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## ORIGINAL ARTICLE

# 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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## Abstract

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

## KEYWORDS

Canadian Prairie fishing, climate change, game fishes, Prairie lakes, Walleye

## 1 | 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-water and cold-water species, such as walleye, *Sander vitreus* (Mitchill), 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 winterkill or summerkill (Wetzel, 2001). Elevated temperatures will also increase lake-water evaporation, potentially resulting in higher solute concentrations and osmotic stress (Starks, Cooper, Leavitt, & Wissel, 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, Kalbe, Milinski, & Reusch, 2008; Whitney et al., 2016).

Game fishes in hard water 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, Cooper, Leavitt, & Pham, 2011). These lakes experience substantial seasonal and inter-annual variation in physical and chemical water parameters due to high climate variability (Pham, Leavitt, McGowan, Wissel, & Wassenaar, 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, there is a need 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 (Marcogliese, Brambilla, Gagné, & Gendron, 2005; Murphy, Willis, & Springer, 1991; Vander Zanden, Vadeboncoeur, & Chandra, 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 using a diverse set of lakes spanning more than an order-of-magnitude in most limnological, physical and chemical features (Appendix Table 1), these lakes were used 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 & Wissel, 2017), yet is a stocked taxon that 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* L., and yellow perch, *Perca flavescens* Mitchell, to evaluate whether stocked and native species respond differentially to environmental change. Although 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. It was thus possible to

test whether it is the presence of game fishes or more detrimental environmental conditions (elevated salinity, poor water quality) that impact population health of forage fishes. This study hypothesised that: (a) game fishes will exhibit variable resource-use, reflecting differences in lake productivity and physical extent of littoral areas; (b) walleye will have poorer body condition index than northern pike and yellow perch because it is not native to these lakes; (c) all three game fishes will exhibit higher parasite loads in years of elevated salinity and poor water quality; and (d) forage fishes will exhibit similar resource-use in both high-complexity and low-complexity lakes due to their increased ability to withstand stress.

## 2 | METHODS

### 2.1 | Study site

Thirteen fish-bearing lakes were sampled to evaluate temporal and spatial variation of fishes among lakes within the Prairie Ecozone of southern Saskatchewan (SK) in central Canada (Appendix Figure 1). These lakes are part of a 21-lake Long-Term Ecological Research Programme 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* (Mitchill), cisco, *Coregonus artedii* Lesueur, and common sucker, *Catostomus commersonii* (Lacépède). 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 channelised 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).

### 2.2 | Sampling and analyses

Lakes were sampled in June and August annually from 2007 to 2014 using standard methods (Cooper & Wissel, 2012a, 2012b; Starks et al., 2014). Water temperature (°C), total dissolved solids (g/L), dissolved oxygen (mg/L) and pH were all measured at 1-m intervals at the location of the deepest point in the lake using a YSI model 556 multiprobe instrument. Depth values were obtained with a Laylin SM-5 electronic depth meter, and water transparency was measured using a 20-cm-diameter Secchi disc. 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  $\mu\text{m}$ ) and stored at  $-15^{\circ}\text{C}$  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 analysed using standard spectrophotometric methods (Wellburn, 1994).

Pelagic zooplankton was sampled using small (80- $\mu\text{m}$  mesh, 30-cm diameter) and large nets (500- $\mu\text{m}$  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 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- $\mu\text{m}$  mesh size) in near-shore habitats. Both sets of isotope samples were contained in filtered lake water and stored at  $-15^{\circ}\text{C}$  prior to analyses.

Near-shore forage fishes were sampled using a beach seine net (2 m  $\times$  30 m, 10-mm mesh size) at midday following Cooper and Wissel (2012a). Fish were identified to species and stored at  $-15^{\circ}\text{C}$  prior to further analyses. Game fishes and benthivores in high-complexity lakes were sampled overnight using a gillnet (1.5 m  $\times$  30 m, 55-mm mesh) placed perpendicular to shore. Fish were stored at  $-15^{\circ}\text{C}$  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 ( $\sim 1$  g) of lateral muscle tissue was removed from each of 5–10 individuals per species and lake for stable isotope analysis (Pinnegar & Polunin, 1999). Fish muscle samples, abundant taxa from large-bodied littoral macroinvertebrates ( $\sim 1$  individual/sample) and zooplankton ( $\sim 30$ – $150$  individuals/sample) were rinsed with deionised water, dried to constant mass at  $50^{\circ}\text{C}$  and packed into tin capsules. Capsules were combusted in a Costech elemental analyser connected to a Thermo Finnigan Delta V isotope ratio mass spectrometer (IRMS). Internal laboratory standards of bovine liver and wheat flour were used as reference materials. Carbon and nitrogen isotopes were reported in the conventional  $\delta$  notation (‰) relative to the international standards Vienna Pee Dee Belemnite (for carbon) and atmospheric  $\text{N}_2$  (for nitrogen) (Peterson & Fry, 1987). Due to the potential impacts of chemical lipid extraction on carbon and nitrogen isotope values (Logan et al., 2008), C:N-based mathematical lipid corrections outlined in Braun, Phillips, and Wissel (2014) were

used to normalise  $\delta^{13}\text{C}$  values prior to analyses and to account for depleted  $^{13}\text{C}$  values with increasing lipid content (Post et al., 2007).

### 2.3 | Numerical analyses

Benthic and pelagic primary production at each site and on each sampling date was calculated using the primary production model of Vadeboncoeur, Peterson, Vander Zanden, and Kalff (2003). Similar to previous studies (Vadeboncoeur et al., 2003; Vander Zanden & Vadeboncoeur, 2002), benthic in this 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 ( $\text{BP}_{\text{max}}$ ) was set at the intermediate value (50  $\text{mg C/m}^2/\text{h}$ ) 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  $\text{BP}_{\text{max}}$  represents light-saturated benthic productivity in mesotrophic lakes, whereas the lowest value (5  $\text{mg C/m}^2/\text{h}$ ) is characteristic of periphyton attached to substrata in low-alkalinity lakes and the highest value (120  $\text{mg C/m}^2/\text{h}$ ) is typical of a wide range of oligotrophic lakes (Vadeboncoeur et al., 2008).

Carbon stable isotope ( $\delta^{13}\text{C}$ ) data were used to characterise resource-use by different fish taxa, in particular their relative reliance on benthic versus 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  $^{13}\text{C}$  due to diffusion processes within the cellular boundary layer (Hecky & Hesslein, 1995; Vander Zanden & 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 & Semmens, 2013) available in the R cran statistical package (version 3.4.1; R Development Core Team 2017). Trophic fractionation factors of  $0.0 \pm 0.5$  for carbon (Vander Zanden & Vadeboncoeur, 2002) and  $3.5 \pm 0.5$  for nitrogen were used (Vander Zanden & 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 & 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 Geweke diagnostic tests for model convergence on the posterior distributions (Stock & Semmens, 2013).

Relationships 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  $f(\text{BP})$  (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 analysed 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, Brown, and Springer (1990) and Blackwell, Brown, and Willis (2000). A body condition index was calculated for each game fish species caught from 2009 to 2014 using the following equation and reported as a whole number;

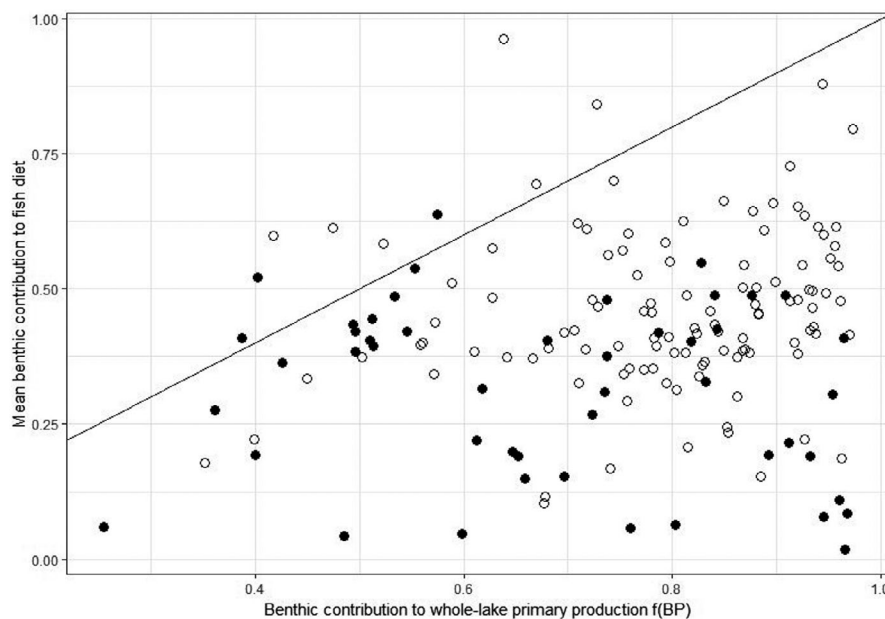
$$W_r = \left( \frac{W}{W_s} \right) \times 100,$$

where  $W_s$  values were calculated for each fish exceeding the required minimum total length (walleye  $> 150$  mm, pike  $> 100$  mm, perch  $> 100$  mm). 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 (Blackwell et al., 2000; Murphy et al., 1990). The number of individuals per sampling period (June or August) varied from 20 to 61 for walleye, 0 to 25 for pike and 0 to 48 for perch. Unusually high relative weight indices were observed for both walleye and northern pike in early 2009 when unstandardised 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 (Cestoda) 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 was 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.

### 3 | RESULTS

Benthic contribution to whole-lake primary production exceeded 50% from 2007 to 2014 in most fish-bearing lakes (Figure 1). Overall



**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)

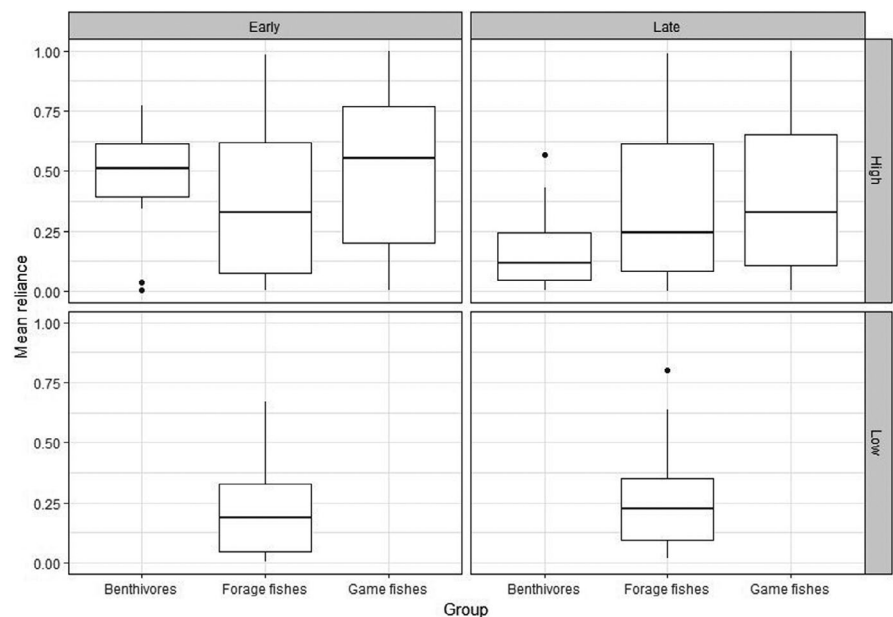
mean ( $\pm$  SD) benthic contribution to whole-lake primary production over the entire sampling period was  $0.68 \pm 0.19$  in low-complexity lakes and  $0.79 \pm 0.14$  in high-complexity lakes, with similar extremes and ranges in both community types. Despite the importance of benthic primary production, 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  $0.31 \pm 0.27$ , with higher values in high-complexity lakes ( $0.36 \pm 0.31$ ) than in sites of low complexity ( $0.23 \pm 0.18$ ) (Figure 2). Similarly, mean benthic reliance for game fishes was  $0.47 \pm 0.32$ , while bottom-feeders exhibited proportionate use of benthic carbon of  $0.31 \pm 0.25$ . 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* Rafinesque, minnows (Cyprinidae) and ninespine stickleback, *Pungitius pungitius* (L.), were all significantly more reliant on benthos than were other taxa in high-complexity lakes, while brassy minnow, *Hybognathus hankinsoni* Hubbs, was more reliant on benthos in low-complexity lakes ( $p < 0.001$ ). Spottail shiner, *Notropis hudsonius* (Clinton), was 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.

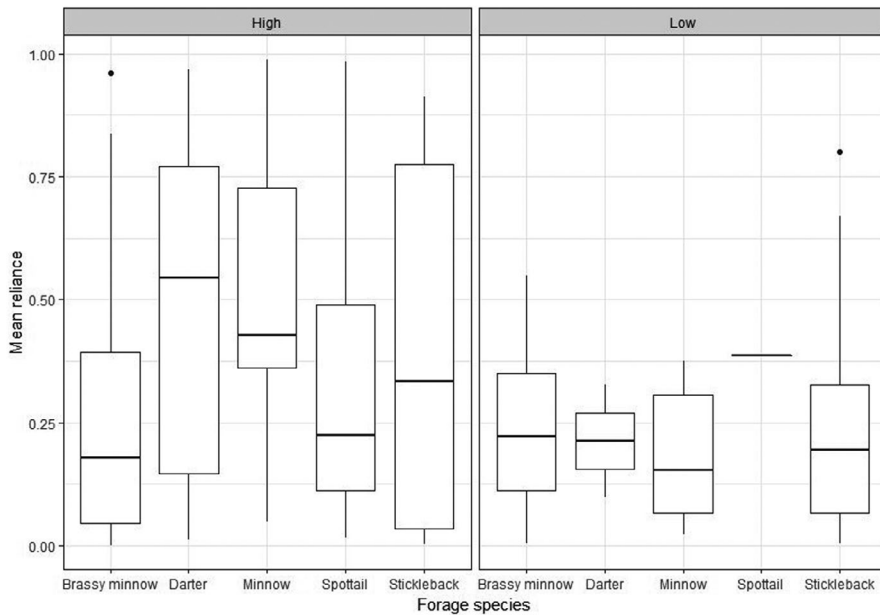
$W_r$  values for 404 walleye, 76 pike and 165 perch individuals were estimated (Table 1). Overall, there were no significant differences among lakes for any of the three species ( $p > 0.05$ ). Walleye achieved mean  $W_r$  indices within the range expected for healthy populations (95–105; Blackwell 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  $W_r$  was 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 3 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

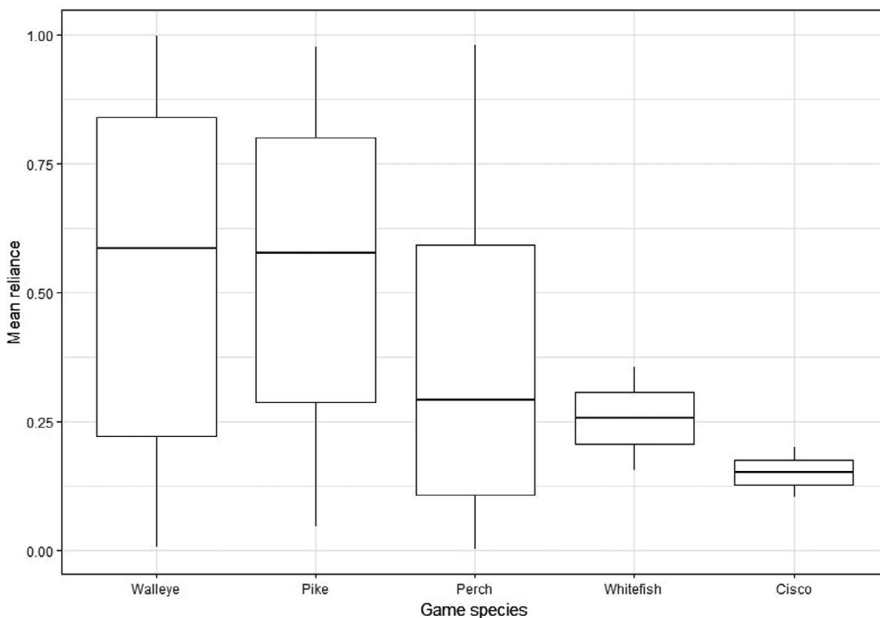


**FIGURE 2** Mean benthic reliance for each fish group. Vertically compared by season (early versus late) and horizontally compared by complexity (high versus low). Mean benthic reliance for each group estimated from Bayesian mixing models (MixSIAR). Black circles indicate outliers





**FIGURE 3** Species-level reliance on benthic carbon for forage fishes. All species except spottail shiner (*Notropis hudsonius*) were found in both low-complexity and high-complexity lakes. Vertically divided by lake complexity (high versus 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*) and 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)

( $r^2 = 0.93$ ,  $p < 0.05$ ) with lake-water salinity (g TSD/L) 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 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.

## 4 | DISCUSSION

In general, use of benthic C sources by fishes was unrelated to the modelled importance (%) of phyto-benthos to total primary production of prairie lakes, with most sites recording an under-utilisation of

benthic resources relative to their abundance (Figure 1). This finding contrasts with Vander Zanden et al. (2011), who documented 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* (L.), exhibited 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 the current 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



**TABLE 1** Body condition ( $W_t$ ) data for the three main game fishes: walleye (*Sander vitreus*); northern pike (*Esox lucius*); and yellow 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)

Note: All fishes used in this analyses exceeded minimum total lengths (walleye > 150 mm, pike > 100 mm, perch > 100 mm). Intercept and slope measures for the  $W_t$  equations for each species from the following sources: Murphy et al., 1990 (walleye); Willis, 1989 (pike); and Willis, Guy, & Murphy, 1991 (perch). Target range for  $W_t$  is 95–105.

studies, the present work focused 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 (e.g. boreal, sub-arctic, grassland).

Higher reliance on benthos during early summer may reflect competitive interactions between periphyton and phytoplankton (Vadeboncoeur et al., 2008), as benthic primary producers often predominate early in the ice-free season, particularly during the clearwater phase (Dröscher, Patoine, Finlay, & Leavitt, 2009), until phytoplankton productivity increases and limits light penetration during summer. Similar to the current findings, García-Berthou and Moreno-Amich (2000) noted a decrease in pumpkinseed, *Lepomis gibbosus* (L.), dependence on benthic prey over the course of the summer (June to August), while Hayden, Harrod and Kahilainen (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, Brock, Ebel, & Patoine, 2006; Starks et al., 2014), ranging from wastewater pollution in Humboldt Lake (Cooper & Wissel, 2012a), to dramatic lake level changes in Lenore Lake, and simplified forage fishes food-web structure in Lake Pelletier (Yellow perch alone, Cooper & 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, Bert, & Zheng, 2000; Jackson, Peres-Neto, & Olden, 2001), differences in overall lake production among low-complexity and high-complexity lakes (Persson, Diehl, Johansson, Andersson, & Hamrin, 1991), or behavioural responses of forage fishes to avoid piscivory (Turner & 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 modelled benthic and planktonic primary production as a function of food-web complexity. While speculative, it was inferred that behavioural 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, Sohel, & Mattila, 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 (Bethke, Vandehey, Fincel, Graeb, & Porath, 2012; Knight, Margraf, & Carline, 1984). Overall, reliance of walleye on amphipods in the prairie lakes was higher than that reported previously (Vander Zanden & Vadeboncoeur, 2002). For example, Quist, Guy, Bernot, and Stephen (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 showed that excessive temperatures may induce thermal stress and result in net energy loss even in the presence of abundant prey (Kitchell, Stewart, & Weininger, 1977; Quist et al., 2002). By contrast, Johnston et al. (2012) reported that adult walleye and sauger, *Sander Canadensis* (Griffith & Smith), growth rates in Lake Winnipeg were not correlated with optimal temperatures, suggesting high site-to-site variation in thermal effects. The current findings suggest that body condition 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, lake-water salinities were in excess of 2.0 g TDS/L in all the game fish-bearing lakes, approaching the upper limit threshold (<3.0 g TDS/L) for freshwater fishes identified by Cooper and Wissel (2012a), whereas salinities were consistently < 1.5 g TDS/L 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, Pech, Sures, Purucker, & Poulin, 2010). Similarly, elevated salinities are known to reduce walleye growth (Wilson & Nagler, 2006), although the critical threshold for population effects is thought to be greater (4–8 g TDS/L) than those recorded in most of the study lakes (Cooper & Wissel, 2012b).

#### 4.1 | Future sustainability of stocked and native prairie fishes

Increased temperatures in the future are expected to decrease the overall fitness of game fish populations by reducing net energy uptake (lower poor body conditions) and increasing parasite loads (Holt & 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 autumn. For example, Quist et al. (2002) reported that warmer temperatures resulted in lower  $W_r$  condition indices, growth rates and higher occurrence of empty stomachs, likely due to decreased foraging. In this study, gut analysis revealed that a high proportion of game fishes had 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 (Barber, Berkhout, & Ismail, 2016; Whitney 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 the study lakes, Macnab and Barber (2012) found that parasitic infection was 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 parasitised fishes (Britton, Pegg, & Williams, 2011).



## 5 | 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 is also considered the most desirable species by regional recreational anglers (Nanayakkara & Wissel, 2017), stocks may be additionally subject to disproportionately high angling pressure. Based on results of this and previous studies (Cooper & 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.

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