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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.**

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:**  
[Link to publication record in Queen's University Belfast Research Portal](#)

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1 Resource-use, body condition and parasite load metrics indicate contrasting health of stocked  
2 and native game fishes in Canadian prairie lakes.

3

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12

13

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.

## 30 **Introduction**

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

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

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

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

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

87

## 88 **Methods**

### 89 *Study site*

90 13 fish-bearing lakes were sampled in June and August from 2007 to 2014 to evaluate  
91 temporal and spatial variation of fishes among lakes within the Prairie Ecoregion of southern  
92 Saskatchewan (SK) in central Canada (Appendix Figure 1). These lakes are part of a 21-lake  
93 Long-Term-Ecological-Research program that has been conducted in most basins since 2002  
94 (Pham et al. 2009). Study lakes comprised five sites of low fish complexity (only forage fishes)  
95 and eight basins with high complexity (forage fishes, benthivores, and game fishes). The term  
96 ‘forage fishes’ herein collectively refers to both potential prey of game fishes in high complexity  
97 lakes and any fishes found in low complexity lakes (Essington et al. 2015). Common game fishes  
98 and bottom-feeding benthivorous species include northern pike, walleye, yellow perch, whitefish  
99 (*Coregonus clupeaformis*), cisco (*Coregonus artedi*) and common sucker (*Catostomus*

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

107

### 108 *Sampling and analyses*

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

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

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

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

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



145 were rinsed with deionized water, dried to constant mass at 50°C, and packed into tin capsules.  
146 Capsules were combusted in a Costech elemental analyzer connected to a Thermo Finnigan  
147 Delta V isotope ratio mass spectrometer (IRMS) at IECS. Internal laboratory standards of  
148 bovine liver and wheat flour were used as reference materials. Carbon and nitrogen isotopes  
149 were reported in the conventional  $\delta$  notation (‰) relative to the international standards Vienna  
150 Pee Dee Belemnite (for carbon) and atmospheric N<sub>2</sub> (for nitrogen) (Peterson and Fry 1987). Due  
151 to the potential impacts of chemical lipid extraction on carbon and nitrogen isotope values  
152 (Logan et al. 2008), we used C:N based mathematical lipid-corrections outlined in (Braun et al.  
153 2014) to normalize  $\delta^{13}\text{C}$  values prior to analyses, to account for depleted  $^{13}\text{C}$  values with  
154 increasing lipid content (Post et al. 2007).

### 155 *Numerical analyses*

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

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

169 Carbon stable isotope ( $\delta^{13}\text{C}$ ) data were used to characterize resource-use by different fish  
170 taxa, in particular their relative reliance on benthic vs. pelagic carbon sources. Use of carbon  
171 isotope data to differentiate between benthic and pelagic primary producers is based on  
172 established trophic relationships in which consumers retain the carbon isotope values of primary  
173 producers, and where periphyton (benthic primary producers) are enriched in  $^{13}\text{C}$  due to diffusion  
174 processes within the cellular boundary layer (Hecky and Hesslein 1995, Vander Zanden and  
175 Vadeboncoeur 2002). Nitrogen stable isotope data (as  $\delta^{15}\text{N}$ ) were used to reconstruct trophic  
176 levels in the study lakes. Primary consumers that were commonly identified in stomach content  
177 analyses of game fishes, amphipods (benthic) and cladocerans (pelagic) were used as end  
178 members in the mixing model instead of primary producers to avoid the high temporal variability  
179 of phytoplankton samples, sampling bias, and high lake-to-lake variability (Vander Zanden et al.  
180 2011).

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

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

195 Relations between fish resource use and lake parameters were quantified using unreplicated  
196 linear regression. Regression models (R cran package “car”, version 2.1-5: Fox and Weisberg  
197 2011) were developed for associations between lake-specific global mean output (mean of all the  
198 species-specific values) for each sampling date, and diverse measures including f(BP) (benthic  
199 contribution to whole-lake production), year, complexity (reference category: high), month  
200 (reference category: August) and lake (reference category: Wakaw). Subsequently, MixSIAR  
201 results for temporal (year, season), spatial (lake), species and group (forage, benthivores and  
202 game fishes)-specific differences on benthic reliance (dependent variable) were analyzed using  
203 analysis of variance (ANOVA) models (R cran packages “car”, version 2.1-5: Fox and Weisberg  
204 2011; “compute.es”, version 0.2-4: Del Re 2013; “ggplot2”, version 2.2.1: Wickham 2009;  
205 “pastecs”, version 1.3-18: Grosjean and Ibanez 2014). ANOVA models were tested for, and  
206 passed, Levene’s test for homogeneity of variances ( $P > 0.05$ ). Linear regressions were run  
207 separately for forage and game fishes to examine the role of environmental predictors (including  
208 maximum depth, salinity, temperature, nutrients and Secchi depth) on benthic reliance of each  
209 group.

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

212 Blackwell et al. (2000). A body condition index was calculated for each game fish species  
213 caught from 2009-2014 using the following equation and reported as a whole number;  
214  $W_r = (W/W_s) \times 100$ ,  
215 where  $W_s$  values were calculated for each fish exceeding the required minimum total length  
216 (walleye >150mm, pike >100mm, perch >100mm). Measures for  $W_s$  were derived from the  
217 regression equations of (Blackwell et al. 2000). Individual body condition index values were  
218 then averaged for each species by month, lake and year. Since  $W_r$  values for individual  
219 populations were not significantly different among sites within each sample period (ANOVA,  
220  $P > 0.05$ ), results from all lakes were combined for each month and species. Values of  $W_r = 95$ -  
221 105 indicate good condition, whereas scores near 80 indicate poor health due to adverse  
222 environmental conditions or lack of food and extremely high scores (>115) imply excess energy  
223 reserves (Murphy et al. 1990, Blackwell et al. 2000). The number of individuals per sampling  
224 period (June or August) varied from 20-61 for walleye, 0-25 for pike, and 0-48 for perch.  
225 Unusually high relative weight indices were observed for both walleye and northern pike in early  
226 2009 when unstandardized measurement protocols were used, and were not included in further  
227 analyses.

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

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

236

## 237 **Results**

238 Benthic contribution to whole-lake primary production exceeded 50% from 2007-2014 in  
239 most fish-bearing lakes (Figure 1). Overall mean ( $\pm$  SD) benthic contribution to whole-lake  
240 primary production over the entire sampling period was  $0.68 \pm 0.19$  in low-complexity lakes and  
241  $0.79 \pm 0.14$  in high-complexity lakes, with similar extremes and ranges in both community types.  
242 Despite the importance of benthic primary production, MixSIAR models suggested that most  
243 taxa were not using benthic carbon sources in proportion to their availability (below the 1:1 line  
244 in Figure 1). Mean reliance on benthic carbon for all fishes was significantly associated with  
245 month, being higher in June than August ( $P < 0.05$ ). Three lakes (Humboldt, Lenore and  
246 Pelletier) exhibited significantly lower reliance on benthic carbon than the reference category  
247 (Wakaw lake,  $P > 0.05$ ). Overall, the proportion of benthic production to whole-lake primary  
248 production (f[BP]) was not associated significantly ( $r^2 = 0.27$ ,  $P > 0.05$ ) with the use of benthic  
249 carbon by fishes.

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

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

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

273          $W_r$  values for 404 walleye, 76 pike, and 165 perch individuals (Table 1) were estimated.  
274 Overall, there were no significant differences among lakes for any of the three species ( $P>0.05$ ).  
275 Walleye achieved mean  $W_r$  indices within the range expected for healthy populations (95-105;  
276 Blackwell et al. 2000, Murphy et al. 1990) in only three of 11 sampling periods, while northern  
277 pike achieved this range in five out of 10 collection periods, and perch mean  $W_r$  were within the  
278 range in six of 10 sampling periods.  $W_r$  of walleye increased through the summer in all years but  
279 2014 (Table 1). Such seasonal increases occurred less frequently for pike and perch (only three

280 years each). Intra-annually, walleye exhibited  $W_r$  values characteristic of healthy populations in  
281 at least one of the two annual sampling periods (June or August) in 2010 and 2011, but had less  
282 than ideal body condition in both sample periods during 2012-2014, with minima recorded in  
283 both June and August 2014. Pike populations were healthy ( $W_r > 95$ ) during at least one of the  
284 two monthly sampling periods every year; during August in 2010-2012 and during June in 2013-  
285 2014. Perch also exhibited good body condition during at least one sampling period each year,  
286 including August 2010 and 2012-2013, June 2012, and both months in 2014.

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

294

## 295 **Discussion**

296 In general, use of benthic C sources by fishes was unrelated to the modeled importance  
297 (%) of phyto-benthos to total primary production of prairie lakes, with most sites recording an  
298 underutilization of benthic resources relative to their abundance (Figure 1). This finding  
299 contrasts Vander Zanden et al. (2011), who document a positive correlation between the two  
300 metrics and a high benthic reliance by fish even when  $f(\text{BP})$  was low. Similarly, Ask et al.  
301 (2009) found benthic energy use by higher trophic levels was tightly coupled with benthic  
302 primary production ( $r^2 = 0.96$ ,  $P < 0.001$ ) whereas (Karlsson and Byström 2005) found arctic char

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

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



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

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

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

349 macroinvertebrates despite potential for reduced growth without fish prey (Knight et al. 1984,  
350 Bethke et al. 2012). Overall, reliance of walleye on amphipods in our lakes was higher than that  
351 reported in past studies (Vander Zanden and Vadeboncoeur 2002). For example, Quist et al.  
352 (2002) found that even when invertebrates were abundant in walleye diets, they did not  
353 substantially contribute to the total biomass consumed relative to vertebrate prey. Taken  
354 together, these findings indicate that the relatively poor body condition of some species may  
355 reflect a decoupling of primary and secondary production in these systems, leading to lower  
356 energy transmission to top predators.

357 Bioenergetic models show that excessive temperatures may induce thermal stress and  
358 result in net energy loss even in the presence of abundant prey (Kitchell et al. 1977, Quist et al.  
359 2002). In contrast, Johnston et al. (2012) reported that adult walleye and sauger growth rates in  
360 Lake Winnipeg were not correlated with optimal temperatures, suggesting high site-to-site  
361 variation in thermal effects. Our findings suggest that body conditions of game fishes in prairie  
362 lakes may be determined by a combination of sub-lethal stressors and prey availability.

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

372 Martínez et al. 2010). Similarly, elevated salinities are known to reduce walleye growth (Wilson  
373 and Nagler 2006), although the critical threshold for population effects is thought to be greater  
374 (4-8 g TDS L<sup>-1</sup>) than those recorded in most of our study lakes (Cooper and Wissel 2012b).

375 *Future sustainability of stocked and native prairie fishes*

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

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

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

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

403

#### 404 **Conclusions**

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

417

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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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.

646 **Figure legends**

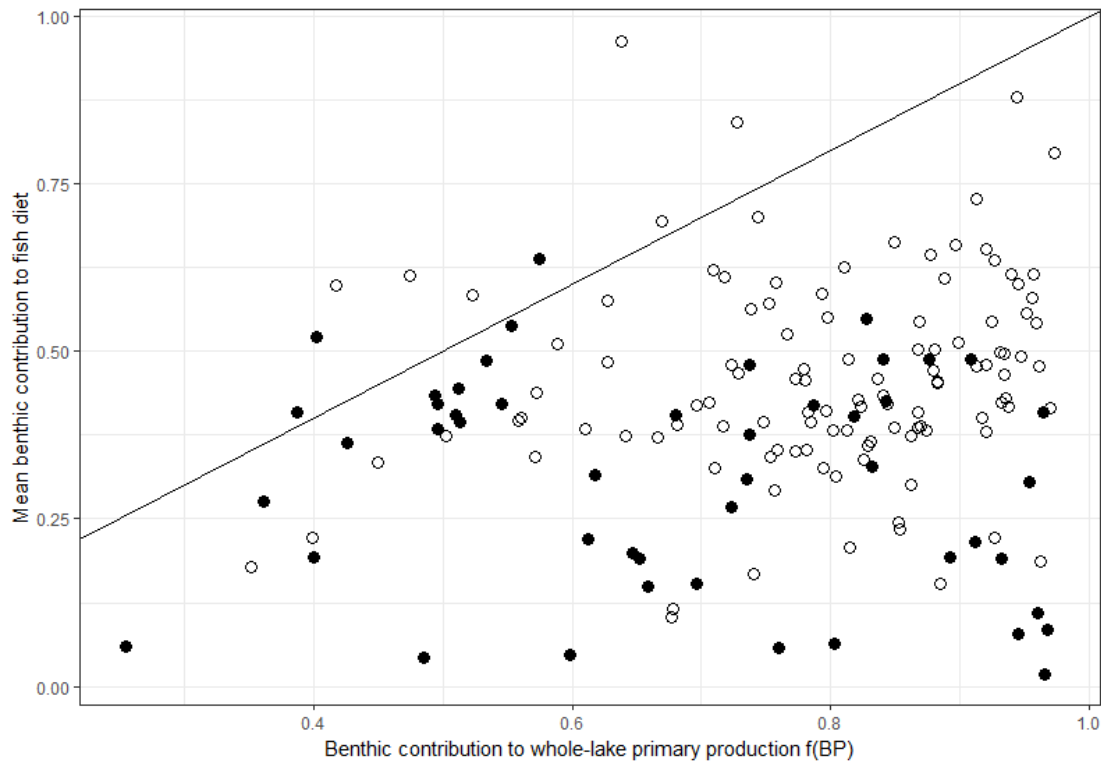
647 **Figure 1.** Comparison of benthic contribution to whole-lake production (x-axis) to mean whole-  
648 lake benthic contribution to fish diets (y-axis). Open circles = high complexity lakes  
649 (includes forage fishes, benthivores and game fishes) and closed circles = low complexity  
650 lakes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

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

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

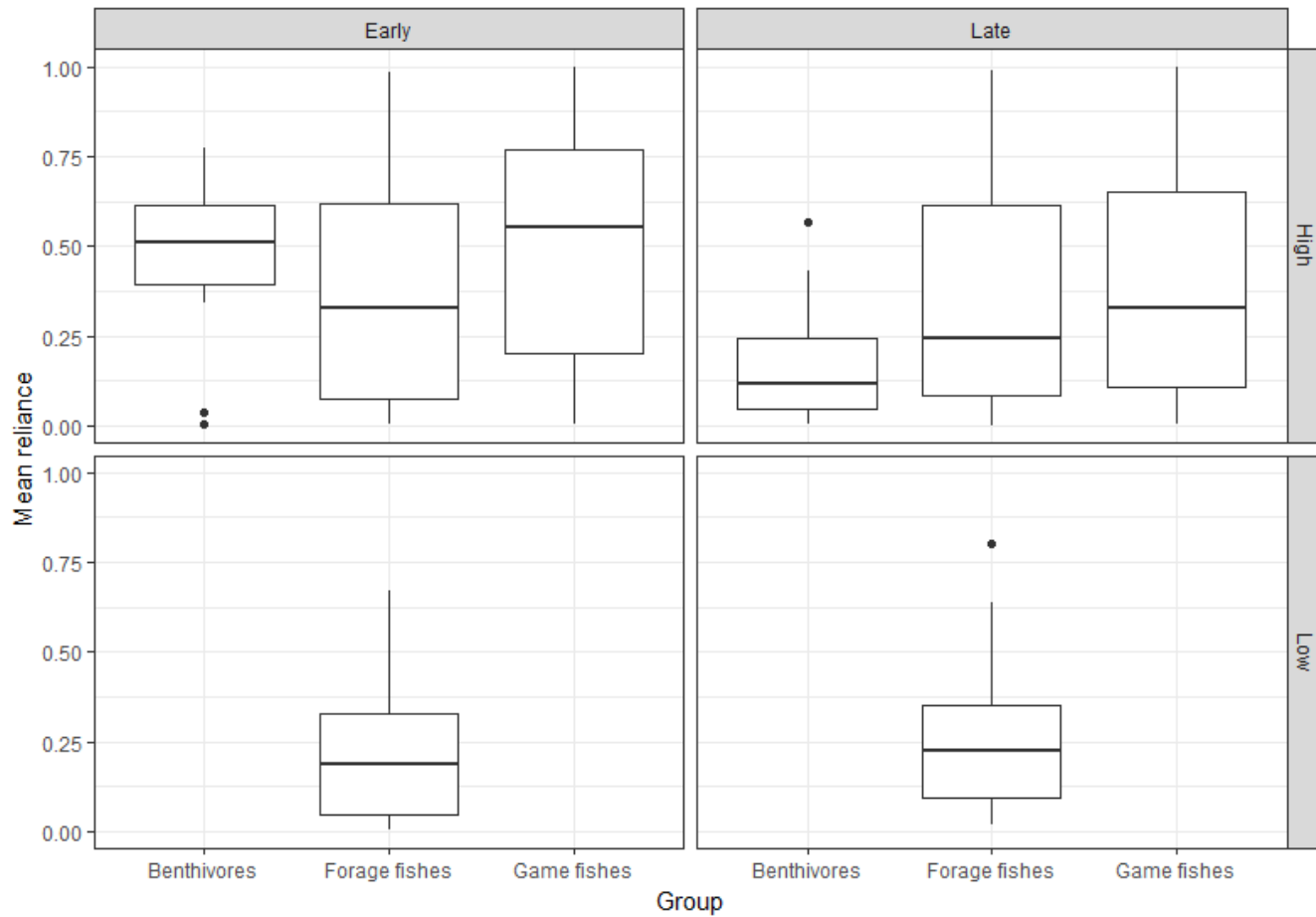
662 **Figure 4.** Species level reliance on benthic carbon for game fishes. Walleye (*Sander vitreus*) and  
663 northern pike (*Esox lucius*) exhibited significantly higher reliance on benthos than did  
664 yellow perch (*Perca flavescens*). Whitefish (*Coregonus clupeaformis*), Cisco (*Coregonus*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

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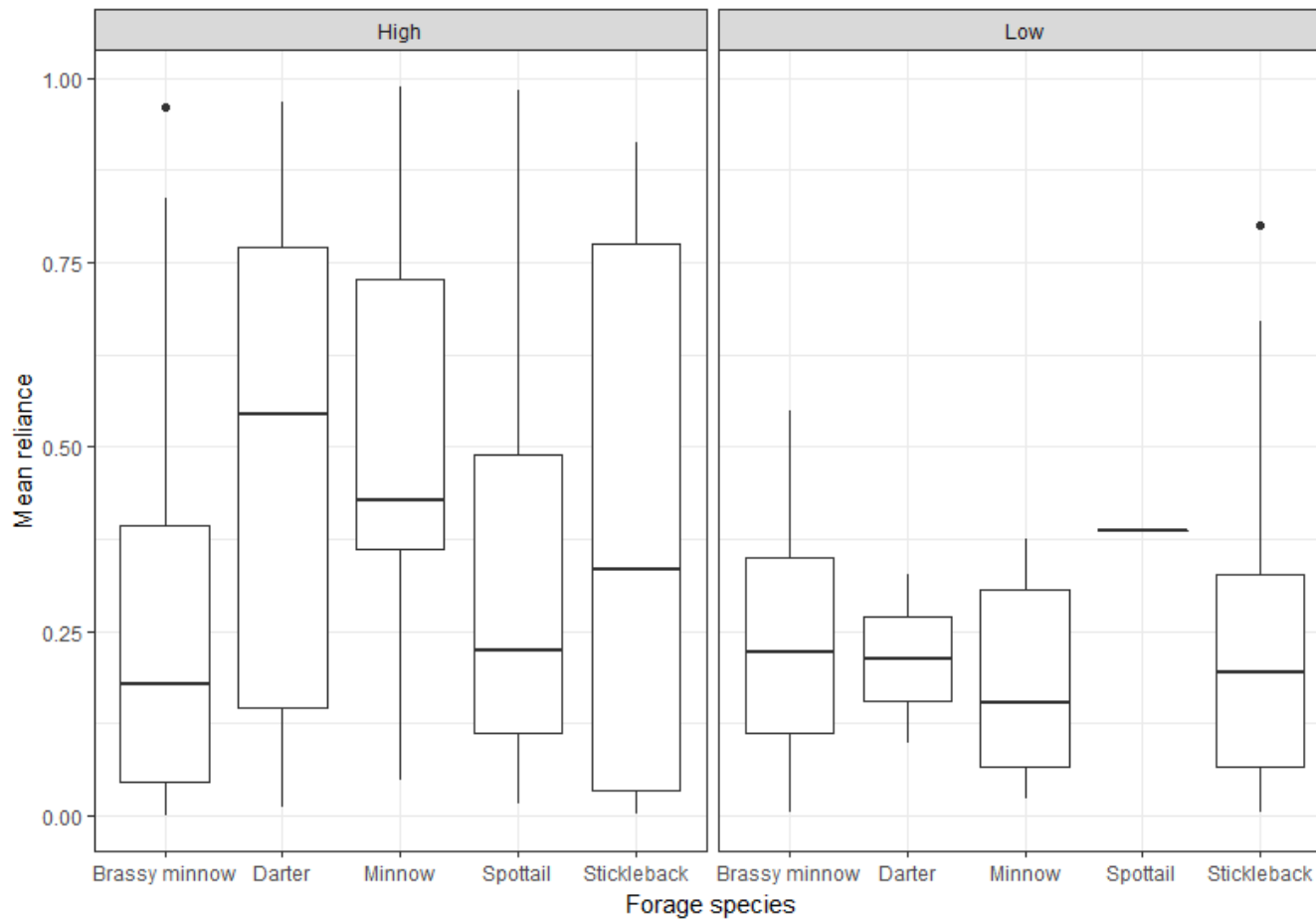
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 671 complexity lakes (only forage fishes). Line indicates 1:1 for benthic contribution for whole-lake production and fish reliance on  
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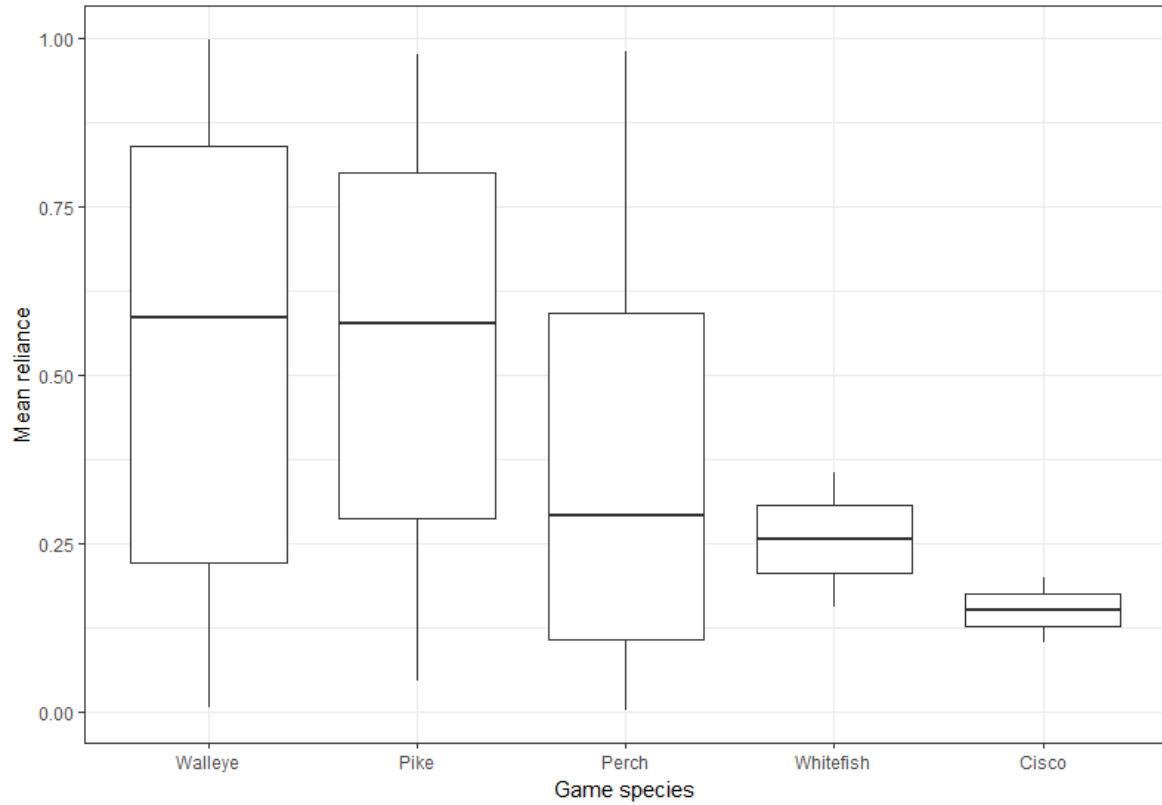
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675 **Figure 2.** Mean benthic reliance for each fish group. Vertically compared by season (Early vs. Late) and horizontally compared by  
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