

1 **Effects of ontogeny and invasive crayfish on feeding ecology and mercury concentrations of**  
2 **predatory fishes**

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## 24 **Abstract**

25 Lake food web structure dictates the flow of energy and contaminants to top predators, and  
26 addition of invasive species can shift these flows. We examined trophic position (TP),  
27 proportional reliance on the littoral zone ( $\text{Prop}_{\text{littoral}}$ ), and mercury (Hg) concentrations across the  
28 life span of two predatory fishes, walleye (*Sander vitreus*) and northern pike (*Esox lucius*), in  
29 lakes with and without invasive virile crayfish (*Faxonius virilis*). The littoral was the dominant  
30 foraging zone for both species regardless of size, accounting for 59% and 80% of the diet of  
31 walleye and pike, respectively. Both species increased in TP and Hg with body size, as did  
32 crayfish. Walleye in crayfish-present lakes had lower  $\text{Prop}_{\text{littoral}}$ , TP and Hg concentrations  
33 compared with non-present lakes, but trophic magnification of Hg through the food web was  
34 consistent across all six lakes. These findings underscore a strong role for the littoral zone in  
35 channeling energy and contaminants to higher trophic levels, and how invasive species can  
36 occupy new habitats at low abundance while altering food web structure and contaminant  
37 bioaccumulation.

38

## 39 **Introduction**

40 The structure of lake food webs has important implications for energy flow and  
41 contaminant bioaccumulation (Vander Zanden et al. 1996). Both horizontal and vertical food  
42 web structure play roles in shaping energy flow from primary producers to apex predators.  
43 Fishes act as couplers of littoral and pelagic zones in lakes by deriving energy from both  
44 pathways through their mobile foraging (Schindler and Scheuerell 2002; Vander Zanden and  
45 Vadeboncoeur 2002). Meanwhile, foraging by fishes at the top of long food chains leads to high  
46 concentrations of potentially harmful compounds such as mercury (Hg) (Cabana and Rasmussen

47 1994) because concentrations increase roughly 5 to 7 times per trophic level (Lavoie et al. 2013).  
48 Also, differential exposure to some chemicals occurs when organisms forage in different food  
49 web compartments (Kidd et al. 2001).

50         Ontogeny is a key process that dictates feeding patterns in lake fishes. Many species  
51 display predictable shifts from the pelagic zone as larvae to the littoral zone as adults (King  
52 2005; Jardine et al. 2015). This shift could affect Hg concentrations because the pelagic zone  
53 can have higher concentrations for a given trophic level (Power et al. 2002; Ethier et al. 2008).  
54 Furthermore, most predatory species exhibit increases in trophic position (TP) throughout their  
55 life span, and for some species, a switch to piscivory occurs very early in development  
56 (Mittelbach and Persson 1998; Post 2003). Progressive shifts to prey with larger sizes that  
57 occupy higher trophic levels is likely responsible for known increases in Hg concentrations with  
58 size and age in fishes (e.g. Jardine et al. 2012).

59         Invasive species have the potential to modulate food web structure, extend or shorten the  
60 length of food chains, and thereby affect contaminant concentrations of apex predators (Cabana  
61 and Rasmussen 1994; Vander Zanden and Rasmussen 1996). Non-native crayfish are expanding  
62 their range, affecting aquatic ecosystems in all continents except Antarctica (Phillips et al. 2009;  
63 Lodge et al. 2012). This includes slow post-glacial expansion by a widely distributed species,  
64 *Faxonius virilis* (Phillips et al. 2009). Different species of crayfish can have different mercury  
65 concentrations and energy densities even when they co-occur, suggesting predation on recently  
66 introduced species could alter concentrations in predators (Johnson et al. 2014). Work in the  
67 United States Midwest shows that lakes invaded by crayfish can have predatory fishes that feed  
68 more in the littoral zone and occupy lower trophic positions (Nilsson et al. 2012; Kreps et al.  
69 2016). Ontogenetic shifts in diet within species could directly influence these patterns.

70 We determined the relative role of ontogeny and the presence of crayfish in determining  
71 feeding ecology and Hg concentrations in predatory fishes in lakes of central Saskatchewan,  
72 Canada. First, we used stable C isotopes to examine if walleye (*Sander vitreus*) and northern  
73 pike (*Esox lucius*) exhibited shifts from the pelagic zone to the littoral zone as they grew. Next,  
74 we determined patterns in TP using stable N isotopes and assessed whether any shifts were  
75 accompanied by changes in Hg concentrations. Finally, we evaluated how the presence of  
76 crayfish (*F. virilis*) affected these three biological endpoints. We conducted these analyses to  
77 help better understand the implications of changing crayfish distributions, and how individual  
78 foraging behaviour dictates contaminant concentrations.

79

## 80 **Methods**

81 Sampling was conducted in 2015 in six prairie lakes (Figure 1), located in South East  
82 Saskatchewan, Canada. The lakes are located in close proximity to each other, are classified as  
83 eutrophic, and share similar substrate, a mixture of mud, sand, gravel and boulder (Water  
84 Security Agency 2016) (Table 1). All are natural lakes with the exception of Theodore Lake,  
85 which is a river valley reservoir.

86 Crayfish have been slow to recolonize these lakes following glaciation (Phillips et al.  
87 2009), in part because of limited hydrological connectivity to downstream waters. Populations  
88 in the region become established through a combination of natural recolonization and human  
89 assistance due to connections established by new water conveyance works. The six lakes have  
90 been actively surveyed in summer since 2007 with snorkel counts of individuals along 10  
91 transects (1 m wide by 10 m long) in 1 – 3 m deep littoral habitats, overturning cobble and other  
92 potential refuge (Table 2). Fishing, Margo and Stoney lakes do not have documented crayfish

93 populations. In addition to snorkeling efforts, baited Gee-minnow traps were set in Stoney Lake  
94 for 56 trap days in 2013, in Fishing Lake for 432 trap days in 2015, and Margo Lake for 416 trap  
95 days in 2015 without catching any crayfish. This, in combination with non-detects in cobble  
96 basket sets and kick and sweep surveys suggest that crayfish were absent from these lakes at the  
97 time of study. Crayfish have since accessed Stoney Lake via a narrow connecting channel from  
98 Whitesand Lake, with densities rising to 2 individuals/m<sup>2</sup> by 2018 (I. Phillips, unpublished data).

99 Crayfish are present in Whitesand, Newburn and Theodore lakes. In addition to densities  
100 ranging from 1 to 44 individuals/m<sup>2</sup> from the snorkelling surveys (Table 2), trapping in 2013  
101 yielded a catch-per-unit effort of 2.1 crayfish trap<sup>-1</sup> day<sup>-1</sup> in Whitesand for two traps set over 20  
102 days. This value is similar to that for *F. virilis* in Wisconsin and Michigan lakes (Kreps et al.  
103 2016). For our other two crayfish-present lakes, kick net sweeps in the littoral zone were used as  
104 the main sampling method for this study, and effort was expended only until sufficient numbers  
105 were collected. Therefore we do not have minnow trap CPUE data for these lakes to compare  
106 with other studies, but densities estimated from snorkeling suggest highest abundance in  
107 Newburn Lake (Table 2).

108 Samples for stable isotope and Hg analysis were collected from various sites in each lake  
109 in the summer of 2015 from mid-June to mid-August. Walleye, northern pike and yellow perch  
110 (*Perca flavescens*) were collected by angling and using three 60-meter nylon monofilament mesh  
111 gill nets with 10 m increments ranging in mesh size from 1.9 cm to 10.2 cm. Gill nets were set  
112 perpendicular to shore for ~12-24 hours overnight. All individuals had their stomach contents  
113 briefly inspected for large prey items, and a subsample of each species spanning a size range  
114 representative of the sample was used to collect dorsal muscle tissue samples for stable isotope  
115 analysis (SIA). The proportion of fish with crayfish in their stomachs in the crayfish-absent lakes

116 was 0 of 60 for Fishing Lake, 0 of 89 for Margo Lake and 0 of 53 for Stoney Lake. In the  
117 crayfish-present lakes, it was 4 of 79 for Whitesand, 0 of 44 for Newburn Lake and 13 of 74 for  
118 Theodore Lake. Measurements of fork length and weight were recorded for all fish species.  
119 Using minnow traps, seine netting and kick net sweeps, a size range of crayfish was sub-sampled  
120 for analysis. Kick net sweeps were conducted along the shore for three minutes at a water depth  
121 of approximately 1 m to 1.5 m to capture additional benthic macroinvertebrates. These samples  
122 were later sorted and analyzed in the laboratory with taxa keyed to the lowest possible  
123 designation. We used snails to represent the littoral zone isotope end-member. For two of the  
124 lakes we used data from a prior sampling event in 2013. To represent the pelagic zone,  
125 zooplankton were collected monthly with a Wisconsin Net with a hoop diameter of 20 cm, a  
126 length of 90 cm, and mesh size of 80  $\mu\text{m}$ . Vertical tows were repeated until a sufficient sample  
127 was collected for SIA. Samples were later hand sorted in the laboratory to attain a concentrated  
128 zooplankton sample from each lake. All samples were stored frozen until analysis.

### 129 *Stable Isotope Preparation and Analysis*

130 Samples were dried at 60°C for ~48 hours before being homogenized with a mortar and  
131 pestle. Whole organisms were dried for all samples except adult fish, where representative dorsal  
132 muscle was used. Snails were removed from their shells prior to drying. Once homogenized,  
133 subsamples were weighed into tin capsules ( $1.0 \pm 0.1$  mg). SIA was performed at the UC-Davis  
134 Stable Isotope Facility using a continuous flow isotope ratio mass spectrometer (CF-IRMS).  
135 Stable isotope ratios for nitrogen and carbon are reported in delta ( $\delta$ ) notation defined as parts  
136 per thousand or permil (‰) deviation from an international standard. The formula for the delta  
137 ( $\delta$ ) notation is as follows:

$$138 \quad \delta X = [(R_{\text{SAMPLE}} / R_{\text{STANDARD}}) - 1] * 1000$$

139 Where: X is the heavy isotope of the particular element being measured (either  $^{15}\text{N}$  for nitrogen  
 140 or  $^{13}\text{C}$  for carbon);  $R_{\text{SAMPLE}}$  is the ratio of the heavy isotope to the light isotope for the particular  
 141 element in the sample ( $^{15}\text{N}/^{14}\text{N}$  for nitrogen or  $^{13}\text{C}/^{12}\text{C}$  for carbon);  $R_{\text{STANDARD}}$  is the ratio of the  
 142 heavy isotope to the light isotope for an international standard (Pee Dee Belemnite limestone for  
 143  $^{13}\text{C}/^{12}\text{C}$  (Craig 1957) and atmospheric nitrogen for  $^{15}\text{N}/^{14}\text{N}$  (Mariotti 1983)). International  
 144 standards are set at delta ( $\delta$ ) values of 0‰. Samples analysed in duplicate ( $n = 20$ ) had an  
 145 average difference of 0.3‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

#### 146 *Calculations and Statistical Analysis*

147 Lipid extraction for animal tissue was not conducted prior to SIA and instead a lipid  
 148 correction factor (Logan et al. 2008) was applied following:  $\delta^{13}\text{C}_{\text{corr}} = \delta^{13}\text{C} - [(-$   
 149  $2.8317 * \text{LN}(C/N) + 2.8838]$  where:  $\delta^{13}\text{C}_{\text{corr}}$  is the lipid-corrected value,  $\delta^{13}\text{C}$  is the  $\delta^{13}\text{C}$  value for  
 150 the particular sample; -2.8317 and 2.8838 are constants; and C/N equals the elemental carbon to  
 151 nitrogen ratio for the particular sample.

152 For each fish and crayfish, the proportion of the diet derived from the littoral zone was  
 153 calculated as  $\text{Prop}_{\text{littoral}} = (\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic}})$  where  $\delta^{13}\text{C}_{\text{pelagic}}$  is the  
 154  $\delta^{13}\text{C}$  value of zooplankton, and  $\delta^{13}\text{C}_{\text{littoral}}$  is the  $\delta^{13}\text{C}$  value of snails. Trophic position was  
 155 determined by accounting for different baseline  $\delta^{15}\text{N}$  in the littoral and pelagic zones using:  $\text{TP} =$   
 156  $2 + [\delta^{15}\text{N}_{\text{consumer}} - (\delta^{15}\text{N}_{\text{littoral}} \times \text{Prop}_{\text{littoral}} + \delta^{15}\text{N}_{\text{pelagic}} \times \text{Prop}_{\text{pelagic}})] / \Delta^{15}\text{N}$  where  $\delta^{15}\text{N}_{\text{pelagic}}$  is the  
 157  $\delta^{15}\text{N}$  value of zooplankton,  $\delta^{15}\text{N}_{\text{littoral}}$  is the  $\delta^{15}\text{N}$  value of snails, and  $\Delta^{15}\text{N}$  is the trophic  
 158 enrichment factor and was estimated as 3.4‰ (Post 2002).

159 Mercury was analysed as total Hg dry weight using a Direct Mercury Analyser (DMA,  
 160 Milestone, Inc.). Samples were weighed at  $20 \pm 1$  mg and thermally decomposed in the DMA

161 before amalgamation and atomic absorption. Blanks were less than 50% of the detection limit  
162 (0.04 ng of Hg), and recoveries of two secondary certified reference materials analysed alongside  
163 samples (DORM-4 dogfish liver and IAEA-85 human hair) were  $102 \pm 6\%$  ( $n = 24$ ) and  $95 \pm 1\%$   
164 ( $n = 12$ ).

165 All statistical analyses were conducted in SPSS version 25 (Chicago, IL). To assess the  
166 effects of body size on  $\text{Prop}_{\text{littoral}}$ , TP and total Hg concentrations, we first used ordinary least-  
167 squares regressions within lakes. To test for the effects of crayfish presence on these three  
168 variables we used a general linear model ANOVA with the random factor ‘lake’ nested within  
169 the fixed factor ‘type’ (crayfish present or absent) and length as a covariate, separately for  
170 walleye and northern pike. Mercury concentrations were log-transformed to improve normality  
171 and reduce heteroscedasticity. To calculate trophic magnification, Hg concentrations of all  
172 organisms in the food web of each of the lakes were regressed against their TPs and a regression  
173 was fit according to  $\text{Log Hg} = m \cdot \text{TP} + b$ . The slopes of these regressions ( $m$ ) were then used to  
174 calculate Trophic Magnification Factors (TMFs) using  $\text{TMF} = 10^m$  (Fisk et al. 2001) where TMF  
175 represents the average increase in Hg concentration for each TL (Lavoie et al. 2013). Slopes and  
176 intercepts were compared among lakes using an Analysis of Covariance with lake as the factor,  
177 log Hg as the response variable, and TP as the covariate.

178

## 179 **Results**

180 Zooplankton and snails appropriately bracketed the  $\delta^{13}\text{C}$  values for the fishes (Figure 2).  
181 Across all lakes, mean zooplankton  $\delta^{13}\text{C}$  was  $-31.4 \pm 2.8\%$  S.D. ( $n = 77$ ) while snails had  $\delta^{13}\text{C} =$   
182  $-27.6 \pm 2.0\%$  S.D. ( $n = 131$ ). Within lakes, the average difference in  $\delta^{13}\text{C}$  between the pelagic  
183 and littoral was  $4.1 \pm 1.1\%$  S.D. The  $\delta^{15}\text{N}$  value of the two baseline organisms were variable

184 across lakes but had similar mean values overall: zooplankton  $\delta^{15}\text{N} = 8.8 \pm 1.9\text{‰}$  S.D. ( $n = 77$ ),  
185 snail  $\delta^{15}\text{N} = 8.2 \pm 1.6\text{‰}$  S.D. ( $n = 131$ ).

186 Walleye and pike showed strong dependence on the littoral zone in five of the six lakes.  
187 Only Theodore Lake had  $\text{Prop}_{\text{littoral}} < 0.5$  for both species, and  $\text{Prop}_{\text{littoral}}$  averaged 0.59 and 0.80  
188 overall in walleye and pike, respectively (Table 3, Figure 3). There was limited evidence for  
189 ontogenetic shifts from the pelagic to the littoral, with only walleye in two lakes (Fishing Lake  
190 and Margo Lake) having significant relationships between  $\text{Prop}_{\text{littoral}}$  and body size (Table 4).  
191 Crayfish, when present, had highly variable  $\delta^{13}\text{C}$  and  $\text{Prop}_{\text{littoral}}$  across lakes, ranging from  $< 0.0$   
192 to  $> 100.0$ , suggesting error in the estimation of end-member values, feeding on other sources  
193 (e.g. terrestrial inputs) or trophic enrichment outside of typical ranges. Like the two fish species,  
194 crayfish in Theodore Lake were strongly dependent on the pelagic zone. In walleye, there were  
195 significant differences in crayfish-present and crayfish-absent lakes, with crayfish-present lakes  
196 having lower  $\text{Prop}_{\text{littoral}}$  ( $F_{1,112} = 141.762$ ,  $p < 0.001$ ), driven largely by low values in Theodore  
197 Lake. For walleye, length was a significant predictor of  $\text{Prop}_{\text{littoral}}$  ( $F_{1,112} = 7.815$ ,  $p = 0.006$ ),  
198 with larger individuals having higher  $\text{Prop}_{\text{littoral}}$ , but this was not the case for pike ( $F_{1,72} = 0.312$ ,  
199  $p = 0.578$ ). Lake type also had no effect on  $\text{Prop}_{\text{littoral}}$  for pike ( $F_{1,72} = 0.075$ ,  $p = 0.784$ ).

200 Both fish species occupied elevated TPs indicative of tertiary consumers, with walleye  
201 ( $3.94 \pm 0.35$ ) having slightly higher mean values than pike ( $3.77 \pm 0.40$ ) and both species  
202 approximately 0.5 to 1.0 TPs above yellow perch that had mean  $\text{TP} = 3.21 \pm 0.23$ . Walleye  
203 increased almost two TPs over the size range that we captured, but the pattern for pike was less  
204 clear (Table 4, Figure 4). Overall TPs for walleye, after accounting for the significant effect of  
205 body size as a co-variate ( $F_{1,111} = 101.357$ ,  $p < 0.001$ ), were slightly lower in crayfish-present  
206 lakes (marginal mean  $\text{TP} = 3.88 \pm 0.03$  SE) compared with crayfish-absent lakes ( $\text{TP} = 4.00 \pm$

207 0.02 SE) ( $F_{1,111} = 10.916$ ,  $p < 0.001$ ), while differences for pike were not significant ( $F_{1,72} =$   
208 0.157,  $p = 0.693$ ). Crayfish were uncommon in the stomachs of both species, appearing in only  
209 two of the 105 walleye and only one of the 46 northern pike examined in crayfish-present lakes,  
210 respectively. Instead, crayfish appeared more often in the diets of yellow perch, with 15 of 45  
211 individuals having crayfish in their stomachs.

212 Mercury concentrations were high in both species, exceeding the Health Canada  
213 guideline of 0.5  $\mu\text{g/g}$  wet weight in 41% (140 of 343) of cases (Figure 5). Mean concentrations  
214 for walleye were above the guideline in four of the six lakes, but none of the lakes had pike with  
215 mean concentrations above the guideline (Table 3). Mercury concentrations increased  
216 consistently with body size for both species (Table 5), and also for crayfish (Figure 6). For the  
217 latter species, this was likely due to increased TP in larger individuals (Figure 6). Both length  
218 ( $F_{1,242} = 234.481$ ,  $p < 0.001$ ) and lake type ( $F_{1,242} = 31.238$ ,  $p < 0.001$ ) had significant effects on  
219 Hg concentrations in walleye, with lower values in the crayfish-present lakes (marginal mean =  
220 2.1  $\mu\text{g/g}$  dry weight) compared with crayfish-absent lakes (1.6  $\mu\text{g/g}$  dry weight). While length  
221 also significantly affected Hg concentrations in pike ( $F_{1,80} = 99.454$ ,  $p < 0.001$ ), there was no  
222 crayfish effect ( $F_{1,80} = 0.772$ ,  $p = 0.382$ ).

223 Trophic magnification of Hg through the food web was strong and consistent across all  
224 lakes (Figure 7). Trophic magnification factors ranged from 3.7 in Stoney Lake to 5.0 in Margo  
225 Lake (Table 6). The interaction term (lake x TP) in the model was not significant ( $F = 1.805$ ,  $p =$   
226 0.111), suggesting parallel slopes and equivalent TMFs across lakes regardless of the presence of  
227 crayfish. After removing the interaction term, TP was significant ( $F = 1652.86$ ,  $p < 0.001$ ) and  
228 there was also a significant lake effect ( $F = 5.977$ ,  $p < 0.001$ ). Post-hoc comparisons indicated

229 that Fishing Lake had a significantly higher marginal mean than the other five lakes, which did  
230 not differ from each other.

231

## 232 **Discussion**

233 Crayfish were associated with unexpected effects on the habitat foraging of top predators  
234 in our study lakes. Past work revealed a greater contribution of the littoral zone (benthos) to the  
235 diet of piscivorous fishes when invasive crayfish were in great abundance (Nilsson et al. 2012;  
236 Kreps et al. 2016). In our case, crayfish presence was associated with more pelagic foraging  
237 rather than littoral foraging, contrary to this earlier work. Much of this was owing to Theodore  
238 Lake, where walleye and pike both fed more in the pelagic zone and at lower trophic levels  
239 compared with other lakes, akin to lake trout shifts following bass invasion (Vander Zanden et  
240 al. 1999). Crayfish in Theodore Lake also had the lowest trophic level and lowest littoral  
241 contribution, suggesting that the food web in this lake is based more on the pelagic zone. This  
242 lake is a long, narrow river valley reservoir formed by the construction of Theodore Dam.  
243 Brinkmann and Rasmussen (2010) showed that pike aligned more closely with zooplankton in a  
244 narrow Prairie reservoir, and in reservoirs such as this with large shoreline water level  
245 fluctuations, benthic production can be compromised leading to greater use of the pelagic zone  
246 by fishes (Black et al. 2003). This indicates that lake shape and hydrological regime may be  
247 more important than community membership in driving fish foraging patterns (Dolson et al.  
248 2009), and warrants further investigation.

249 Crayfish forage extensively on benthic macroinvertebrates and they can appear in the diet  
250 of fishes, suggesting they could add a trophic level to the food chain (Phillips et al. 2009; Nilsson  
251 et al. 2012). Yet Kreps et al. (2016) reported a lower TP for walleye when invasive rusty

252 crayfish were present in large numbers, consistent with our findings for *F. virilis*. In our case,  
253 the two top predators did not feed on crayfish, instead consuming mostly small fish, *Gammarus*  
254 sp., or having empty stomachs. Only yellow perch preyed heavily on small crayfish, particularly  
255 in Theodore Lake, but this did not lengthen the food chain in crayfish-present lakes since yellow  
256 perch were also generally not consumed by walleye and pike. Larger crayfish escape predation  
257 (Dorn and Mittelbach 1999; Hein et al. 2006) and therefore can act as a trophic “dead-end” in the  
258 food web (Cremona et al. 2008) rather than contributing to biomass production at higher trophic  
259 levels and lengthening food chains.

260 Crayfish occupied TPs that were approximately one level above herbivores, and TP  
261 increased with body size in all three lakes where they were present. This is consistent with  
262 earlier studies that concluded crayfish were predators (Whitledge and Rabeni 1997; Roth et al.  
263 2006), and could also indicate that predation on small fish occurs in largest individuals that had  
264  $TP > 3.0$ . It is unknown if crayfish in these systems deplete benthic macroinvertebrate  
265 populations upon invasion, as has been demonstrated elsewhere (Nilsson et al. 2012), but their  
266 relatively low abundance suggests this is unlikely. Crayfish Hg concentrations (mean = 0.32  $\mu\text{g/g}$   
267 dry weight for all lakes) were within the reported range of 0.1 to 1.4  $\mu\text{g/g}$  dry weight (Mueller  
268 and Serdar 2002; Kouba et al. 2010) and significant, positive relationships between size/age and  
269 Hg concentrations, as we observed here, are common in crayfish populations (Allard and Stokes  
270 1989).

271 We found little evidence for ontogenetic habitat shifts in our two study fish species. The  
272 littoral zone accounted for ~60% of the diet of both species across all body sizes, consistent with  
273 earlier estimates for lake fish populations (Vander Zanden and Vadeboncoeur 2002) and further  
274 pointing to the littoral zone as deserving of equal attention as the pelagic zone in governing lake-

275 wide productivity. The littoral contribution to diet was higher than expected for both species.  
276 Vander Zanden and Vadeboncoeur (2002) previously reported a limited contribution of  
277 zoobenthos to the diets of these species based on gut contents (14%), where isotope studies were  
278 limited. However, as piscivores, walleye and pike were believed to consume benthic prey  
279 indirectly by eating fishes from the littoral zone, accounting for ~45% of their diet (Vander  
280 Zanden and Vadeboncoeur 2002). Our data suggest that this is the case. Elsewhere, both species  
281 were strongly aligned isotopically with benthic prey in boreal shield lakes (Bertolo et al. 2005)  
282 and % littoral was as high as 96% and never lower than 68% for walleye in four Michigan lakes  
283 (Herbst et al. 2016). These findings highlight the importance of the littoral zone as a source of  
284 energy and contaminants to higher trophic levels, and how contamination of the nearshore  
285 environment from industrial activity can lead to high concentrations of toxic chemicals in the  
286 tissues of top predators (Eagles-Smith et al. 2008).

287 Both species had lower mean TPs compared to literature summaries (Vander Zanden et  
288 al. 1997; Paradis et al. 2008; Depew et al. 2013a), which is supported by gut content  
289 observations for these lakes and dietary flexibility to include non-fish prey (Beaudoin et al. 1999;  
290 Venturelli and Tonn 2005; Paradis et al. 2008). Yet despite these relatively low TPs, Hg  
291 concentrations were often above guidelines and greater than median concentrations for the two  
292 species summarized elsewhere (Depew et al. 2013a). This could be related to slow growth in  
293 these species near the northern edge of their distribution (Lavigne et al. 2010). Both walleye and  
294 northern pike increased their TP as they grew, leading to higher Hg concentrations in larger,  
295 older fish. The strength of these relationships varied across lakes, suggesting a decoupling of  
296 body size, TP and Hg concentrations at the individual level in some lakes. Increases in TP with  
297 body size were consistent with expectations that increasing gape size allows consumption of

308 larger, higher trophic level prey as fishes attain larger body sizes (Mittelbach and Persson 1998).  
309 Others have argued that  $^{15}\text{N}$  could accumulate with age in long-lived fishes independent of  
310 dietary switches to higher trophic levels (Overman and Parrish 2001), but stomach data showed  
311 that the largest walleye in our sample set tended to have fish in their stomachs, further supporting  
312 their position as apex predators in these lakes.

313         There are three possible processes that lead to differential Hg concentrations in top  
314 predators, including stronger trophic magnification through the food web, longer food chains and  
315 higher baseline Hg concentrations (Kidd et al. 2012). Trophic magnification factors differed  
316 little among lakes, and were very near the global average of 4.7 for total Hg (Lavoie et al. 2013).  
317 Given the similarities in species composition and their geographic proximity to one another, it is  
318 not surprising that TMFs fell in such a narrow range. Food chain length was also similar at all  
319 lakes, with large walleye occupying the highest TP, though Theodore Lake walleye and pike had  
320 lowest mean TPs and consequently the lowest total Hg concentrations. A higher baseline  
concentration may be responsible for the higher marginal mean observed in Fishing Lake, where  
significant flooding had occurred in the two years prior to sampling (Water Security Agency  
2016). This lake also had the highest concentrations in zooplankton and snails at the base of the  
food web. The many individual walleye and pike above the Hg consumption guideline highlight  
how prairie lakes are not immune to Hg contamination despite many suggesting that Western  
North America has lower atmospheric Hg deposition (Prestbo and Gay 2009) and hence lower  
risk to fish-eating consumers (Depew et al. 2013b). Concentrations in the two species were  
higher in all six of our study lakes compared with historical provincial records for these lakes  
(Depew et al. 2013a). This could owe, in part to recent high water levels in the region (Water  
Security Agency 2016) as flooding of soils and associated organic matter is known to elevate

321 baseline Hg concentrations in shallow flooded areas (Hall et al. 2009; Watras et al. in press).  
322 While we have shown that crayfish invasion appears to have modest effects on food web  
323 structure and Hg bioaccumulation, the productive littoral zones of these lakes are clearly  
324 transferring Hg to higher trophic levels.

325 Our work shows effects of *F. virilis* on food web properties, but other species may have  
326 stronger effects. For example, rusty crayfish (*F. rusticus*) likely modify habitats (Wilson et al.  
327 2004; Phillips et al. 2009) more strongly than *F. virilis* in part because they achieve higher  
328 relative abundance (Kreps et al. 2016). Because there are little differences among species in  
329 their overall effects (Twardochleb et al. 2013), abundance becomes a key element of an invasive  
330 species' potential to modify ecosystems (Hansen et al. 2013). In our lakes, CPUE of crayfish  
331 was well below that measured for *F. rusticus* in Wisconsin lakes (Nilsson et al. 2012; Kreps et al.  
332 2016), where catch rates were typically 20-40 individuals per trap per day and as high as 70  
333 individuals per trap per day. As such, provided that invasive crayfish remain at low relative  
334 abundance, their food web effects are likely to be modest. We recommend additional paired  
335 studies that include measurements of contaminants such as mercury, with more crayfish species  
336 such as *F. rusticus* that achieve higher abundances (Wilson et al. 2004; Olden et al. 2006). Such  
337 studies will reveal whether we should anticipate additional changes to food webs and  
338 contaminant risks as animal distributions continue to change across the landscape.

339

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347

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507 **Table 1.** Characteristics of the six lakes studied

Lake	Lat	Long	Crayfish	Area (ha)	Mean Depth (m) (max)	TP (mg/L)	TN (mg/L)
Fishing Lake	51.833	-103.533	Absent	3967	25 (NA)	0.060	1.3
Margo Lake	51.816	-103.363	Absent	250	NA (5)	0.090	1.5
Stoney Lake	51.788	-103.364	Absent	286	5 (8)	0.070	1.7
Whitesand Lake	51.764	-103.345	Present	495	3 (11)	0.050	1.6
Newburn Lake	51.693	-103.177	Present	156	NA (6)	0.050	1.6
Theodore Lake	51.453	-102.845	Present	304	NA (NA)	NA	NA

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527 **Table 2.** Estimated crayfish densities (individuals/m<sup>2</sup>) from snorkel surveys (10 transects per lake) in the six lakes. Empty cells  
528 indicate that the lake was not surveyed in that year.

Lake	Year								
	2007	2008	2009	2010	2011	2012	2013	2014	2015
Fishing Lake	0	0	0		0	0	0		0
Margo Lake	0	0	0		0	0	0	0	0
Stoney Lake	0	0	0		0	0	0	0	0
Whitesand Lake		3.3 ± 2.5	4.3 ± 2.1		2.2 ± 2.0	3.2 ± 2.0	2.2 ± 1.8	2.2 ± 1.7	2.0 ± 2.2
Newburn Lake			26.0 ± 32.7		43.5 ± 25.8	21.6 ± 22.6	20.2 ± 17.7		25.4 ± 21.5
Theodore Lake			16.4 ± 19.0						

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533 **Table 3.** Mean ( $\pm$  S.D.) body size, trophic position, proportion littoral dependence ( $\text{Prop}_{\text{littoral}}$ )  
 534 and total mercury concentrations of walleye and northern pike in six lakes in the Northern Great  
 535 Plains. Assuming 75% moisture, the mercury guideline for human consumption is 2.0 ug/g dry  
 536 weight.

#### Walleye

Lake	Fork length (cm)	TP	$\text{Prop}_{\text{littoral}}$	[Hg] (ug/g dry wgt)
Fishing Lake	43.0 $\pm$ 3.6	4.07 $\pm$ 0.15	0.78 $\pm$ 0.09	2.83 $\pm$ 1.05
Margo Lake	41.0 $\pm$ 5.0	3.81 $\pm$ 0.29	0.72 $\pm$ 0.14	1.92 $\pm$ 0.90
Stoney Lake	40.7 $\pm$ 8.0	4.07 $\pm$ 0.37	0.53 $\pm$ 0.10	2.04 $\pm$ 0.58
Whitesand Lake	44.7 $\pm$ 4.7	4.09 $\pm$ 0.20	0.72 $\pm$ 0.06	2.08 $\pm$ 0.68
Newburn Lake	46.3 $\pm$ 9.5	3.82 $\pm$ 0.24	0.58 $\pm$ 0.12	2.24 $\pm$ 0.89
Theodore Lake	42.6 $\pm$ 11.6	3.73 $\pm$ 0.36	0.04 $\pm$ 0.08	1.80 $\pm$ 1.19

#### Pike

Lake	Fork length (cm)	TP	$\text{Prop}_{\text{littoral}}$	[Hg] (ug/g dry wgt)
Fishing Lake	51.2 $\pm$ 14.3	3.50 $\pm$ 0.26	0.75 $\pm$ 0.08	1.56 $\pm$ 0.98
Margo Lake	57.1 $\pm$ 5.6	3.58 $\pm$ 0.24	0.69 $\pm$ 0.12	1.38 $\pm$ 0.44
Stoney Lake	52.7 $\pm$ 3.4	4.12 $\pm$ 0.27	0.80 $\pm$ 0.17	1.99 $\pm$ 0.62
Whitesand Lake	51.6 $\pm$ 8.7	3.84 $\pm$ 0.41	0.79 $\pm$ 0.10	1.69 $\pm$ 0.66
Newburn Lake	52.6 $\pm$ 6.3	4.02 $\pm$ 0.31	0.95 $\pm$ 0.21	1.97 $\pm$ 0.54
Theodore Lake	39.9 $\pm$ 10.0	3.18 $\pm$ 0.34	0.45 $\pm$ 0.16	0.84 $\pm$ 0.30

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547 **Table 4.** Relationship between trophic position and fork length for walleye and pike in the six  
 548 study lakes, with regression equations for significant regressions.

Walleye				
Lake	Equation	r <sup>2</sup>	p	n
Fishing Lake	Trophic position = 0.030*fork length+2.72	0.44	0.001	20
Margo Lake	Trophic position = 0.025*fork length+2.78	0.34	0.001	27
Stoney Lake	Trophic position = 0.031*fork length+2.90	0.75	<0.001	19
Whitesand Lake	Trophic position = 0.024*fork length+3.03	0.38	0.001	26
Newburn Lake	Trophic position = 0.015*fork length+3.16	0.46	0.045	9
Theodore Lake	Trophic position = 0.032*fork length+2.52	0.64	<0.001	18

Pike				
Lake	Equation	r <sup>2</sup>	p	n
Fishing Lake	Trophic position = 0.011*fork length+2.95	0.48	0.002	17
Margo Lake		0.02	0.723	10
Stoney Lake	Trophic position = -0.066*fork length+7.59	0.60	0.041	7
Whitesand Lake	Trophic position = 0.037*fork length+1.92	0.62	<0.001	21
Newburn Lake		0.12	0.186	20
Theodore Lake		0.22	0.532	4

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562 **Table 5.** Relationship between log total Hg concentration and fork length for walleye and pike in  
 563 the six study lakes, with regression equations for significant regressions

Walleye				
Lake	Equation	r <sup>2</sup>	p	n
Fishing Lake	Log Hg = 0.036*fork length-1.129	0.64	<0.001	31
Margo Lake	Log Hg = 0.036*fork length-1.244	0.53	<0.001	77
Stoney Lake	Log Hg = 0.011*fork length-0.142	0.52	<0.001	45
Whitesand Lake	Log Hg = 0.016*fork length-0.421	0.35	<0.001	51
Newburn Lake	Log Hg = 0.017*fork length-0.465	0.97	<0.001	9
Theodore Lake	Log Hg = 0.019*fork length-0.648	0.85	<0.001	35
Pike				
Lake	Equation	r <sup>2</sup>	p	n
Fishing Lake	Log Hg = 0.014*fork length-0.567	0.68	<0.001	25
Margo Lake		0.32	0.086	10
Stoney Lake	Log Hg = 0.043*fork length-1.994	0.60	0.041	7
Whitesand Lake	Log Hg = 0.019*fork length-0.768	0.62	<0.001	21
Newburn Lake	Log Hg = 0.009*fork length-0.172	0.22	0.036	20
Theodore Lake		0.75	0.135	4

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577 **Table 6** Best-fit equations for Log total Hg versus Trophic Position (TP) for six Northern Great  
 578 Plains lakes.

Lake	Equation	r <sup>2</sup>	p	n
Fishing Lake	Log Hg = 0.700*TP-2.347	0.94	<0.001	57
Margo Lake	Log Hg = 0.703*TP-2.531	0.82	<0.001	56
Stoney Lake	Log Hg = 0.567*TP-2.052	0.85	<0.001	36
Whitesand Lake	Log Hg = 0.659*TP-2.405	0.85	<0.001	65
Newburn Lake	Log Hg = 0.662*TP-2.429	0.82	<0.001	71
Theodore Lake	Log Hg = 0.696*TP-2.546	0.78	<0.001	53

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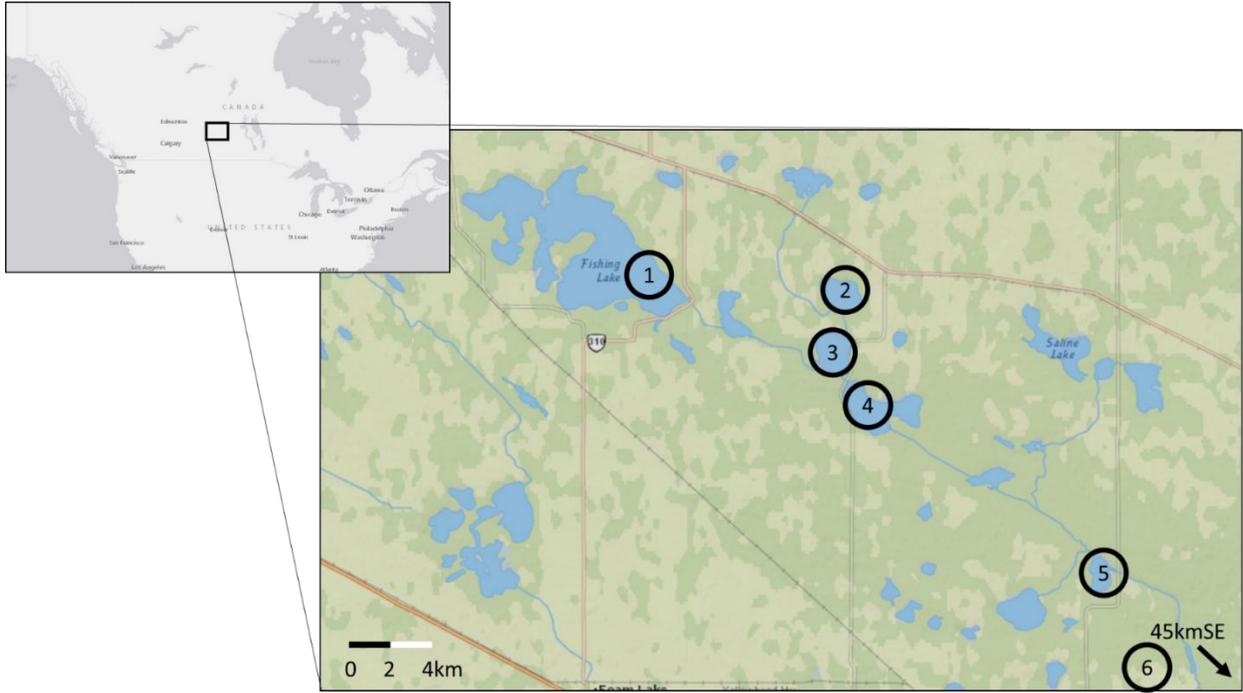
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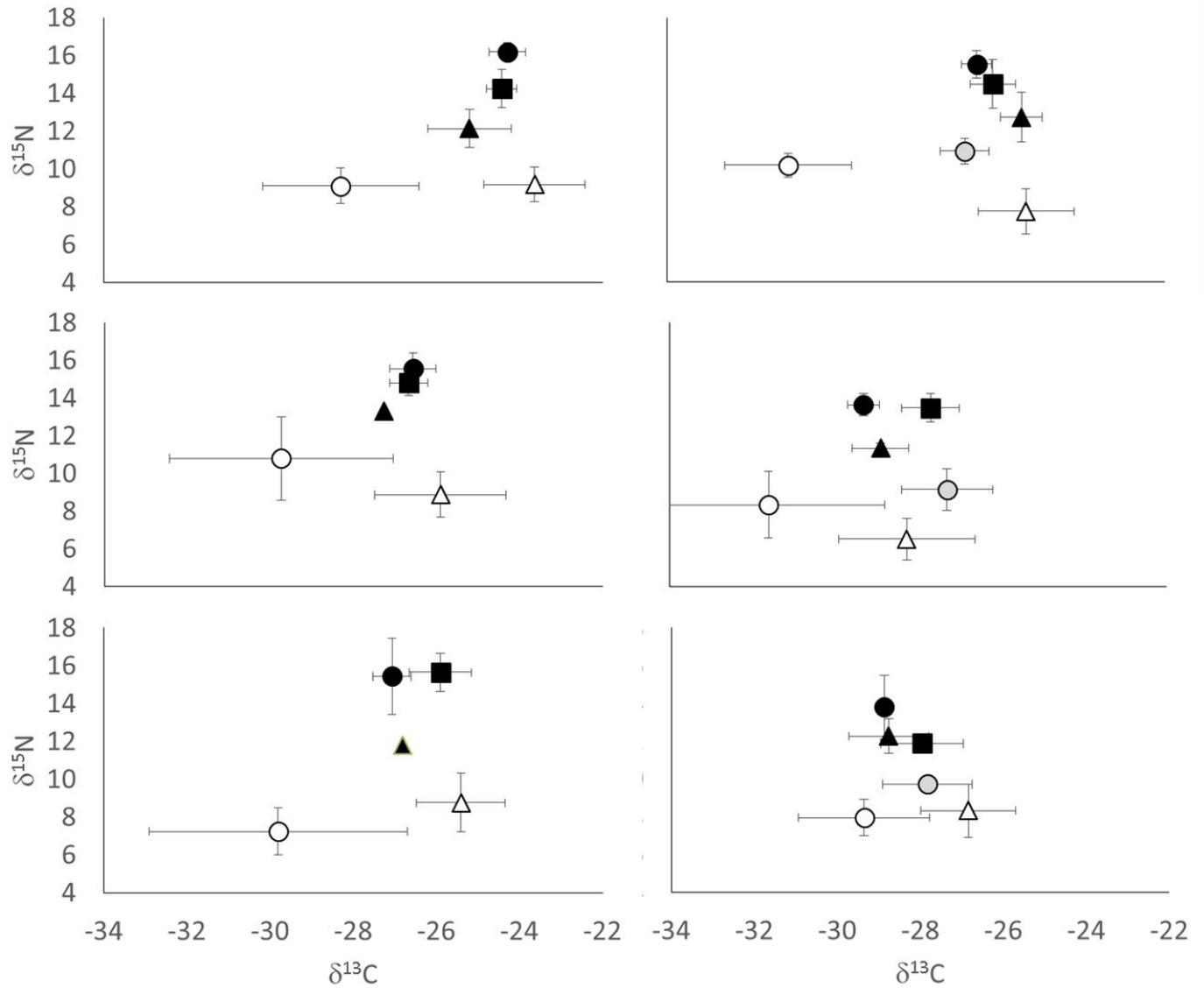
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598 **Figure 1.** Location of lakes with crayfish (1 – Fishing Lake, 2 – Margo Lake, 3 – Stoney Lake)  
599 and without crayfish (4 – Whitesand Lake, 5 – Newburn Lake, 6 – Theodore Lake, not shown) in  
600 the Northern Great Plains.



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613 **Figure 2.** Scatterplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for the food webs of the six lakes. Solid symbols  
 614 are fish (circles = walleye, squares = pike, triangles = yellow perch), open symbols are baseline  
 615 organisms (circles = zooplankton, triangles = snails) and shaded circles are crayfish.



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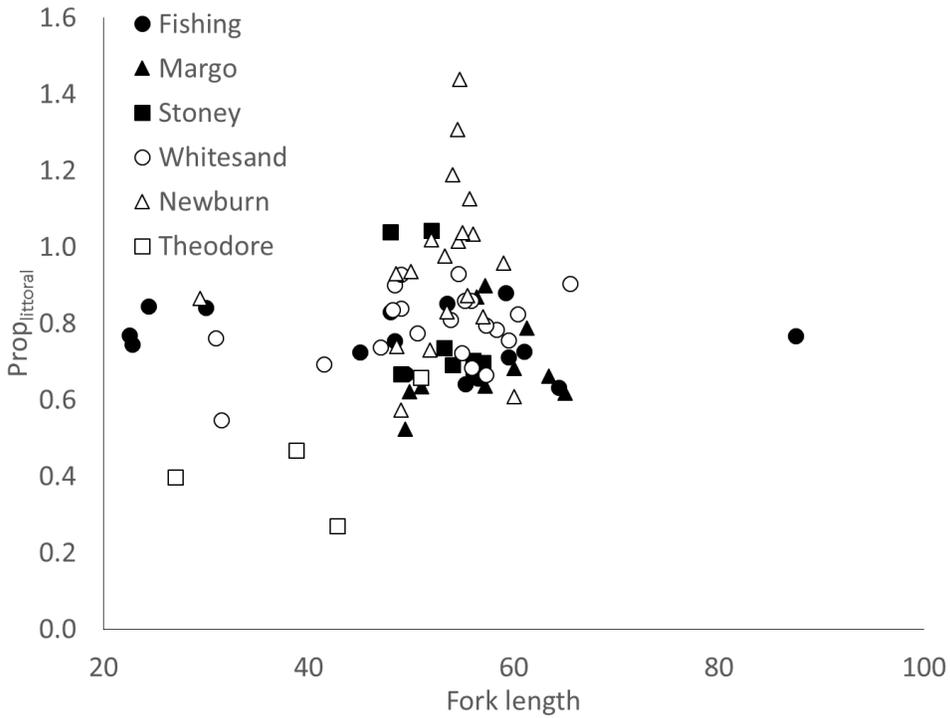
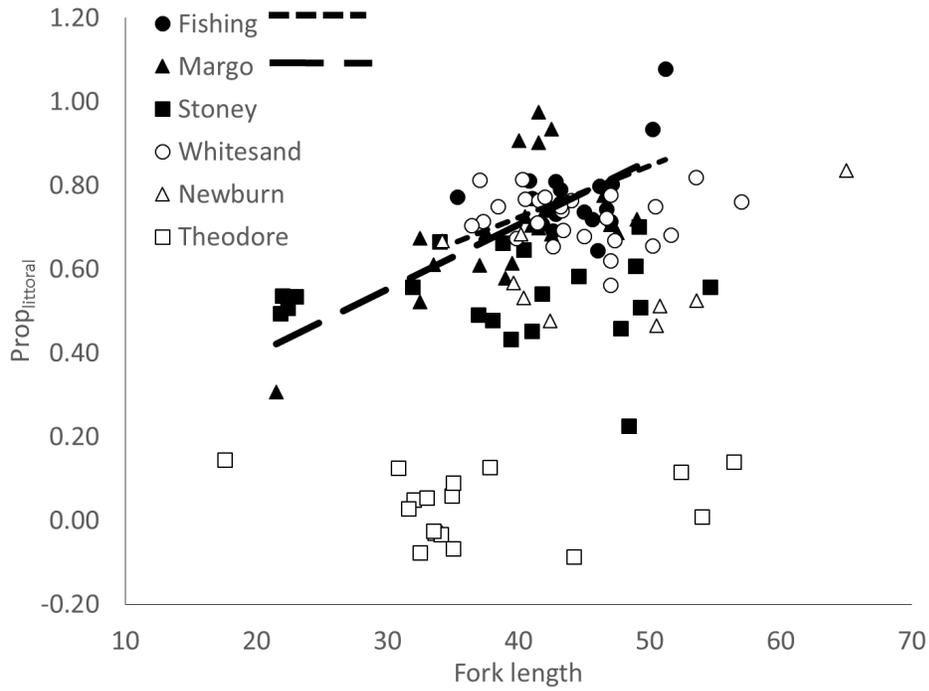
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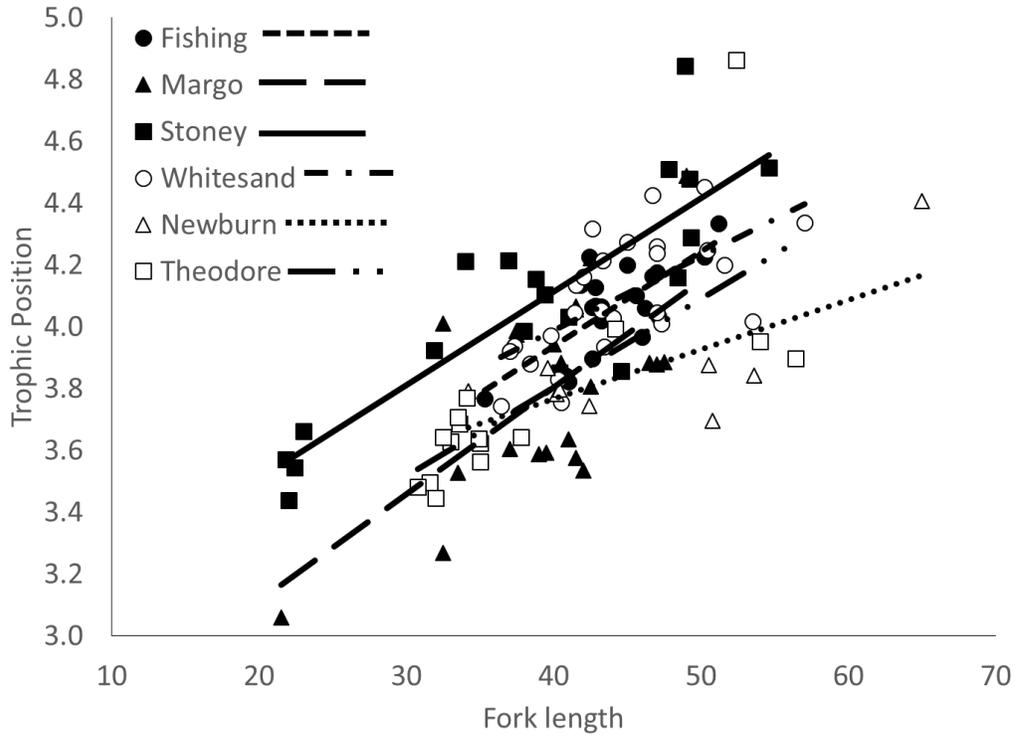
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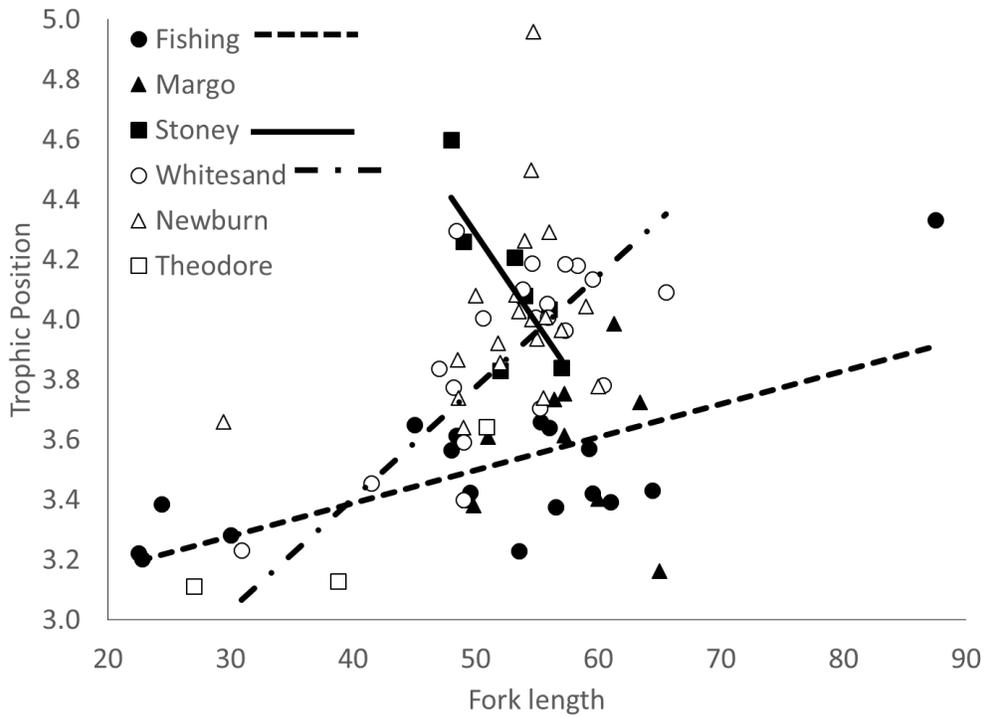
621 **Figure 3.** Proportional littoral dependence ( $Prop_{littoral}$ ) vs. body size for walleye (A) and northern  
 622 pike (B) in northern Great Plains lakes with (open symbols) and without (solid symbols)  
 623 crayfish.



626 **Figure 4.** Trophic position vs. body size for walleye (A) and northern pike (B) in northern Great  
 627 Plains lakes with (open symbols) and without (solid symbols) crayfish.

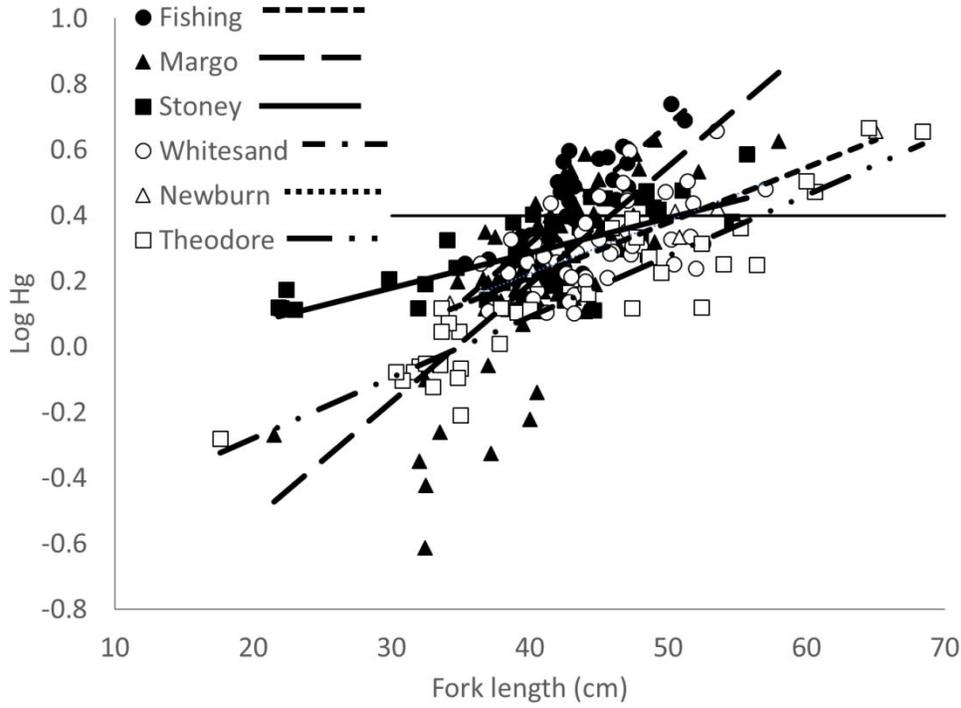


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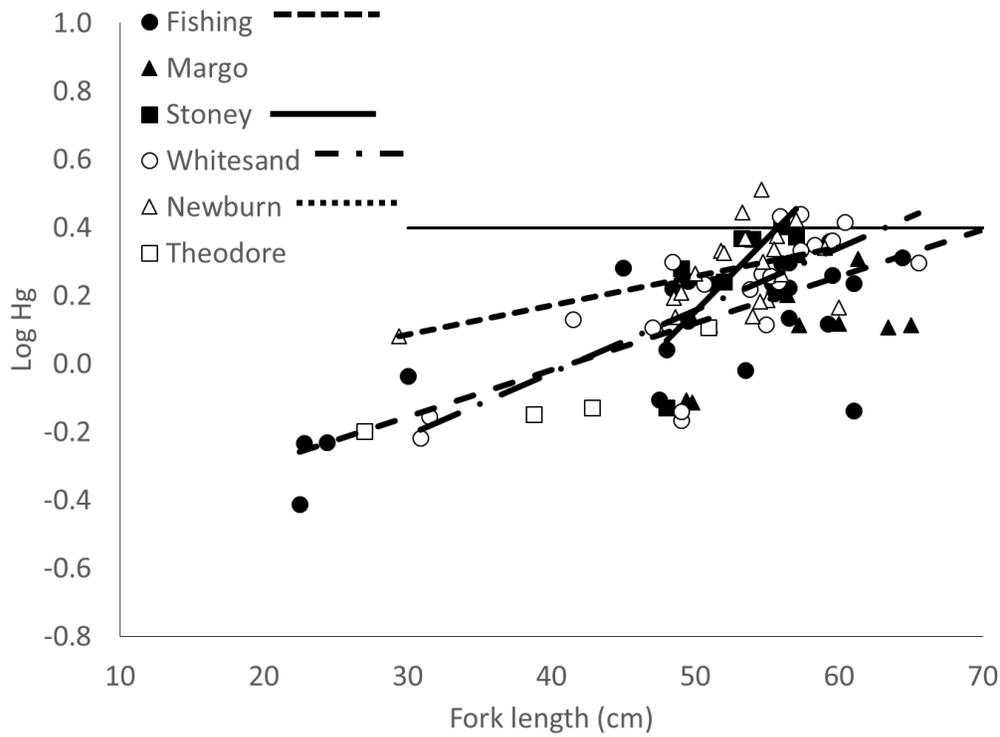


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630 **Figure 5.** Mercury vs body size for walleye (A) and northern pike (B) in northern Great Plains  
631 lakes with (open symbols) and without (solid symbols) crayfish.

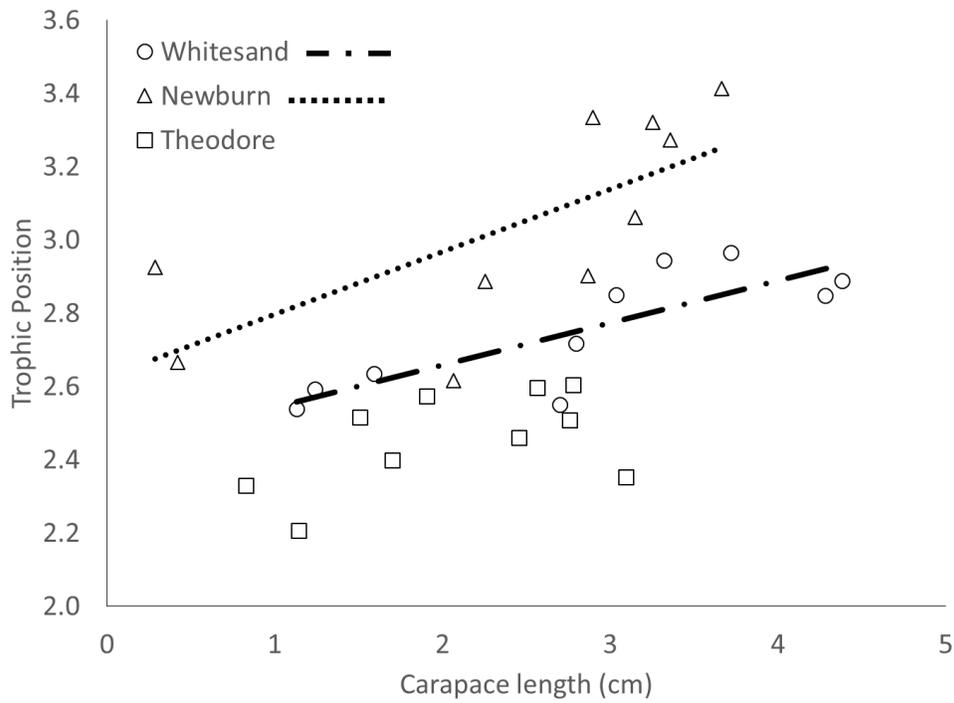


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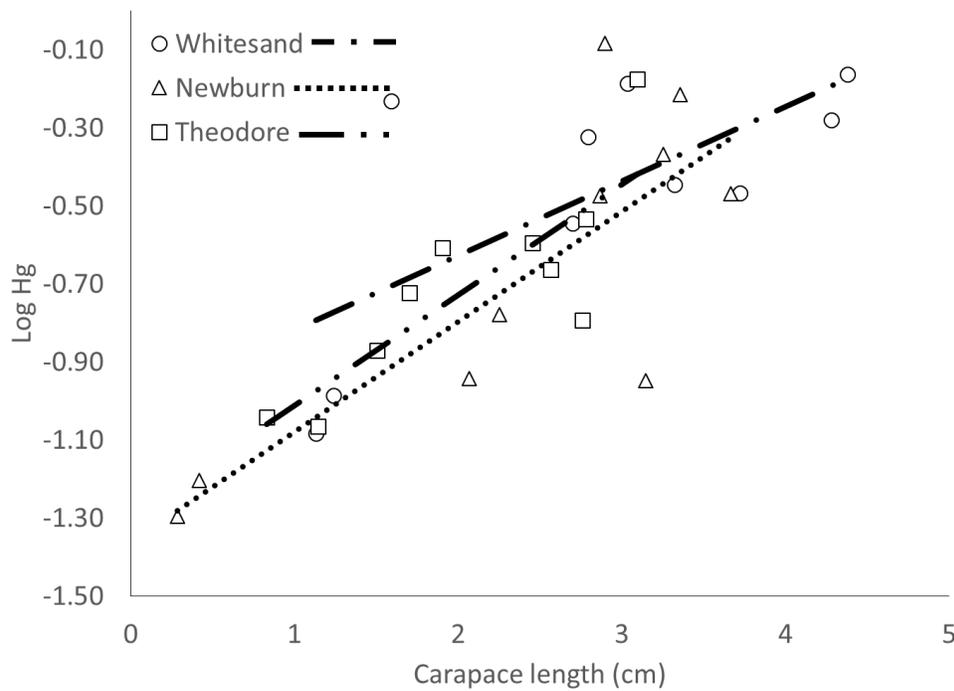


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634 **Figure 6** Trophic position and log total Hg concentrations in crayfish versus body size in three  
635 northern Great Plains lakes. Significant regressions are indicated with best fit lines.



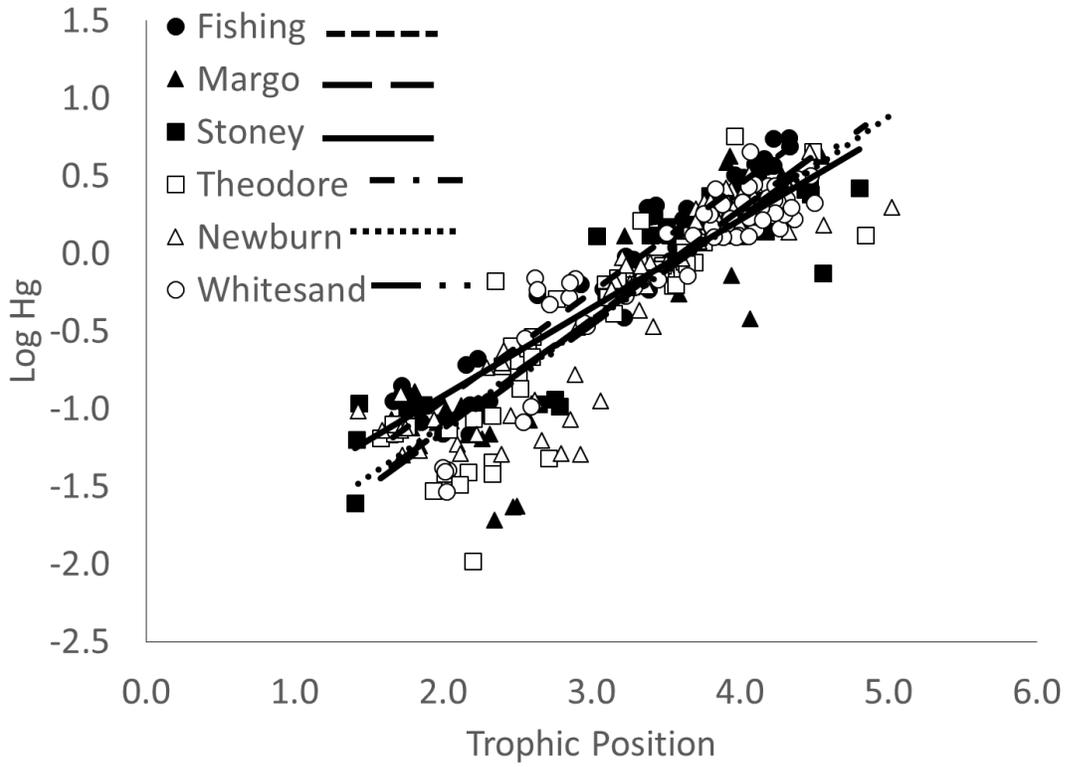
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639 **Figure 7** Log total Hg concentrations versus trophic position in northern Great Plains lakes with  
640 (open symbols) and without (solid symbols) crayfish.



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