleted ^{13}C values with increasing lipid content (Post et al. 2007).

Numerical analyses

Benthic and pelagic primary production at each site and on each sampling date were calculated using the primary production model of Vadeboncoeur et al. (2008). Similar to previous studies (Vander Zanden and Vadeboncoeur 2002, Vadeboncoeur et al. 2008) ‘benthic’ in our study refers to littoral production. Benthic production and contribution to whole-lake production was estimated from analysis of lake surface area, basin volume, Chl *a* content, lake depth (maximum and mean), depth ratio, shape factor and day length. Model input for maximum benthic primary production (BP_{max}) was set at the intermediate value ($50 \text{ mg C m}^{-2} \text{ h}^{-1}$) to account for the possibly confounding balance of large littoral areas and high trophic status, and because prairie lakes are more productive relative to other lake-types. This value for BP_{max} represents light-saturated benthic productivity in mesotrophic lakes whereas the lowest value ($5 \text{ mg C m}^{-2} \text{ h}^{-1}$) is characteristic of periphyton attached to substrata in low-alkalinity lakes and the

highest value ($120 \text{ mg C m}^{-2} \text{ h}^{-1}$) is typical of a wide range of oligotrophic lakes (Vadeboncoeur et al. 2008).

Carbon stable isotope ($\delta^{13}\text{C}$) data were used to characterize resource-use by different fish taxa, in particular their relative reliance on benthic vs. pelagic carbon sources. Use of carbon isotope data to differentiate between benthic and pelagic primary producers is based on established trophic relationships in which consumers retain the carbon isotope values of primary producers, and where periphyton (benthic primary producers) are enriched in ^{13}C due to diffusion processes within the cellular boundary layer (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002). Nitrogen stable isotope data (as $\delta^{15}\text{N}$) were used to reconstruct trophic levels in the study lakes. Primary consumers that were commonly identified in stomach content analyses of game fishes, amphipods (benthic) and cladocerans (pelagic) were used as end members in the mixing model instead of primary producers to avoid the high temporal variability of phytoplankton samples, sampling bias, and high lake-to-lake variability (Vander Zanden et al. 2011).

Contributions of each carbon source to fish diets were estimated using the Bayesian mixing model package *MixSIAR* (Stock and Semmens 2013) available in the R cran statistical package (version 3.4.1; R Development Core Team 2017). Trophic fractionation factors of 0.0 ± 0.5 for carbon (Vander Zanden and Vadeboncoeur 2002) and 3.5 ± 0.5 for nitrogen were used (Vander Zanden and Rasmussen 2001). Preliminary analyses revealed sufficient isotopic separation between end-members ($>3\text{‰}$) to obtain robust results. As a result, two main sources of variability in isotope values were accounted for by entering ‘process errors’ (e.g., variability in consumer isotope values due to chance) and ‘residual errors’ (e.g., individual differences in rate of assimilation) into the model configuration (Stock and Semmens 2016). Mixing models were

run for each sampling date from 2007 to 2014. To obtain accurate posterior distributions, models were run at “long” (300,000, burn-in 200,000) or “very long” (1,000,000, burn-in 500,000) Markov Chain Monte Carlo (MCMC) measures. All models passed the Gelman-Rubin and Gewke diagnostic tests for model convergence on the posterior distributions (Stock and Semmens 2013).

Relations between fish resource use and lake parameters were quantified using unreplicated linear regression. Regression models (R cran package “car”, version 2.1-5: Fox and Weisberg 2011) were developed for associations between lake-specific global mean output (mean of all the species-specific values) for each sampling date, and diverse measures including f(BP) (benthic contribution to whole-lake production), year, complexity (reference category: high), month (reference category: August) and lake (reference category: Wakaw). Subsequently, MixSIAR results for temporal (year, season), spatial (lake), species and group (forage, benthivores and game fishes)-specific differences on benthic reliance (dependent variable) were analyzed using analysis of variance (ANOVA) models (R cran packages “car”, version 2.1-5: Fox and Weisberg 2011; “compute.es”, version 0.2-4: Del Re 2013; “ggplot2”, version 2.2.1: Wickham 2009; “pastecs”, version 1.3-18: Grosjean and Ibanez 2014). ANOVA models were tested for, and passed, Levene’s test for homogeneity of variances ($P > 0.05$). Linear regressions were run separately for forage and game fishes to examine the role of environmental predictors (including maximum depth, salinity, temperature, nutrients and Secchi depth) on benthic reliance of each group.

Fish condition was estimated from calculation of relative weight (W_r) indices (body condition) for walleye, northern pike and yellow perch following Murphy et al. (1990) and

Blackwell et al. (2000). A body condition index was calculated for each game fish species caught from 2009-2014 using the following equation and reported as a whole number;

$$W_r = (W/W_s) \times 100,$$

where W_s values were calculated for each fish exceeding the required minimum total length (walleye >150mm, pike >100mm, perch >100mm). Measures for W_s were derived from the regression equations of (Blackwell et al. 2000). Individual body condition index values were then averaged for each species by month, lake and year. Since W_r values for individual populations were not significantly different among sites within each sample period (ANOVA, $P > 0.05$), results from all lakes were combined for each month and species. Values of $W_r = 95-105$ indicate good condition, whereas scores near 80 indicate poor health due to adverse environmental conditions or lack of food and extremely high scores (>115) imply excess energy reserves (Murphy et al. 1990, Blackwell et al. 2000). The number of individuals per sampling period (June or August) varied from 20-61 for walleye, 0-25 for pike, and 0-48 for perch. Unusually high relative weight indices were observed for both walleye and northern pike in early 2009 when unstandardized measurement protocols were used, and were not included in further analyses.

Parasite densities sufficient for analysis were only found in walleye samples, consequently, parasite loads of gut tapeworms were compared between lakes over time for that species alone. The quantity of tapeworms found in each fish and the proportion of the population infected were recorded for each lake and date. These values were subsequently regressed against environmental measures using unreplicated linear regressions. The influence of sex and season were evaluated using t-tests and the effects of year and lake were

assessed by one-way ANOVAs (IBM SPSS version 20). The abundance of other parasites (e.g., nematodes) was insufficient to be included in the analysis.

Results

Benthic contribution to whole-lake primary production exceeded 50% from 2007-2014 in most fish-bearing lakes (Figure 1). Overall mean ($\pm$ SD) benthic contribution to whole-lake primary production over the entire sampling period was 0.68 ± 0.19 in low-complexity lakes and 0.79 ± 0.14 in high-complexity lakes, with similar extremes and ranges in both community types. Despite the importance of benthic primary production, MixSIAR models suggested that most taxa were not using benthic carbon sources in proportion to their availability (below the 1:1 line in Figure 1). Mean reliance on benthic carbon for all fishes was significantly associated with month, being higher in June than August ($P < 0.05$). Three lakes (Humboldt, Lenore and Pelletier) exhibited significantly lower reliance on benthic carbon than the reference category (Wakaw lake, $P > 0.05$). Overall, the proportion of benthic production to whole-lake primary production (f[BP]) was not associated significantly ($r^2 = 0.27$, $P > 0.05$) with the use of benthic carbon by fishes.

Both forage and game fishes exhibited high variability in use of benthic resources; mean reliance for all forage fishes was 0.31 ± 0.27 , with higher values in high complexity lakes (0.36 ± 0.31) than in sites of low complexity (0.23 ± 0.18) (Figure 2). Similarly, mean benthic reliance for game fishes was 0.47 ± 0.32 , while bottom-feeders exhibited proportionate use of benthic carbon of 0.31 ± 0.25 . A two-way ANOVA for group and seasonal difference on benthic reliance for the three groups of fishes revealed that game fishes were significantly more reliant on benthic resources throughout the growing season ($P < 0.01$) and all three fish groups were more reliant on

benthos early on in the season ($P<0.05$) (Figure 2). Forage fishes were significantly more reliant on benthic carbon in high complexity lakes than in low complexity lakes ($P<0.05$) (Figure 2). Subsequent one-way ANOVA showed that johnny darters (*Etheostoma nigrum*), minnows (*Cyprinidae*) and ninespine stickleback (*Pungitius pungitius*) were all significantly more reliant on benthos than were other taxa in high complexity lakes, while brassy minnows (*Hybognathus hankinsoni*) were more reliant on benthos in low complexity lakes ($P<0.001$). Spottail shiner's (*Notropis hudsonius*) were only found in one low complexity lake (Figure 3).

There were no significant associations between use of benthic carbon and environmental measures for either forage or game fishes (each $P>0.05$), although species-level analysis revealed that walleye and northern pike were significantly more reliant on benthic resources than were yellow perch ($P<0.01$) (Figure 4). While benthic reliance for whitefish and cisco seemed low, insufficient sample sizes precluded their inclusion in species-specific analyses. Direct estimates of dietary composition revealed that walleye consumed forage fishes more than twice as frequently as they did amphipods. Northern pike consumed forage fishes four times as much as they did amphipods, but yellow perch diets were almost-evenly composed of cladocerans and amphipods.

W_r values for 404 walleye, 76 pike, and 165 perch individuals (Table 1) were estimated. Overall, there were no significant differences among lakes for any of the three species ($P>0.05$). Walleye achieved mean W_r indices within the range expected for healthy populations (95-105; Blackwell et al. 2000, Murphy et al. 1990) in only three of 11 sampling periods, while northern pike achieved this range in five out of 10 collection periods, and perch mean W_r were within the range in six of 10 sampling periods. W_r of walleye increased through the summer in all years but 2014 (Table 1). Such seasonal increases occurred less frequently for pike and perch (only three

years each). Intra-annually, walleye exhibited W_r values characteristic of healthy populations in at least one of the two annual sampling periods (June or August) in 2010 and 2011, but had less than ideal body condition in both sample periods during 2012-2014, with minima recorded in both June and August 2014. Pike populations were healthy ($W_r > 95$) during at least one of the two monthly sampling periods every year; during August in 2010-2012 and during June in 2013-2014. Perch also exhibited good body condition during at least one sampling period each year, including August 2010 and 2012-2013, June 2012, and both months in 2014.

Walleye were infected with significantly more parasites in 2009 than in 2010. Parasite load was correlated positively and strongly ($r^2 = 0.93$, $P < 0.05$) with lake water salinity (g TSD L⁻¹) in 2009 but not in 2010, and not with other environmental predictors in either year. Salinities were significantly higher in 2009 ($P < 0.05$). Tapeworm load was also significantly correlated with fish size (total length), with individuals > 10 cm hosting more parasites than did smaller fish ($P < 0.05$). Despite similar infection rates in 2009, females were infected with a significantly higher quantity of tapeworms ($P < 0.05$) in 2009. No males were infected in 2010.

Discussion

In general, use of benthic C sources by fishes was unrelated to the modeled importance (%) of phytobenthos to total primary production of prairie lakes, with most sites recording an underutilization of benthic resources relative to their abundance (Figure 1). This finding contrasts Vander Zanden et al. (2011), who document a positive correlation between the two metrics and a high benthic reliance by fish even when $f(BP)$ was low. Similarly, Ask et al. (2009) found benthic energy use by higher trophic levels was tightly coupled with benthic primary production ($r^2 = 0.96$, $P < 0.001$) whereas (Karlsson and Byström 2005) found arctic char

(*Salvelinus alpinus*) exhibit high reliance (62-94%) on benthic energy despite availability of prey fish. Interestingly, mean benthic contribution to whole-lake production in prairie lakes was higher than reported in previous studies (Ask et al. 2009, Vander Zanden et al. 2011). Similar to our analysis, Vander Zanden et al. (2011) also found no significant association between mean benthic reliance and limnological, morphological and environmental measures. Thus, in contrast to the predominantly boreal and subarctic lakes of these previous studies, the present work focuses on eutrophic hardwater lakes, basins which constitute ~50% of the global inland water volume (Finlay et al. 2015). This observation suggests that benthic resource-use by fishes may differ among continental lake districts (boreal, subarctic, grassland, etc.).

Higher reliance on benthos during early summer may reflect competitive interactions between periphyton and phytoplankton (Vadeboncoeur et al. 2003), as benthic primary producers often predominate early in the ice-free season, particularly during the clearwater phase (Dröscher et al., 2009), until phytoplankton productivity increases and limits light penetration during summer. Similar to our findings, García-Berthou and Moreno-Amich (2000) noted a decrease in pumpkinseed (*Lepomis gibbosus*) dependence on benthic prey over the course of the summer (June to August), while Hayden et al. (2014) found seasonal decreases in dependence on benthic prey by fish species in subarctic lakes. However, despite generally high use of benthic resources in early summer (Figure 2), there remains a high degree of variation among prairie survey lakes. Although speculative, high among-lake variation may reflect the wide gradient of human and hydrological controls in regional ecosystems (Leavitt et al. 2006, Starks et al. 2014), ranging from wastewater pollution in Humboldt Lake (Cooper and Wissel 2012a), to dramatic lake level changes in Lenore Lake, and simplified forage fishes food-web structure in Lake Pelletier (Yellow perch alone, Cooper and Wissel 2012b). Alternately, high variation in benthic

production and use among lakes in June may arise because of differences in timing and strength of the June clearwater phase (Dröscher et al. 2009). During that period, herbivorous zooplankton can clear the water of particles, increase light penetration to the bottom of shallow lakes, and stimulate benthic primary production (McGowan et al. 2005). Further research will be required to distinguish among these possibilities.

Benthic energy pathways were similarly important to forage and game fishes in these study lakes (Figure 2). In general, a higher reliance of forage fishes on benthic resources occurred in lakes of high food-web complexity. Such increased reliance can reflect variations in forage fishes community composition as a result of predation pressure (Findlay et al. 2000, Jackson et al. 2001), differences in overall lake production among low- and high-complexity lakes (Persson et al. 1991), or behavioral responses of forage fishes to avoid piscivory (Turner and Mittelbach 1990). It was inferred that community composition did not influence the use of benthic resources by forage fishes, as all forage species except spottail shiners were present in all lakes. Similarly, there was no significant difference in modeled benthic and planktonic primary production as a function of food-web complexity. While speculative, it was inferred that behavioral responses of fishes to avoid predation affected forage fishes diets, with these taxa spending a higher proportion of the day in shallow littoral habitats where benthic production is greatest and where the more heterogeneous environment provides refugia from predation (Ajemian et al. 2015).

While fish dominated the diets of both walleye and northern pike, amphipods were common in both species-specific assessments and may indicate a lack of vertebrate prey. Additionally, diets of adult yellow perch were almost equally split between zooplankton and amphipods, consistent with the tendency of percids to supplement their diets with

macroinvertebrates despite potential for reduced growth without fish prey (Knight et al. 1984, Bethke et al. 2012). Overall, reliance of walleye on amphipods in our lakes was higher than that reported in past studies (Vander Zanden and Vadeboncoeur 2002). For example, Quist et al. (2002) found that even when invertebrates were abundant in walleye diets, they did not substantially contribute to the total biomass consumed relative to vertebrate prey. Taken together, these findings indicate that the relatively poor body condition of some species may reflect a decoupling of primary and secondary production in these systems, leading to lower energy transmission to top predators.

Bioenergetic models show that excessive temperatures may induce thermal stress and result in net energy loss even in the presence of abundant prey (Kitchell et al. 1977, Quist et al. 2002). In contrast, Johnston et al. (2012) reported that adult walleye and sauger growth rates in Lake Winnipeg were not correlated with optimal temperatures, suggesting high site-to-site variation in thermal effects. Our findings suggest that body conditions of game fishes in prairie lakes may be determined by a combination of sub-lethal stressors and prey availability.

Water chemistry may have interacted with infection by endoparasites to further reduce the body condition of some prairie fishes. For example, salinity was significantly associated with the load and prevalence of parasites in walleye during 2009, although it was not significantly correlated with the body condition index of this species. During 2009, lakewater salinities were in excess of 2.0 g TDS L⁻¹ in all the gamefish-bearing lakes, approaching the upper limit threshold (<3.0 g TDS L⁻¹) for freshwater fishes identified by Cooper and Wissel (2012a), whereas salinities were consistently <1.5 g TDS L⁻¹ throughout 2010. Previous studies have documented significant correlations between environmental stressors and parasite loads and identified parasites as useful bioindicators of environmental impacts on fish condition (Vidal-

Martínez et al. 2010). Similarly, elevated salinities are known to reduce walleye growth (Wilson and Nagler 2006), although the critical threshold for population effects is thought to be greater (4-8 g TDS L⁻¹) than those recorded in most of our study lakes (Cooper and Wissel 2012b).

Future sustainability of stocked and native prairie fishes

Increased temperatures in the future are expected to decrease the overall fitness of game fishes populations by reducing net energy uptake (lower poor body conditions) and increasing parasite loads (Holt and Jørgensen 2015). Without sufficient energy reserves, walleye may not be able to sustain net positive secondary production during summers until water-column temperatures decrease again in fall. For example, Quist et al. (2002) reported that warmer temperatures resulted in lower W_t condition indices, growth rates and higher occurrence of empty stomachs, likely due to decreased foraging. In our lakes, gut analysis revealed that a high proportion of game fishes exhibited empty stomachs for both walleye (30-60%) and northern pike (35-40%). In dimictic lakes, walleye seek a thermal refuge and decrease forage activity when water temperatures exceed 22 °C (Quist et al. 2002); however, this option is unavailable in these polymictic basins which lack deepwater thermal refuges. As projected temperature maxima may exceed 30 °C in the Prairies (Barrow 2009), walleye may be eliminated from these shallow systems due to a combination of limited feeding activity, higher metabolic costs, and other factors leading to low growth rates (Quist et al. 2002, Whitney et al. 2016).

Walleye in prairie lakes may be more susceptible to synergistic effects of lake warming and osmotic stress than were northern pike or yellow perch, particularly in concert with endoparasitic infections. Projected temperature increases of 5 °C by 2050 (Barrow 2009) will favour evaporative concentration of prairie lakes (Pham et al. 2009, Wissel et al. 2011) and

salinity-induced suppressions of immune systems that may make walleye more susceptible to parasitic infections in the future (Whitney et al. 2016, Barber et al. 2016). However, there is no indication that temperatures are currently exceeding a point at which parasitic infections cause issues.

Although parasite load was not significantly related to temperature in our lakes, Macnab and Barber (2012) found that parasitic infection were positively correlated with increasing temperatures in other aquatic systems, both because of increased rates of life-cycle completion and provision of warmer fish tissues required for parasite proliferation. Such factors are expected to combine to decrease body conditions of parasitized fishes (Britton et al. 2011).

Conclusions

Comparison of resource-use, body condition, and parasite load suggested that stocked walleye were less resilient to environmental change than were native prairie fishes. In particular, walleye in prairie lakes are more reliant on macroinvertebrates, exhibited poorer body conditions, and are more susceptible to parasitic infections than were native fishes. Current status of walleye populations indicates a stressed taxon with high susceptibility to the unique and interactive effects of climate change, intensified land-use, and invasive species. As walleye are also considered the most desirable species by regional recreational anglers (Nanayakkara and Wissel 2017), they may be additionally subject to disproportionately high angling pressure. Based on results of this and previous studies (Cooper and Wissel 2012b, Starks et al. 2014), the long-term habitability of these lakes for large game fishes may depend on the balance between osmotic and thermal stress brought on by climate change, susceptibility to parasitic infections, their influence on body condition and fluctuations in winterkill risk.

418 **Acknowledgements**

419 This research was conducted on Treaty 4 and Treaty 6 lands, which consists of the traditional
420 territories of the Cree, Dene, Blackfoot, Saulteaux, Nakoda, Dakota, and Lakota peoples and the
421 homeland of the Métis Nation. Funding for this study was provided by a Natural Sciences and
422 Engineering Research Council of Canada (NSERC) grants to BW, and Teaching Assistance and
423 Research scholarships from the University of Regina to LN and Government of Saskatchewan
424 Fisheries and Wildlife Development Fund grants to BW and LN. Canada Foundation for
425 Innovation, the Province of Saskatchewan and NSERC are thanked for funding for research
426 infrastructure. Field assistance during sample collection was provided by D. Bateson, D. Braun,
427 B. Hesjedal, K. Murphy, and M. Beaton.

428

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 640

641 **Table 1.** Body condition (Wr) data for the three main game fishes; Walleye (*Sander vitreus*), Northern pike (*Esox lucius*) and Yellow
642 perch (*Perca flavescens*).

Year	Month	Walleye	Pike	Perch
2009	June	156 (n=21)	157 (n=8)	91 (n=48)
	August	95 (n=49)	NA	92 (n=35)
2010	June	81 (n=23)	84 (n=25)	89 (n=27)
	August	105 (n=36)	117 (n=3)	123 (n=11)
2011	June	93 (n=44)	94 (n=19)	139 (n=17)
	August	99 (n=61)	101 (n=8)	94 (n=7)
2012	June	90 (n=38)	93 (n=5)	NA
	August	91 (n=54)	97 (n=2)	98 (n=1)
2013	June	89 (n=24)	97 (n=3)	94 (n=2)
	August	90 (n=29)	81 (n=3)	97 (n=4)
2014	June	85 (n=20)	95 (n=5)	95 (n=4)
	August	83 (n=26)	91 (n=3)	96 (n=9)

643 Note. All fishes used in this analyses exceeded minimum total lengths (Walleye >150mm, pike >100mm, perch >100mm). Intercept
644 and slope measures for the W_s equations for each species from the following sources: Murphy et al. 1990 (Walleye), Willis 1989
645 (pike), Willis et al. 1991 (perch). Target range for W_r is 95 – 105.

Figure legends

Figure 1. Comparison of benthic contribution to whole-lake production (x-axis) to mean whole-lake benthic contribution to fish diets (y-axis). Open circles = high complexity lakes (includes forage fishes, benthivores and game fishes) and closed circles = low complexity lakes (only forage fishes). Line indicates 1:1 for benthic contribution for whole-lake production and fish reliance on benthic carbon. $f(\text{BP})$ values estimated from the Vadeboncoeur et al. (2008) productivity model and mean benthic contribution estimated from Bayesian mixing models (MixSIAR).

Figure 2. Mean benthic reliance for each fish group. Vertically compared by season (Early vs. Late) and horizontally compared by complexity (High vs. Low). Mean benthic reliance for each group estimated from Bayesian mixing models (MixSIAR). Black circles indicate outliers.

Figure 3. Species level reliance on benthic carbon for forage fishes. All species except spottail shiner (*Notropis hudsonius*) were found in both low and high complexity lakes. Vertically divided by lake complexity (High vs. Low). Mean estimates of benthic reliance obtained from Bayesian mixing models (MixSIAR). Black circles indicate outliers.

Figure 4. Species level reliance on benthic carbon for game fishes. Walleye (*Sander vitreus*) and northern pike (*Esox lucius*) exhibited significantly higher reliance on benthos than did yellow perch (*Perca flavescens*). Whitefish (*Coregonus clupeaformis*), Cisco (*Coregonus artedii*) are not discussed in the manuscript because of low sample sizes. Mean benthic reliance estimates were obtained from Bayesian mixing models (MixSIAR).

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674

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