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

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

2   **predatory fishes**

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Abstract

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

Introduction

The structure of lake food webs has important implications for energy flow and contaminant bioaccumulation (Vander Zanden et al. 1996). Both horizontal and vertical food web structure play roles in shaping energy flow from primary producers to apex predators. Fishes act as couplers of littoral and pelagic zones in lakes by deriving energy from both pathways through their mobile foraging (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). Meanwhile, foraging by fishes at the top of long food chains leads to high 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^2 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^2 from the snorkelling surveys (Table 2), trapping in 2013

101   yielded a catch-per-unit effort of 2.1 crayfish trap^{-1} day^{-1} 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 μm. 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 ± 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 (δ) notation defined as parts

136   per thousand or permil (‰) deviation from an international standard. The formula for the delta

137   (δ) notation is as follows:

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

139   Where: X is the heavy isotope of the particular element being measured (either ^{15}N for nitrogen

140   or ^{13}C for carbon); R_{SAMPLE} is the ratio of the heavy isotope to the light isotope for the particular

141   element in the sample (^{15}N/^{14}N for nitrogen or ^{13}C/^{12}C for carbon); $R_{STANDARD}$ is the ratio of the

142   heavy isotope to the light isotope for an international standard (Pee Dee Belemnite limestone for

143   ^{13}C/^{12}C (Craig 1957) and atmospheric nitrogen for^{15}N/^{14}N (Mariotti 1983)). International

144   standards are set at delta (δ) values of 0‰. Samples analysed in duplicate (n = 20) had an

145   average difference of 0.3‰ for both δ^{13}C and δ^{15}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: $\delta^{13}C_{corr} = \delta^{13}C-[(-$

149    $2.8317*LN(C/N))+2.8838]$ where: $\delta^{13}C_{corr}$ is the lipid-corrected value, δ^{13}C is the δ^{13}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 $Prop_{littoral} = (\delta^{13}C_{consumer} - \delta^{13}C_{pelagic})/(\delta^{13}C_{littoral} - \delta^{13}C_{pelagic})$ where $\delta^{13}C_{pelagic}$ is the

154   δ^{13}C value of zooplankton, and $\delta^{13}C_{littoral}$ is the δ^{13}C value of snails. Trophic position was

155   determined by accounting for different baseline δ^{15}N in the littoral and pelagic zones using: TP =

156    $2 + [\delta^{15}N_{consumer} - (\delta^{15}N_{littoral} \times Prop_{littoral} + \delta^{15}N_{pelagic} \times Prop_{pelagic})]/\Delta15N$ where $\delta^{15}N_{pelagic}$ is the

157   δ^{15}N value of zooplankton, $\delta^{15}N_{littoral}$ is the δ^{15}N value of snails, and $\Delta15N$ 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 ± 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 $Prop_{littoral}$, 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 Log Hg = m*TP + b. The slopes of these regressions (m) were then used to

174   calculate Trophic Magnification Factors (TMFs) using $TMF = 10^m$ (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 $\delta^{13}C$ values for the fishes (Figure 2).

181   Across all lakes, mean zooplankton $\delta^{13}C$ was $-31.4 \pm 2.8‰$ S.D. ($n = 77$) while snails had $\delta^{13}C =$

182    $-27.6 \pm 2.0‰$ S.D. ($n = 131$). Within lakes, the average difference in $\delta^{13}C$ between the pelagic

183   and littoral was $4.1 \pm 1.1‰$ S.D. The $\delta^{15}N$ value of the two baseline organisms were variable

184   across lakes but had similar mean values overall: zooplankton $\delta^{15}N$ = 8.8 ± 1.9‰ S.D. (n = 77),

185   snail $\delta^{15}N$ = 8.2 ± 1.6‰ 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 $Prop_{littoral}$ <0.5 for both species, and $Prop_{littoral}$ 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 $Prop_{littoral}$ and body size (Table 4).

191   Crayfish, when present, had highly variable $\delta^{13}C$ and $Prop_{littoral}$ 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 $Prop_{littoral}$ ($F_{1,112}$ = 141.762, p < 0.001), driven largely by low values in Theodore

197   Lake. For walleye, length was a significant predictor of $Prop_{littoral}$ ($F_{1,112}$ = 7.815, p = 0.006),

198   with larger individuals having higher $Prop_{littoral}$, but this was not the case for pike ($F_{1,72}$ = 0.312,

199   p = 0.578). Lake type also had no effect on $Prop_{littoral}$ 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 ± 0.35) having slightly higher mean values than pike (3.77 ± 0.40) and both species

202   approximately 0.5 to 1.0 TPs above yellow perch that had mean TP = 3.21 ± 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 TP = 3.88 ± 0.03 SE) compared with crayfish-absent lakes (TP = 4.00 ±

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 µg/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 µg/g dry weight) compared with crayfish-absent lakes (1.6 µg/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 µg/g

267   dry weight for all lakes) were within the reported range of 0.1 to 1.4 µg/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

298   larger, higher trophic level prey as fishes attain larger body sizes (Mittelbach and Persson 1998).

299   Others have argued that ^{15}N could accumulate with age in long-lived fishes independent of

300   dietary switches to higher trophic levels (Overman and Parrish 2001), but stomach data showed

301   that the largest walleye in our sample set tended to have fish in their stomachs, further supporting

302   their position as apex predators in these lakes.

303   There are three possible processes that lead to differential Hg concentrations in top

304   predators, including stronger trophic magnification through the food web, longer food chains and

305   higher baseline Hg concentrations (Kidd et al. 2012). Trophic magnification factors differed

306   little among lakes, and were very near the global average of 4.7 for total Hg (Lavoie et al. 2013).

307   Given the similarities in species composition and their geographic proximity to one another, it is

308   not surprising that TMFs fell in such a narrow range. Food chain length was also similar at all

309   lakes, with large walleye occupying the highest TP, though Theodore Lake walleye and pike had

310   lowest mean TPs and consequently the lowest total Hg concentrations. A higher baseline

311   concentration may be responsible for the higher marginal mean observed in Fishing Lake, where

312   significant flooding had occurred in the two years prior to sampling (Water Security Agency

313   2016). This lake also had the highest concentrations in zooplankton and snails at the base of the

314   food web. The many individual walleye and pike above the Hg consumption guideline highlight

315   how prairie lakes are not immune to Hg contamination despite many suggesting that Western

316   North America has lower atmospheric Hg deposition (Prestbo and Gay 2009) and hence lower

317   risk to fish-eating consumers (Depew et al. 2013b). Concentrations in the two species were

318   higher in all six of our study lakes compared with historical provincial records for these lakes

319   (Depew et al. 2013a). This could owe, in part to recent high water levels in the region (Water

320   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^2) 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 (± S.D.) body size, trophic position, proportion littoral dependence ($Prop_{littoral}$)

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

Pike

Lake	Fork length (cm)	TP	$Prop_{littoral}$	[Hg] (ug/g dry wgt)
Fishing Lake	51.2 ± 14.3	3.50 ± 0.26	0.75 ± 0.08	1.56 ± 0.98
Margo Lake	57.1 ± 5.6	3.58 ± 0.24	0.69 ± 0.12	1.38 ± 0.44
Stoney Lake	52.7 ± 3.4	4.12 ± 0.27	0.80 ± 0.17	1.99 ± 0.62
Whitesand Lake	51.6 ± 8.7	3.84 ± 0.41	0.79 ± 0.10	1.69 ± 0.66
Newburn Lake	52.6 ± 6.3	4.02 ± 0.31	0.95 ± 0.21	1.97 ± 0.54
Theodore Lake	39.9 ± 10.0	3.18 ± 0.34	0.45 ± 0.16	0.84 ± 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	r2	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	r2	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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Table 5. Relationship between log total Hg concentration and fork length for walleye and pike in the six study lakes, with regression equations for significant regressions

Walleye

Lake	Equation	r^2	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^2	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	r2	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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Figure 1. Location of lakes with crayfish (1 – Fishing Lake, 2 – Margo Lake, 3 – Stoney Lake) and without crayfish (4 – Whitesand Lake, 5 – Newburn Lake, 6 – Theodore Lake, not shown) in the Northern Great Plains.
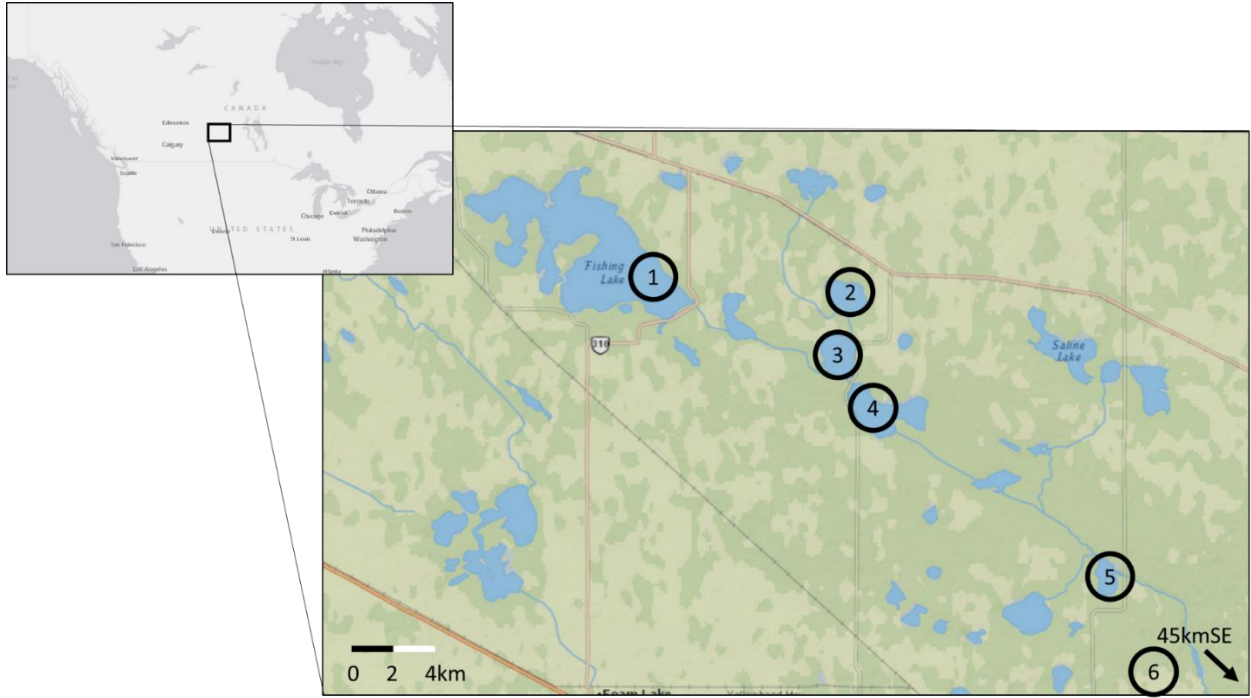
Figure 2. Scatterplot of δ¹³C and δ¹⁵N values for the food webs of the six lakes. Solid symbols are fish (circles = walleye, squares = pike, triangles = yellow perch), open symbols are baseline organisms (circles = zooplankton, triangles = snails) and shaded circles are crayfish.
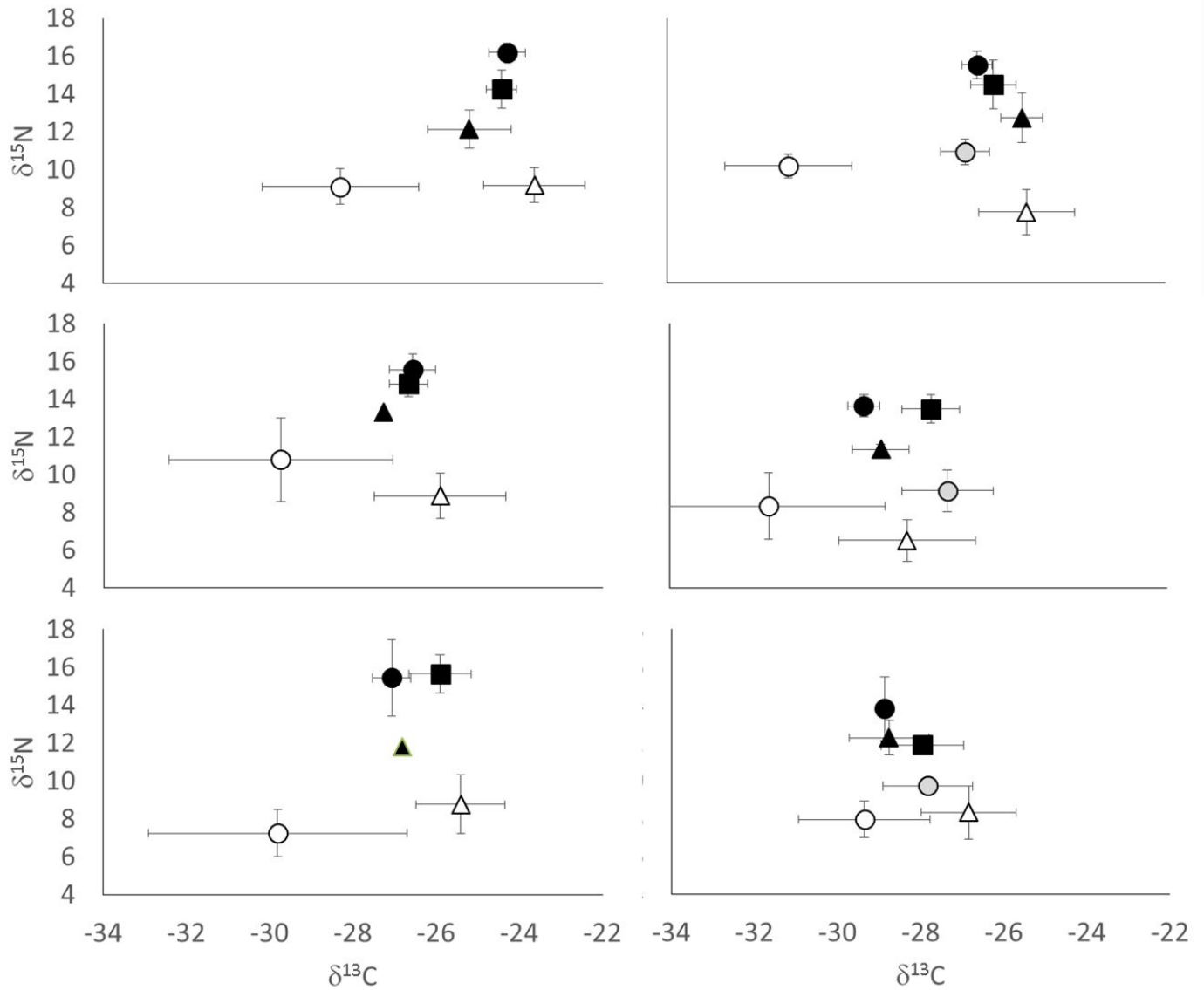
621   **Figure 3.** Proportional littoral dependence (Prop$_{littoral}$) vs. body size for walleye (A) and northern

622   pike (B) in northern Great Plains lakes with (open symbols) and without (solid symbols)

623   crayfish.

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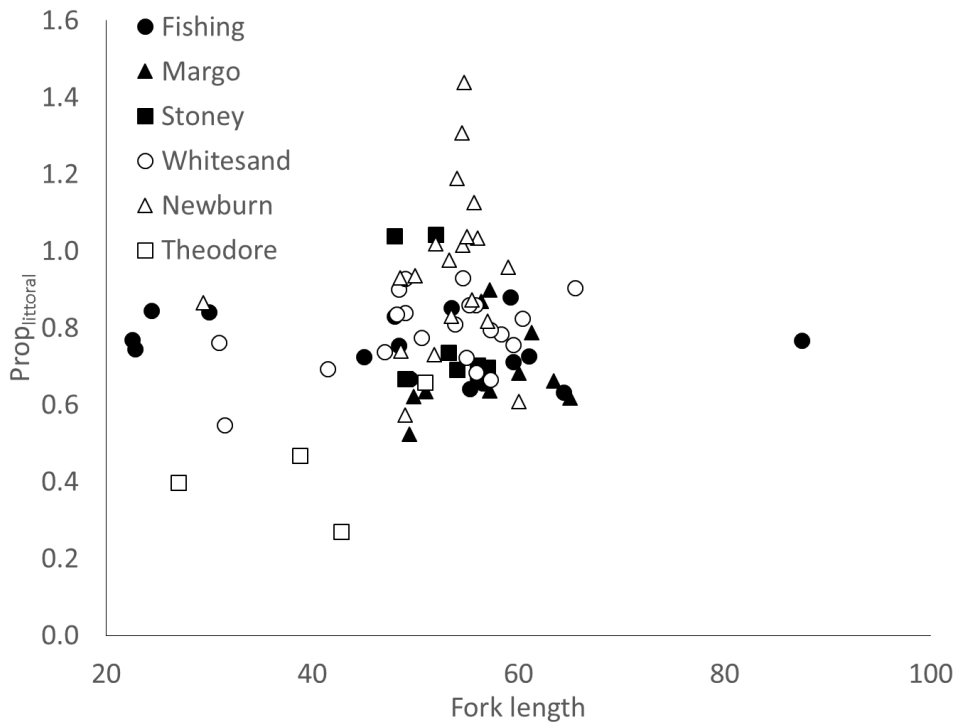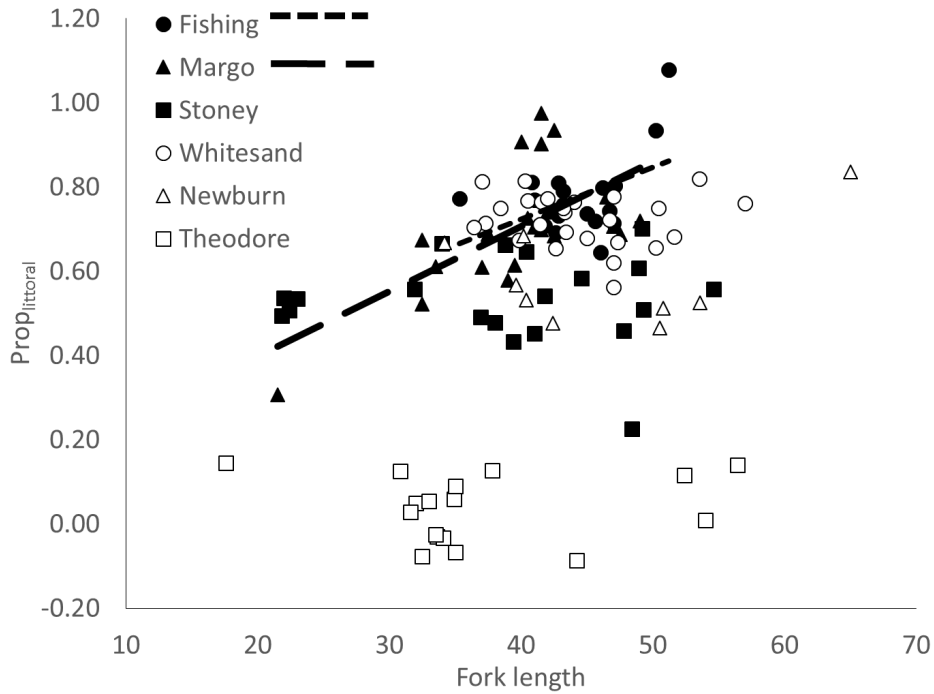
626 **Figure 4.** Trophic position vs. body size for walleye (A) and northern pike (B) in northern Great

627 Plains lakes with (open symbols) and without (solid symbols) crayfish.
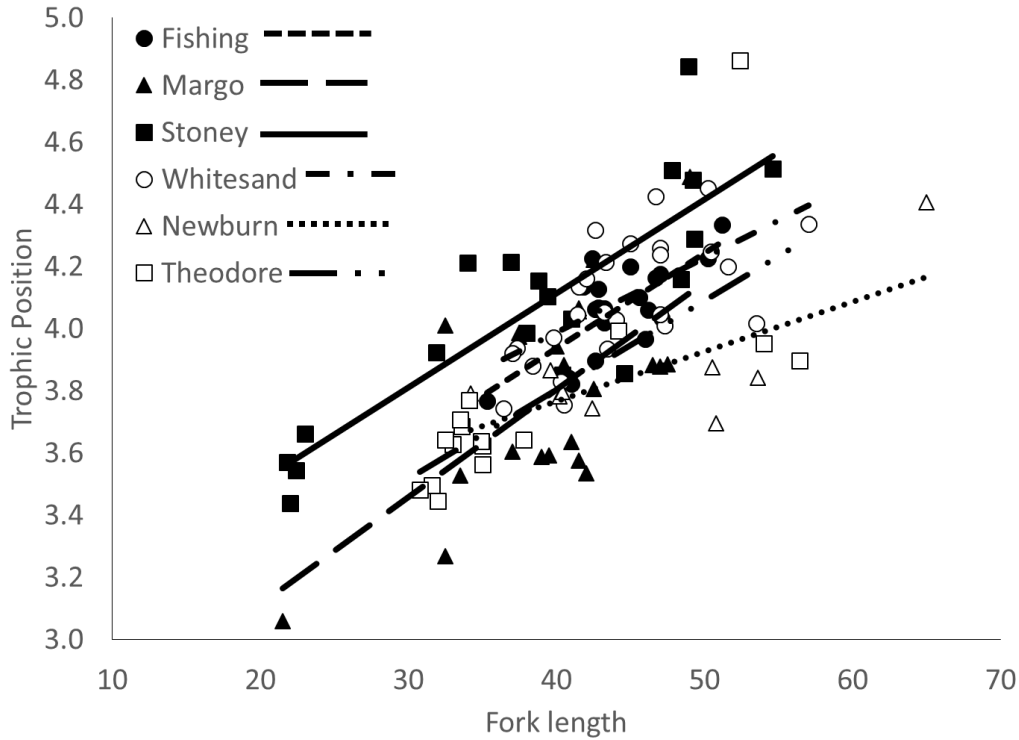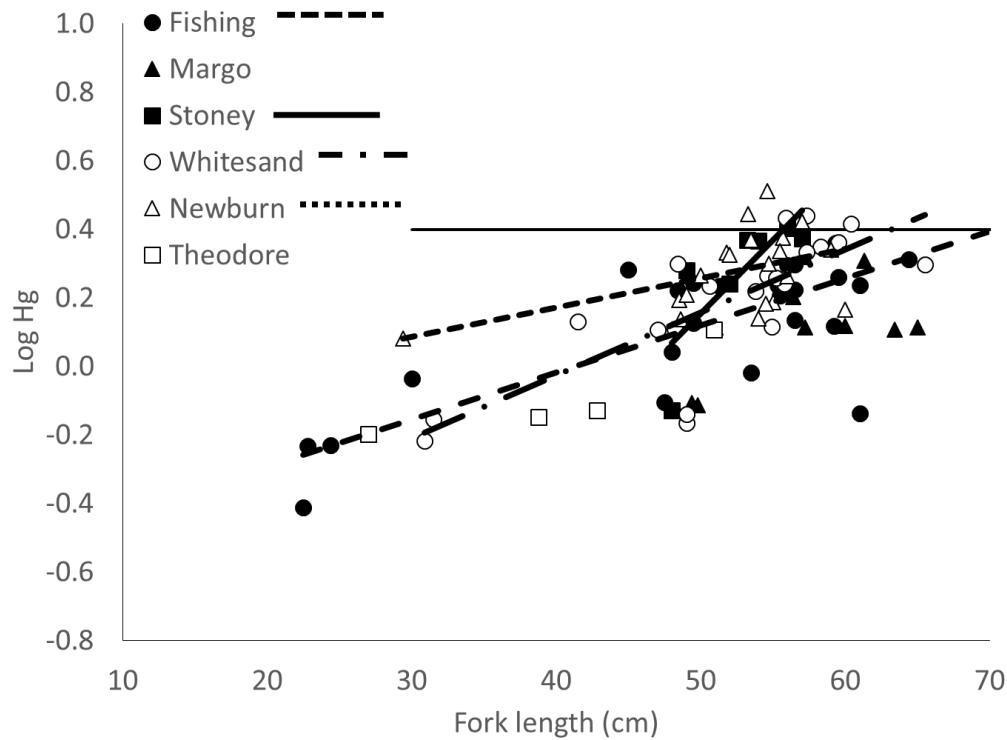

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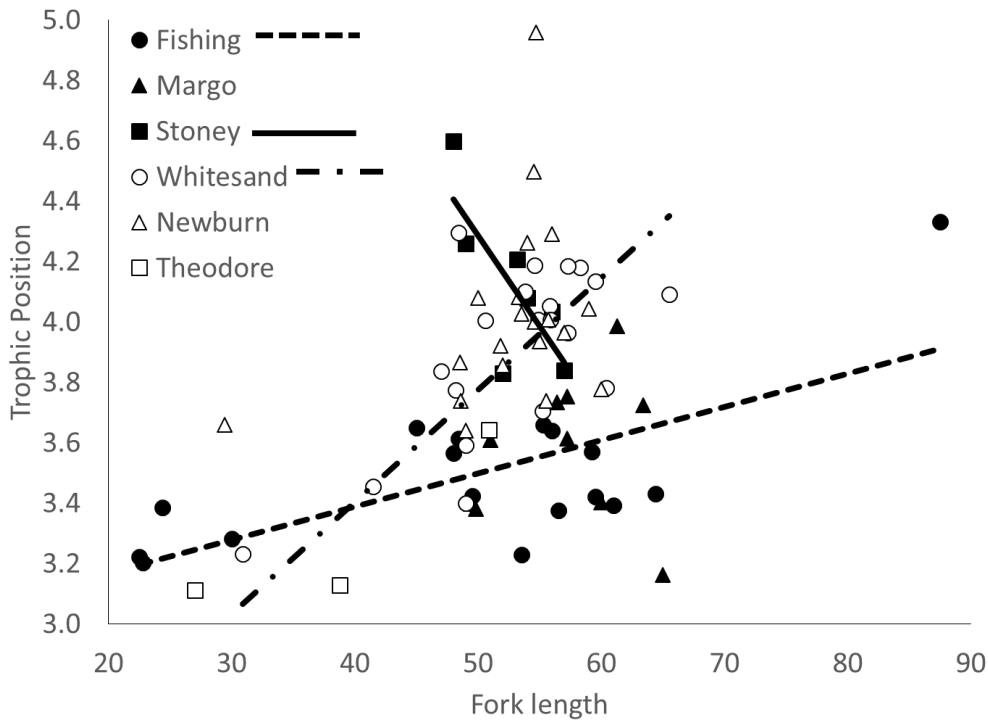
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630 **Figure 5.** Mercury vs body size for walleye (A) and northern pike (B) in northern Great Plains

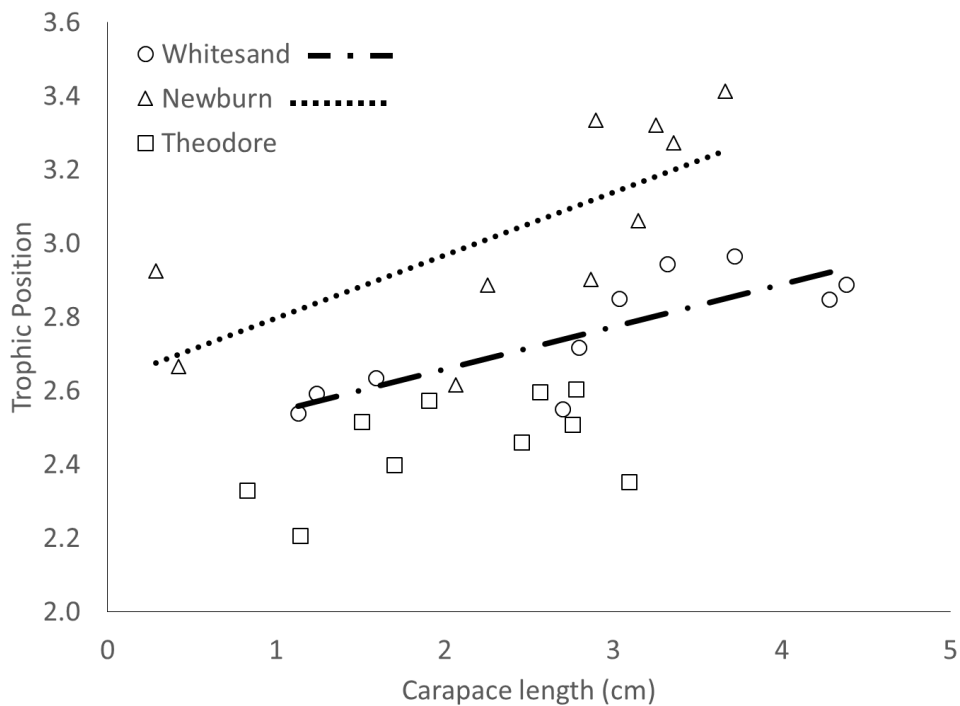631 lakes with (open symbols) and without (solid symbols) crayfish.
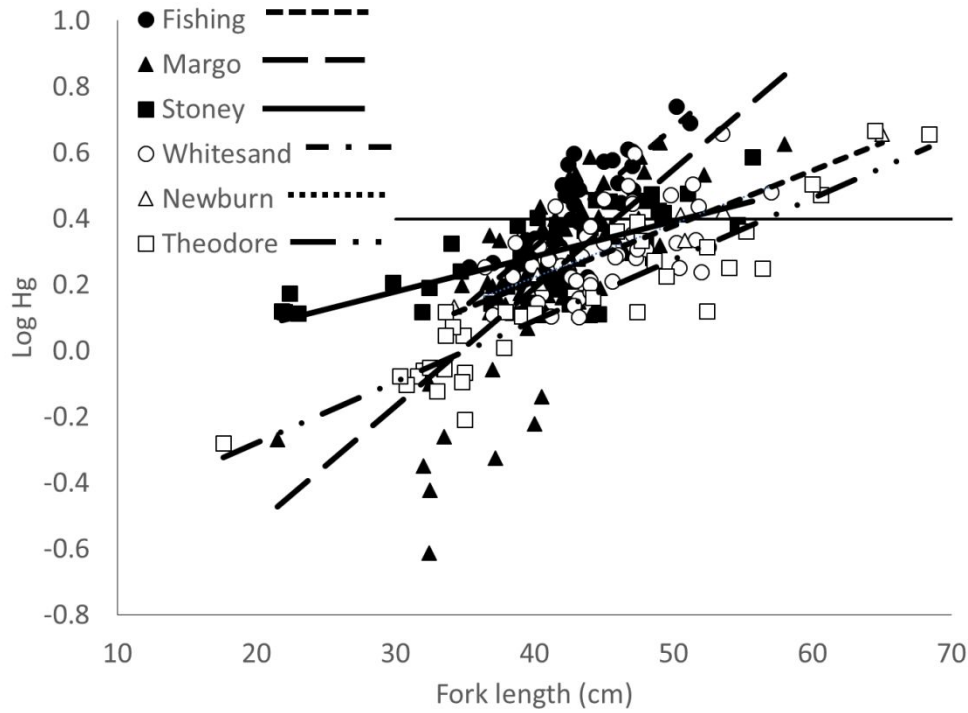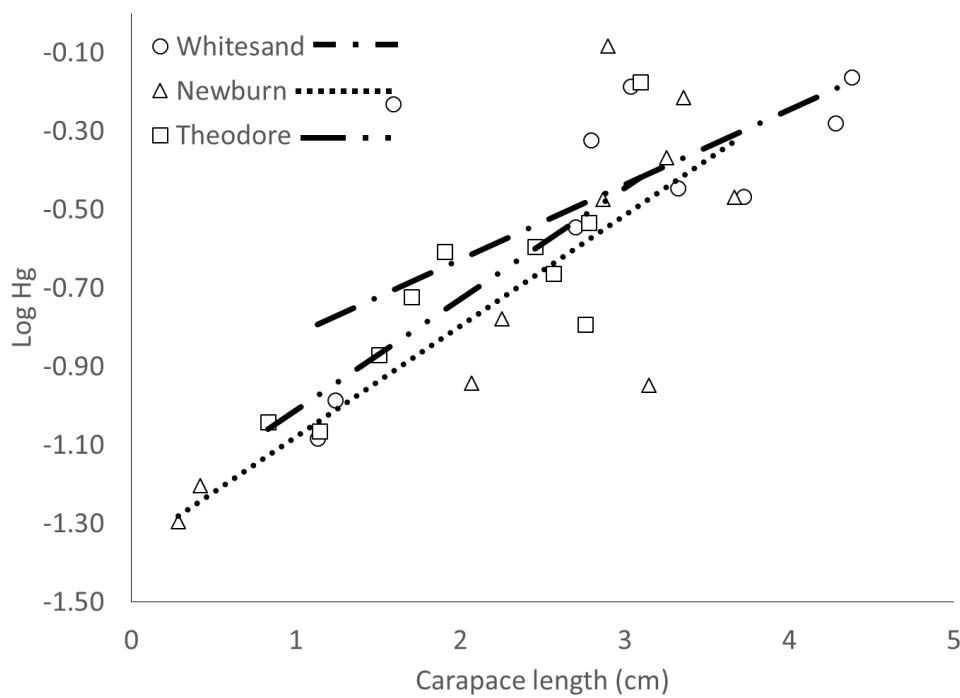

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634 **Figure 6** Trophic position and log total Hg concentrations in crayfish versus body size in three

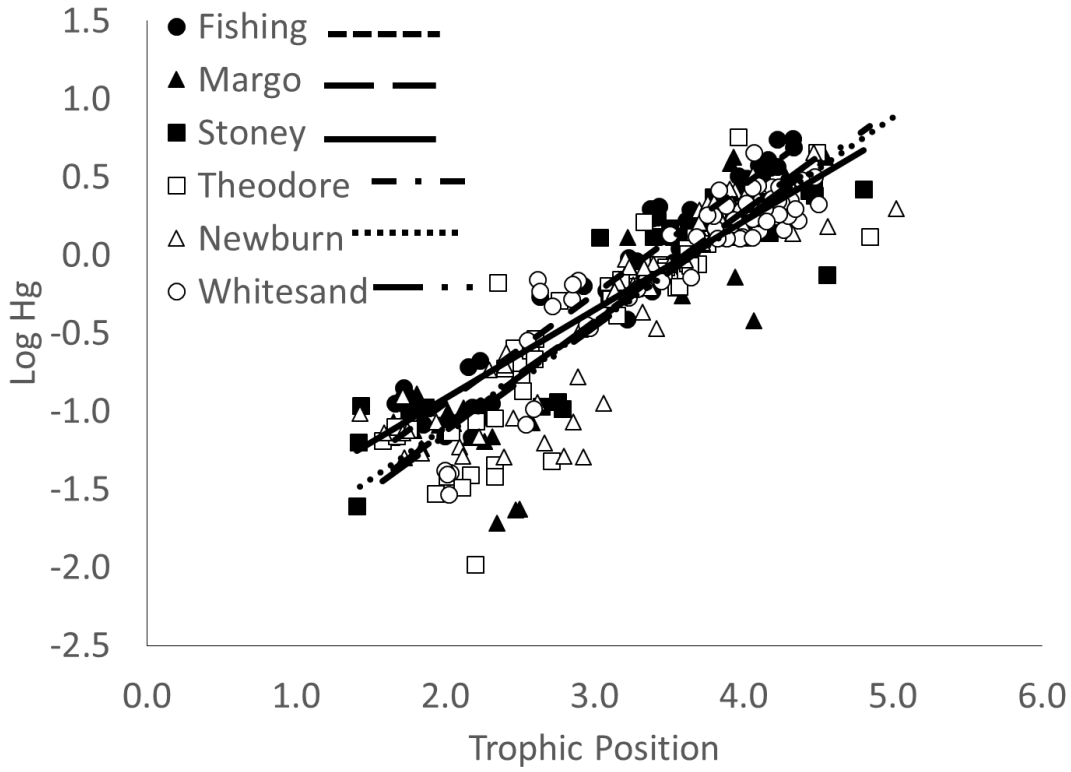635 northern Great Plains lakes. Significant regressions are indicated with best fit lines.

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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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