

1 Contemporary Diets of Lake Superior Lake Whitefish off the Keweenaw Peninsula and Changes  
2 in Condition from the 1980s to 2010s

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5 Grant Woodard<sup>1</sup>, Travis O. Brenden<sup>1,\*</sup>, and William P. Mattes<sup>2</sup>

6

7 <sup>1</sup>Quantitative Fisheries Center

8 Department of Fisheries and Wildlife

9 Michigan State University

10 East Lansing, MI 48824

11

12 <sup>2</sup>Biological Services - Great Lakes Section

13 Great Lakes Indian Fish and Wildlife Commission

14 Odanah, WI 54861

15

16 Correspondence

17 Travis O. Brenden

18 Quantitative Fisheries Center

19 Department of Fisheries and Wildlife

20 Michigan State University

21 375 Wilson Rd, 101 UPLA

22 East Lansing, MI 48824

23 [brenden@msu.edu](mailto:brenden@msu.edu)

24 517-355-0003

25

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27 Running title: Lake Superior lake whitefish diet and condition

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29

30 **Abstract**

31 Over the last two decades, declines in lake whitefish (*Coregonus clupeaformis*) recruitment and  
32 growth in many areas of the Laurentian Great Lakes have raised concerns about the status of this  
33 important species. Although Lake Superior populations have been less affected than those in  
34 other Great Lakes, these populations still face multiple threats. We characterized lake whitefish  
35 diets collected off the Keweenaw Peninsula between 2015-2017 and compared results to  
36 previous Lake Superior studies. We additionally estimated length-weight relationships to  
37 determine whether lake whitefish body condition (i.e., expected weight-at-length) had changed  
38 since the 1980s. Diet diversity was low, although individual specialization was moderate to high.  
39 Fish transitioned from consuming *Diporeia* in the spring to *Mysis* and fish eggs during fall and  
40 winter; sphaeriids composed 20-30% of diets across all seasons. Compared to findings for other  
41 Lake Superior regions, lake whitefish diets comprised lower percentages of high energy items  
42 (e.g., *Diporeia*, *Mysis*) and higher percentages of low energy items (e.g., sphaeriids). Expected  
43 weights in the 2000s and 2010s were lower in the 400- and 500-mm length groups but similar in  
44 larger lengths groups compared to the 1980s; condition was highest across all lengths in the  
45 1990s. The observed decline in condition since the 1990s in the 400- and 500-mm length groups,  
46 in combination with possibly greater consumption of less energetically profitable items, suggests  
47 that lake whitefish < 600 mm or preferred prey resources in this lake region may be experiencing  
48 stressors leading to condition declines, although what these stressors are remain unknown.

49

50 Keywords: Lake Superior, lake whitefish, diet, quantile regression, condition, *Diporeia*, *Mysis*

51

52 **Introduction**

53 Lake whitefish (*Coregonus clupeaformis*) is a coregonid species indigenous to northern  
54 latitudes of North America, including the Laurentian Great Lakes (Ebener et al., 2008).  
55 Historically, Native American tribes and First Nation communities in the Great Lakes basin  
56 relied heavily on lake whitefish through subsistence fishing, and the species continues to be  
57 culturally important to indigenous peoples in the region (Cleland, 1982; Ebener et al., 2008;  
58 Mohr and Ebener, 2005). After European settlement, commercial fisheries for Great Lakes lake  
59 whitefish developed and populations were heavily exploited through the 1800s and early 1900s  
60 (Ebener et al., 2008; Wells and McLain, 1973, 1972). Substantial abundance declines occurred  
61 across all the lakes from the late-1800s to mid-1900s from overharvest, parasitism by invasive  
62 sea lamprey (*Petromyzon marinus*), competition with invasive planktivorous fishes [e.g.,  
63 rainbow smelt (*Osmerus mordax*)], and declining water quality (Christie, 1973, 1972; Nalepa et  
64 al., 2005b). Beginning in the 1960s and continuing into the 1990s, lake whitefish abundances  
65 increased due to a variety of factors, including reductions in abundances of invasive species as a  
66 consequence of control efforts (in the case of sea lamprey; Ebener et al., 2008; Eck and Wells,  
67 1987; Schneeberger et al., 2005) or elevated predation levels (in the case of rainbow smelt; Cook  
68 et al., 2005), more restrictive harvest regulations (Ebener et al., 2008), and improvements in  
69 water quality (Cook et al., 2005; Ebener et al., 2008). Additionally, efforts to rehabilitate lake  
70 trout (*Salvelinus namaycush*) populations in the Great Lakes through stocking reduced sea  
71 lamprey parasitism on lake whitefish due to the former being a more preferred food source than  
72 the latter (Wells and McLain, 1972).

73 Despite increasing abundances since the mid-1900s, recent declines in growth, condition,  
74 and recruitment levels have renewed concerns about Great Lakes lake whitefish populations.  
75 Declines in recruitment have occurred across Lakes Erie (Lake Erie Coldwater Task Group,  
76 2017), Ontario (Hoyle et al., 1999), Huron (Lenart and Caroffino, 2018), and Michigan (Lenart  
77 and Caroffino, 2018). Lake-wide declines in lake whitefish growth and condition have been  
78 observed in Lakes Huron (Lenart and Caroffino, 2018), Michigan (Lenart and Caroffino, 2018;  
79 Pothoven et al., 2001; Schneeberger et al., 2005), and Ontario (Hoyle, 2005), with some  
80 localized declines observed in Lake Superior (Rennie, 2013). The identification of factors  
81 contributing to declines in recruitment is an active area of research in the Great Lakes basin.  
82 Declines in growth and condition were initially attributed to increased lake whitefish

83 abundances; declines since the early 2000s are believed to have been caused by declining  
84 abundances of deepwater amphipods *Diporeia* spp. (hereafter *Diporeia*; Hoyle, 2005; Nalepa et  
85 al., 2005b; Pothoven et al., 2001), which historically were an important food resource for Great  
86 Lakes lake whitefish (Gardner et al., 1985; Kainz et al., 2010; McNickle et al., 2006). Declines  
87 in *Diporeia* abundance ostensibly were caused by invasion and expansion of *Dreissena*  
88 *polymorpha* and *D. bugensis* (hereafter *Dreissena*; Barbiero et al., 2011; Dermott, 2001; Lozano  
89 et al., 2001). Hypotheses for how *Dreissena* invasion contributed to *Diporeia* declines include  
90 reduced food availability due to *Dreissena* filtering (Nalepa et al., 2005a, 2007, 1998), the  
91 associated competition with *Dreissena* (Dermott and Kerec, 1997), exposure to toxins from  
92 *Dreissena* pseudofeces (Dermott et al., 2005), and disease outbreaks from pathogens carried by  
93 *Dreissena* or possibly other sources (Cave and Strychar, 2015; Dermott et al., 2005; Winters et  
94 al., 2014). In addition to the link between *Dreissena* and reductions in availability of lake  
95 whitefish's preferred food resource, *Dreissena* establishment has been associated with  
96 modifications in resource use by lake whitefish, such as increased use of nearshore benthic food  
97 sources and shifts in occupied water depths (Fera et al., 2017; Rennie et al., 2015, 2012).

98         Although Lake Superior lake whitefish populations are believed to have fared better than  
99 those in the other Great Lakes due to limited *Dreissena* establishment in Lake Superior, concerns  
100 remain over the multitude of threats that populations in the lake currently or may soon face.  
101 Declines in lake whitefish growth and condition were observed in some areas of Lake Superior  
102 from the late 1990s to early 2000s (Rennie, 2013). The reasons for these declines are unknown,  
103 but are unlikely related to *Dreissena* because of limited establishment in Lake Superior (Rennie,  
104 2013). Growth rates of Lake Superior lake whitefish from age-1 to age-2 did not change  
105 (Thunder and Whitefish Bays) or increased slightly (Apostle Islands) from the 1990s to the late-  
106 2000s (Fera et al., 2015). Comparisons of current condition or growth rates of Lake Superior lake  
107 whitefish to earlier time periods have been limited.

108         One ostensible threat to Lake Superior lake whitefish populations is climate change.  
109 Open-water summer surface temperatures in Lake Superior have risen approximately 3.5°C over  
110 the last century, with most of the change in the last 30 years (Austin and Colman, 2008).  
111 Warming temperatures in Lake Superior may promote the colonization of non-native species that  
112 could compete with lake whitefish for food resources or prey upon lake whitefish at different life  
113 stages (Collingsworth et al., 2017). Furthermore, increased temperatures may reduce lake

114 whitefish egg survival and recruitment and increase age-at-maturity (Rennie, 2013). Water  
115 temperature is also an important factor, along with productivity and calcium levels, that has  
116 limited *Dreissena* expansion in Lake Superior (Grigorovich et al., 2003; Whittier et al., 2008). If  
117 Lake Superior water temperatures continue to increase, *Dreissena* populations in Lake Superior  
118 could expand given observations that veligers are widely distributed at low densities in the lake  
119 (Trebitz et al., 2019).

120 The purpose of this study was to describe contemporary diets of lake whitefish collected  
121 off the Keweenaw Peninsula of Lake Superior. Our expectations based on previous diet and  
122 stable isotope studies for Lake Superior lake whitefish (e.g., Anderson and Smith, 1971; Fera et  
123 al., 2017; Gamble et al., 2011; Rennie et al., 2012) were that diets would be heavily dominated  
124 by prey types such as *Diporeia* and *Mysis*. We additionally evaluated changes in lake whitefish  
125 body condition (i.e., expected weight-at-length) in Lake Superior over time (1980s to 2010s) to  
126 determine whether populations continue to be resilient to changes in demographics and dynamics  
127 that other Great Lakes lake whitefish populations have experienced. Our expectation was that  
128 lake whitefish condition in this region of Lake Superior would be temporally stable unlike  
129 condition in lakes where dreissenids invaded and *Diporeia* abundances decreased. We also did  
130 not anticipate density-dependence effects to cause changes in condition because abundance has  
131 not increased in this region of Lake Superior (Mattes, 2019).

132

## 133 **Methods**

### 134 *Data collection*

135 Lake whitefish diet data were obtained from fish collected between April 2015 and June  
136 2017 from four management units in Lake Superior off the Keweenaw Peninsula (Figure 1). Fish  
137 were sampled by Great Lakes Indian Fish and Wildlife Commission fishery technicians from  
138 commercial fishing and assessment gill nets deployed in nearshore waters less than 73.2 m deep.  
139 Stretch-measure mesh sizes of commercial and assessment gillnet panels ranged from 50.8 to  
140 152.4 mm. Commercial nets ranged from 305 to 1,829 m in length and 3.1 to 4.6 m in height.  
141 Assessment nets were 91.44 m in length and 1.8 m in height. Duration of net sets ranged from  
142 overnight to 3 days. During the summer and fall, nets were generally set overnight unless  
143 weather conditions prevented retrieval. During winter and spring, multiple day sets were more  
144 common. After fish were collected, stomachs were removed whole and then frozen. Once

145 returned to the laboratory, stomachs were thawed and dissected. Stomach contents were  
146 identified to the lowest taxonomic level possible, weighed, and enumerated. Consumed items  
147 were assigned to one of 12 prey types using a categorization system for fish diet studies  
148 developed and agreed upon by the Lake Superior Technical Committee (Lake Superior Technical  
149 Committee, unpublished report; Table 1). Items infrequently found in fish stomachs, such as  
150 chironomids and other aquatic insects, were combined into an “other” prey type.

151 Lake whitefish diets were described seasonally by averaging across sampling years. Due  
152 to variation in sample sizes across years, we averaged across years to reduce the effect of years  
153 with disproportionately larger number of observations. Seasonal classifications corresponded to  
154 spring (March to May), summer (June to August), autumn (September to November), and winter  
155 (December to February).

156 Length-weight data for Lake Superior lake whitefish were obtained from fish collected  
157 from commercial gillnet fishers between 1984 to 2017 in the same management units from which  
158 stomach samples were collected. Fish were measured for total length to the nearest 1/10<sup>th</sup> of an  
159 inch, which was subsequently converted to the nearest mm for analysis. Weight measurements  
160 were made in either round weight (entire fish) or dressed weight (gutted fish) to the nearest 0.05  
161 kg. Dressed weights were converted to round weights using a conversion factor of 1.17 (W.  
162 Mattes, unpublished data).

163  
164 *Diet characterization and analyses*

165 Lake whitefish diets were described using two measures of average diversity: richness  
166 and Shannon diversity (Shannon, 1948). Richness was simply the count of the number of diet  
167 item types consumed by a lake whitefish. Shannon diversity was calculated as  $\sum_i p_i \log_{10} p_i$   
168 where  $p_i$  was the proportion by weight that the  $i$ -th diet item composed of all the items consumed  
169 by a fish.

170 Lake whitefish diets were characterized in terms of importance and  
171 specialization/generalization using the graphical assessment method of Amundsen et al. (1996).  
172 This method compares prey-specific abundance for predators that consumed that particular prey  
173 type versus frequency of occurrence of that prey type across all predators; the spread and  
174 location of the prey-type observations on the plot characterizes both prey importance and feeding  
175 strategy (Amundsen et al., 1996). In particular, prey types with high frequency of occurrence and

176 high prey-specific abundance are considered important items, prey types with low frequency of  
177 occurrence and high prey-specific abundance are considered indicative of individual predators  
178 specializing on certain items, and prey types with high frequency of occurrence and low prey-  
179 specific abundance are considered indicative of a generalized feeding strategy by fish  
180 (Amundsen et al., 1996; Chipps and Garvey, 2007; Willis et al., 2015).

181 We calculated individual diet specialization as a measure of intraspecific variation in  
182 resource use among individuals in the region. High individual diet specialization occurs when  
183 individuals consume a small number of available food resources that are different than what  
184 other individuals consume, which can be evidence of intraspecific competition (Araújo et al.,  
185 2008). Our expectation was that individual diet specialization would be low under the hypothesis  
186 that most sampled individuals would rely heavily on *Diporeia* and *Mysis*. Individual diet  
187 specialization was estimated using a network theory method (Araújo et al., 2008). This method  
188 involves constructing a niche overlap network based on the diet overlap among pairs of  
189 individuals – once this network is constructed, the density of overlap values (i.e., connections)  
190 around individual fish (i.e., nodes) is used to organize individuals into clusters that consume the  
191 same set of resources. A weighted clustering coefficient is then used as an overall measure of  
192 clustering and the measure of individual specialization is calculated by subtracting the weighted  
193 clustering coefficient from 1 (Araújo et al., 2008). The measure of individual specialization  
194 values can range from 0 to 1, where 0 indicates all individuals have the same diet and 1 indicates  
195 maximum variation in diets among individuals (Araújo et al., 2008). An individual specialization  
196 value greater than 0.6 has been used as a threshold for identifying significant or strong among-  
197 individual diet variation (Araújo et al., 2008). Individual specialization calculations were  
198 performed in R (R Core Team, 2018) using the RInSp package (Zaccarelli et al., 2013).

199 Similarities in lake whitefish diets among seasons were assessed using the Schoener diet  
200 overlap index (Schoener, 1970) calculated from the mean percentages by weight of the prey  
201 types. The Schoener diet overlap index ranges in value from 0 (no overlap) to 1 (perfect overlap).  
202 An index value greater than 0.6 is commonly interpreted as representing biologically significant  
203 overlap between the groups of organisms being compared (Zaret and Rand, 1971).

204 For richness, Shannon diversity, individual specialization, and Schoener diet overlap  
205 values, 95% confidence intervals were constructed by bootstrapping. For individual  
206 specialization, 95% confidence intervals were constructed by jackknifing (Araújo et al., 2008).

207 Bootstrapping the Schoener diet overlap index followed Smith (1985). Bootstrapping the  
208 richness and Shannon diversity values were conducted by sampling with replacement diet data of  
209 individual fish (i.e., stomachs of individuals were the sampling unit). For each metric, the  
210 number of bootstrap iterations was set at 1,000. Ninety-five percent confidence intervals for the  
211 indices that bootstrapped were generated using the percentile method of Hall (1992), which uses  
212 the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the bootstrap distribution for the evaluated index along with a  
213 bias-adjustment to generate the confidence intervals.

214 We compared lake whitefish diet results from this study to the results from previous  
215 studies conducted for the species on Lake Superior (Anderson and Smith, 1971; Gamble et al.,  
216 2011; Rennie et al., 2012; Stockwell et al. 2014). The main prey categories that we compared  
217 among studies were *Diporeia*, *Mysis*, sphaeriids, and fish eggs. For some of these studies, diet  
218 summaries were provided monthly. In those cases, we calculated weighted averages of the  
219 percentages by weight or volume of the prey types based on the number of non-empty stomachs  
220 that were examined in each month.

221

#### 222 *Temporal changes in lake whitefish condition*

223 We assessed temporal changes in condition (i.e., expected weight-at-length) by using  
224 quantile regression (Cade and Noon, 2003) to fit a log<sub>10</sub>-transformed allometric growth model to  
225 the length-weight data provided by commercial fishers for the Keweenaw Peninsula region of  
226 Lake Superior. The model included a categorical grouping factor for the decade (i.e., 1980s,  
227 1990s, 2000s, 2010s) that length-weight data were collected, which allowed for decade-specific  
228 growth model coefficients to be estimated (Cade et al., 2008). To assess whether allometric  
229 growth models differed by decade, we fit alternative versions of the model with different decade  
230 groupings and used Akaike Information Criterion (AIC) to determine which model was most  
231 supported by available data. The other models that were fit were 1) common model (i.e., shared  
232 coefficients) across all decades; 2) a model with unique coefficients for 1990s and shared  
233 coefficients for the 1980s, 2000s, and 2010s; 3) a model with shared coefficients for the 1980s  
234 and 1990s and shared coefficients for the 2000s and 2010s; 4) a model with unique coefficients  
235 for the 1980s and 1990s and shared coefficients for 2000s and 2010s; 5) a model with shared  
236 coefficients for 1980s, 1990s and 2000s and unique coefficients for 2010s. For the AIC model  
237 comparison, quantile regression models were fit at quantiles of 0.10, 0.25, 0.5, 0.75, and 0.90.



238 Using the AIC-selected allometric growth model, we estimated predicted quantiles of  
239 weight for the different decades at reference lengths ranging from 400 to 800 mm in 100-mm  
240 length increments. Predicted quantiles of weight were estimated by re-centering the intercept of  
241 the AIC-selected allometric growth model to the evaluated reference lengths (Cade et al., 2008).  
242 When predicting weight, we used quantiles ranging from 0.10 to 0.90 in 0.05 increments.  
243 Bootstrapping based on the Markov chain marginal bootstrap approach was used to estimate  
244 95% confidence intervals for predicted weights (He and Hu, 2002). Quantile regressions were  
245 conducted in R using the rq() function in the quantreg package (Koenker, 2018).

246

## 247 **Results**

248 A total of 208 lake whitefish were collected in 2015, 581 fish in 2016, and 343 fish in  
249 2017. Lengths of sampled lake whitefish ranged from approximately 250 to 750 mm, with  
250 approximately 92% of sampled fish between 400 and 600 mm in length. Percentages of non-  
251 empty stomachs were 75% in 2015, 73% in 2016, and 89% in 2017. Consequently, diet data  
252 were available for 157 fish in 2015, 425 fish in 2016, and 307 fish in 2017. For seasons, sample  
253 size ranges across years were: 70 to 189 fish with non-empty stomachs in spring, 24 to 200 fish  
254 with non-empty stocks in summer, 0 to 58 fish with non-empty stomachs in fall (0 fish with non-  
255 empty stomachs were collected in fall 2017), and 5 to 70 fish with non-empty stomachs in  
256 winter.

257

### 258 *Overall description of diet*

259 Diets of lake whitefish consisted primarily of *Mysis* (31% of diet by weight), *Diporeia*  
260 (28%), and sphaeriids (26%). The other and fish egg diet categories composed 7 and 5% of diets  
261 by weight. None of the other diet item categories composed more than 2% of diets by weight.  
262 Overall richness and Shannon diversity of lake whitefish diets were approximately 2 and 0.28,  
263 respectively, suggesting that on average the stomachs of lake whitefish contained few types of  
264 the possible diet items. Comparison of prey-specific abundance for predators that consumed a  
265 particular prey type versus frequency of occurrence of that prey type across all predators  
266 suggests that collected lake whitefish exhibited a mixed feed strategy (Amundsen et al., 1996).  
267 For diet items such as fish and terrestrial invertebrates, some individual specialization (i.e., low  
268 frequency of occurrence but high prey-specific abundance) was evident; whereas for other items

269 such as sphaeriids, feeding was more generalized (high frequency of occurrence but low prey-  
270 specific abundance; Figure 2). The most important (i.e., high frequency occurrence and prey-  
271 specific abundance) diet items were *Diporeia* and *Mysis* (Figure 2). The estimated individual diet  
272 specialization for the entire lake whitefish sample was 0.694 (95% confidence interval: 0.693 –  
273 0.694) indicating strong among individual variation in lake whitefish diets (Araújo et al., 2008),  
274 which is additional evidence of a mixed feeding strategy by lake whitefish.

275

#### 276 *Seasonal diets*

277 During spring, *Diporeia* and sphaeriids composed approximately 42 and 30% of fish  
278 diets by weight, respectively (Figure 3). *Diporeia* was the most important prey type for lake  
279 whitefish during the spring with a frequency of occurrence of approximately 65% and prey-  
280 specific abundance of approximately 70% (Figure 4). Frequency of occurrence for coregonids  
281 was low (< 2%), but in lake whitefish that consumed them the prey-specific abundance was  
282 greater than 50% (Figure 4). Conversely, lake whitefish in the spring exhibited more generalized  
283 feeding for sphaeriids with a frequency of occurrence greater than 50%, but low (< 25%) average  
284 contribution by weight to the stomach contents of the fish that consumed them (Figure 4).

285 Lake whitefish diets during summer comprised primarily *Mysis* (47% of diet by weight),  
286 *Diporeia* (27%), and sphaeriids (21%; Figure 3). All three of these prey types were consumed by  
287 a majority of fish with non-empty stomachs; however, their average contribution by weight to  
288 the stomach contents of the fish that consumed them was less than 50% (Figure 4). In particular,  
289 frequency of occurrence of sphaeriids in lake whitefish stomachs during the summer was near  
290 80%, but the average contribution by weight to the stomach contents of the fish that consumed  
291 them was only around 20%. Diets of a few individual lake whitefish during the summer were  
292 found to consist entirely of sculpins and terrestrial invertebrates (Figure 4).

293 During fall, lake whitefish diets comprised primarily *Mysis*, other prey types, and  
294 sphaeriids (Figure 3). Combined, these prey types composed approximately 94% of fish diets by  
295 weight. *Mysis* in particular was an important prey type with a frequency of occurrence of  
296 approximately 65% and an average contribution by weight to the fish that consumed them of  
297 approximately 80% (Figure 4). Similar to summer, diets of a few individual lake whitefish were  
298 found to consist entirely of either unknown fish or terrestrial invertebrates (Figure 4). As with the

299 other seasons, lake whitefish exhibited a generalized feeding strategy for sphaeriids during the  
300 fall (Figure 4).

301 *Mysis*, sphaeriids, and fish eggs composed approximately 82% of fish diets by weight in  
302 winter (Figure 3). Based on the combination of frequency of occurrence and prey-specific  
303 abundance, fish eggs were the most important prey type during the winter, although the  
304 frequency of occurrence was only around 40% (Figure 4). Although we did not attempt to  
305 identify the species of all the fish eggs that were consumed, genetic testing of some of the  
306 collected eggs indicated they were from cisco (*Coregonus artedii*; B. Mattes, Great Lakes Indian  
307 Fish and Wildlife Commission, *unpublished data*) although we cannot rule out that some eggs  
308 were produced by other fall- or winter-spawning fish, such as other coregonids, burbot (*Lota*  
309 *lota*), or lake trout (*Salvelinus namaycush*). *Mysis* and sphaeriids were consumed by a majority  
310 of lake whitefish during the winter, however, their average contribution by weight to the fish that  
311 consumed them was generally low (Figure 4).

312 In terms of seasonal similarities, diets were most similar between spring and summer and  
313 summer and fall with Schoener (1980) overlap values  $> 0.60$  (Table 2). The 95% confidence  
314 intervals for the diet overlaps encompassed 0.6 suggesting just moderate levels of overlap (Table  
315 2). Diets were most dissimilar between spring and fall and fall and winter with overlap values of  
316 0.27 (spring and fall) and 0.35 (fall and winter; Table 2).

317 Richness and Shannon diversity of lake whitefish diets were the highest in the summer  
318 and lowest in the fall (Table 3). In summer, winter, and spring, richness and Shannon diversity  
319 were greater than 2 and 0.25; in fall, richness and Shannon diversity were 1.543 and 0.216,  
320 respectively (Table 3). Individual specialization was highest during the spring (0.650), declined  
321 during the summer (0.582) and fall (0.525), but increased again during the winter (0.557; Table  
322 3). During spring, the 95% confidence interval for individual specialization was entirely greater  
323 than 0.6, suggesting strong among-individual diet variation for lake whitefish (Table 3). For all  
324 other seasons, the 95% confidence intervals for the specialization values were between 0.5 and  
325 0.6 suggesting moderate among-individual diet variation (Table 3).

326

### 327 *Comparison with other Lake Superior lake whitefish diet studies*

328 The extent to which lake whitefish in Lake Superior relied on *Diporeia* and *Mysis* varied  
329 across studies (Table 4). In some studies, *Diporeia* composed a higher percentage of stomach

330 contents than *Mysis* (Anderson and Smith, 1971; Rennie et al., 2012); in other studies, however,  
331 *Mysis* composed a higher percentage of stomach contents than *Diporeia* (Gamble et al., 2011).  
332 Our findings were intermediate between these studies with *Diporeia* composing a larger  
333 percentage of stomach contents than *Mysis* in spring, with the opposite being true in the other  
334 seasons. The percentages that *Diporeia* composed of stomach contents in our study for summer,  
335 fall, and winter seasons were on the lower end of what was reported in most other studies (Table  
336 4).

337 For most studies, *Diporeia* and *Mysis* composed the majority of stomach contents by wet  
338 weight or volume, with the highest reported percentages by Gamble et al. (2011) across all  
339 assessed seasons (> 90%), Rennie et al. (2012) for the Thunder Bay region of Lake Superior in  
340 2005 (79%), and Anderson and Smith (1971) for western Lake Superior during the winter (78%;  
341 Table 4). Conversely, *Diporeia* and *Mysis* were found to compose between 0 and 12% of lake  
342 whitefish diets collected from western Lake Superior in winter and spring months (Stockwell et  
343 al., 2014; Table 4). Again, our results were intermediate between these extremes. During  
344 summer, we found that *Diporeia* and *Mysis* composed almost three-quarters of the stomach  
345 contents of fish, but during the other seasons these items composed one-third to one-half of fish  
346 stomach contents. The percentages that *Diporeia* and *Mysis* composed stomach contents in our  
347 study for summer, fall, and winter seasons were on the lower end of what was reported in most  
348 other studies with the exception of Stockwell et al. (2014) and Rennie et al. (2012) for the  
349 Apostle Islands region of Lake Superior (Table 4). Little consistency among studies was evident  
350 as to which season lake whitefish were most reliant on *Diporeia and Mysis*. In some studies,  
351 winter was the season when *Diporeia* and *Mysis* composed the largest percentage of stomach  
352 contents (Anderson et al., 1971), whereas in other studies *Diporeia* and *Mysis* were not found in  
353 stomachs during the winter months (Stockwell et al., 2014).

354 With respect to sphaeriids, none of the other diet studies of Lake Superior lake whitefish  
355 reported this item composing more than 15% of consumed items (Table 4). Conversely, we  
356 found sphaeriids composed between 20 and 30% of stomach contents across seasons.

357 The extent that fish eggs were consumed by lake whitefish was highly variable among  
358 studies, although this could reflect when fish were collected for the different studies or the  
359 typically low sample sizes in winter. In western Lake Superior during winter months, coregonid  
360 eggs composed 99% of stomach contents; during spring the contribution of fish eggs declined to

361 15% of stomach contents (Stockwell et al., 2014; Table 4). We observed the second highest  
362 percentage (27%) of fish eggs composing stomach contents; this also occurred during winter.  
363 During spring, the contribution declined to 3%. As indicated previously, we suspect that fish  
364 eggs consumed in our study were mostly from cisco or other coregonid species. The only other  
365 Lake Superior diet study to report consumption of fish eggs was from western Lake Superior in  
366 the 1960s during winter months (Anderson and Smith, 1971). In that study, coregonid eggs  
367 composed 3% of stomach contents (Anderson and Smith, 1971; Table 4).

368 With respect to other items that were consumed by Lake Superior lake whitefish,  
369 copepods, ostracods, chironomids, and plant material were reported in diets in western Lake  
370 Superior in the 1960 (Anderson and Smith, 1971). Chironomids and leeches were also reported  
371 in diets in western Lake Superior in spring in the 2010s (Stockwell et al., 2014). For the Apostle  
372 Islands region of Lake Superior in summer 2004, *Bythotrephes*, chironomids, and plant material  
373 were other diet items that lake whitefish consumed (Rennie et al., 2012). For the Thunder Bay  
374 region of Lake Superior in 2005, chironomids and plant material were consumed by lake  
375 whitefish (Rennie et al., 2012).

376

### 377 *Trends in fish condition over time*

378 For all evaluated quantiles, the allometric growth model with the lowest AIC value was  
379 the model with separate coefficients for each of the four decades. The second-best performing  
380 model across all evaluated quantiles was the model with unique coefficients for the 1980s and  
381 1990s and combined coefficients for the 2000s and 2010s. However, the delta AICs for the  
382 second-best performing models across the evaluated quantiles ranged from 40 to approximately  
383 180, which indicated essentially no empirical support for these models based on available data  
384 (Burnham and Anderson, 2002).

385 Based on the predicted weights from the quantile regressions of the allometric growth  
386 model with decade as a categorical grouping factor, condition (i.e., expected weight-at-length) of  
387 Lake Superior lake whitefish collected off the Keweenaw Peninsula increased from the 1980s to  
388 1990s, but subsequently declined in the 2000s. For the 400- and 500-mm reference length  
389 categories, condition also was lower in the 2010s than it was in the 2000s (Figure 5). For the  
390 400-mm reference length, expected weights in the 1990s were between 1 and 25 g greater in the  
391 1990s than in the 1980s depending on the evaluated quantile. However, expected weights in the

392 2000s were between 27 and 46 g less than in the 1990s depending on the evaluated quantile;  
393 expected weights in the 2010s were between 54 and 66 g less than in the 2000s (Figure 5). For  
394 the 500-mm reference length, expected weights in the 1990s were between 55 and 76 g greater  
395 than in the 1980s, but were between 84 and 112 g less in the 2000s than in the 1990s. Expected  
396 weights were 13 to 34 g less in the 2010s than in the 2000s for the 500-mm reference length. For  
397 both the 400 and 500-mm reference lengths, expected weights at length were lower in the 2000s  
398 and 2010s than in the 1980s (Figure 5).

399 For the 600-, 700-, and 800-mm reference lengths, expected weights increased by  
400 approximately 100 to 230 g (600 mm), 173 to 502 g (700 mm), and 270 to 918 g (800 mm) from  
401 the 1980s to 1990s depending on the evaluated quantile with the largest increases generally for  
402 the upper quantiles. In the 2000s and 2010s, expected weights declined to the levels observed in  
403 the 1980s (Figure 5). For the 600-mm reference length, expected weights in the 2010s were only  
404 around 22 to 52 g less than what observed in the 1980s. For the 700-mm reference length,  
405 differences in expected weights in the 2010s compared to the 1980s ranged from -39 to +64 g  
406 depending on the evaluated quantile. For the 800-mm reference length, differences in expected  
407 weights in the 2010s compared to the 1980s ranged from -3 to +221 g depending on the  
408 evaluated quantile.

409

## 410 **Discussion**

411 Our expectation was that diets of lake whitefish collected off Lake Superior's Keweenaw  
412 Peninsula would be heavily dominated by *Mysis* and *Diporeia*. Although our findings partly  
413 aligned with these expectations, the extent to which lake whitefish relied on these prey types was  
414 perhaps not as high as initially expected. Rather, we found lake whitefish to exhibit more of a  
415 mixed feeding strategy, with *Diporeia*, *Mysis*, and fish eggs strong contributors to the diet but  
416 other prey types contributing as an apparent result of varying degrees of specialization (e.g., fish,  
417 terrestrial invertebrates) and generalization (e.g., sphaeriids). A similar mixed feeding strategy  
418 was reported for lake whitefish from Lake Huron post-*Dreissena* invasion (Pothoven and  
419 Nalepa, 2006). Seasonally, lake whitefish appeared to shift feeding from *Diporeia* during the  
420 spring to *Mysis* and fish eggs in the fall and winter. Although items such as *Diporeia*, *Mysis*, and  
421 sphaeriids composed the majority of fish diets across the seasons, the apparent specialization on  
422 fish and terrestrial invertebrates by some individuals suggests some opportunistic foraging

423 behavior by lake whitefish, which has also been reported in lake whitefish diet studies conducted  
424 in waterbodies after *Dreissena* establishment (Pothoven and Nalepa, 2006; Herbst et al., 2013).

425 One possible reason why our results did not align with expectations was that we  
426 underestimated the variability in previous descriptions of Lake Superior lake whitefish diets. In  
427 particular, we did not expect *Diporeia* and *Mysis* to range from 0 to nearly 100% of lake  
428 whitefish diets (Gamble et al., 2011; Stockwell et al., 2014). One factor that could contribute to  
429 this variability across studies is the small number of non-empty stomachs examined in some  
430 previous studies ( $n < 30$ ), which raises a question as to representativeness of lake whitefish diets  
431 in these studies. Also, as described in greater detail below, diet studies such as those conducted  
432 on Lake Superior lake whitefish provide only a coarse snapshot of what fish are consuming  
433 because they only reflect what fish consumed within a couple of hours of capture (Bolnick et al.,  
434 2002). Despite this unexpected amount of variability, the percentages of fish diets consisting of  
435 *Diporeia* and *Mysis* in our study during the spring, fall, and winter months (37 to 59%) were on  
436 the lower end of what most other Lake Superior lake whitefish diet studies have reported (57% to  
437 100%; Anderson and Smith, 1971; Gamble et al., 2011; Rennie et al., 2012). Conversely, we  
438 found sphaeriids composed a larger percentage of stomach contents than what other Lake  
439 Superior lake whitefish diet studies have reported.

440 Our observation that lake whitefish consumed fish eggs during winter and spring matches  
441 observations from previous Lake Superior studies, although the extent to which fish may rely on  
442 fish eggs during these seasons is uncertain. Similar to the results for *Diporeia* and *Mysis*, the  
443 percentage of fish eggs in diets of lake whitefish was highly variable (3 to 99%) across studies  
444 (Anderson and Smith, 1971; Stockwell et al., 2014). In Lake Champlain, rainbow smelt and  
445 coregonid eggs were consumed by lake whitefish during the spring, composing around 42% of  
446 fish diets by weight for individuals  $< 800$  g (Herbst et al., 2013). From an energetic standpoint,  
447 fish eggs have very high energy densities compared to other items consumed by lake whitefish  
448 (Stockwell et al., 2014). Consequently, even if fish eggs do not compose a majority of fish diets  
449 by weight during the winter in Lake Superior, a majority of the seasonal energetic intake of lake  
450 whitefish could be derived from this food source (Stockwell et al., 2014).

451 As with any diet study, the representativeness or scalability of our results may be limited  
452 by where and how data were collected. First, lake whitefish were only collected off the  
453 Keweenaw Peninsula of Lake Superior. While this region has been an important spawning and

454 rearing area for lake whitefish in Lake Superior (Goodyear et al., 1982), our ability to draw  
455 definitive conclusions when comparing our results to previous studies or to other areas of Lake  
456 Superior is limited. As well, because we collected lake whitefish with gill nets, our results could  
457 be biased against certain prey types, such as soft-bodied organisms, because they may be  
458 digested more quickly than other prey types while fish were entangled in the gear (Garvey and  
459 Chipps, 2012). Regurgitation of stomach contents during gillnet entanglement also could be a  
460 factor influencing our study results (Sutton et al., 2004; Treasurer, 1988). Additionally, the vast  
461 majority of our samples ranged from 400 to 600 mm in length, which were the sizes of fish most  
462 selected by the assessment and commercial fishing nets. Consequently, our ability to make  
463 inferences regarding fish diets is limited to lake whitefish within this length range. Finally, any  
464 study that relies on field capture of individuals provides only a coarse snapshot of diet because  
465 observed prey items are only those that were consumed within a couple of hours of capture; as a  
466 consequence, the observed diets may not reflect actual fish consumption over the assessed time  
467 period. In particular, this snapshot approach to characterize diets may skew results towards  
468 inferences of specialized feeding strategies as even a generalist predator will likely take  
469 advantage of a readily available prey resource when presented with the opportunity (Bolnick et  
470 al., 2002).

471         Given that we do not have diet data for lake whitefish from the Keweenaw Peninsula  
472 region of Lake Superior from years prior to this study, we do not know how different  
473 contemporary lake whitefish diets are from earlier time periods. Further, the variability in results  
474 from other lake whitefish diet studies in Lake Superior and the fact that studies were generally  
475 conducted in different locations and at least 5 years apart makes comparisons with earlier studies  
476 also challenging. Despite these limitations, the differences that we observed in lake whitefish  
477 diets from the Keweenaw Peninsula region of Lake Superior versus other studies from the lake  
478 warrants further investigation. In particular, the lower percentage that *Diporeia* and *Mysis* in lake  
479 whitefish diets and the higher percentage of sphaeriids we observed, compared to what other  
480 studies have found for some regions of the lake, may be of concern. In the lower Great Lakes,  
481 lake whitefish shifted from feeding heavily on *Diporeia* to consuming items such as *Dreissena*,  
482 sphaeriids, chironomids, and gastropods after *Dreissena* invasion (Pothoven et al., 2001),  
483 although immediately after invasion lake whitefish in some lakes initially shifted to consuming  
484 *Mysis* (Owens and Dittman, 2003; Pothoven et al., 2001). In Lakes Huron and Michigan, post-



485 invasion consumption of mollusks (i.e., *Dreissena*, gastropods, and sphaeriids) was 2 to 5 times  
486 greater during the post-invasion period than pre-invasion (Pothoven and Madenjian, 2008). If  
487 consumption of sphaeriids in the Keweenaw Peninsula is increasing while consumption of  
488 *Diporeia* and *Mysis* is decreasing, this could be problematic because the energy density of  
489 sphaeriids is approximately 60 to 70% lower than that of *Diporeia* and *Mysis* (Kočovský, 2019;  
490 Madenjian et al., 2006; Rennie et al., 2012). In the lower Great Lakes, shifts in feeding of lake  
491 whitefish and other species towards food resources with lower energy densities post *Dreissena*  
492 invasion led to reductions in whole body energy densities (Pothoven et al., 2006; Rennie et al.,  
493 2012). Consequently, we would expect similar declines in lake whitefish energy densities in the  
494 Keweenaw Region of Lake Superior if conditions shifted to push lake whitefish to rely more  
495 heavily on sphaeriids than *Diporeia* and *Mysis*.

496         Although we do not have historical or current energy density for lake whitefish from the  
497 Keweenaw Peninsula region of Lake Superior, our condition estimates for lake whitefish based  
498 on the fitted allometric growth model suggests energy densities for at least some sizes of lake  
499 whitefish in the region have declined. Our expectation at the outset of this research was that  
500 current and historical condition (i.e., expected weight-at-length) of lake whitefish would be  
501 similar under the prevailing belief that lake whitefish were not under the influence of stressors  
502 that have been affecting lake whitefish populations in the other Great Lakes. Our expectations  
503 were supported for lake whitefish in the 600-, 700-, and 800-mm length categories, but were not  
504 supported for lake whitefish in the 400- and 500-mm length categories. The distributions of  
505 weights at the 400- and 500-mm lengths in the 2010s were approximately 10% lower than they  
506 were in the 1990s and 5% lower than they were in the 1980s. The decrease in condition from the  
507 1990s to 2010s for these two length groups is comparable to decreases in condition in lake  
508 whitefish in the lower Great Lakes after *Dreissena* invasion (DeBruyne et al., 2008; Lumb et al.,  
509 2007; Pothoven et al., 2001). For the 600-, 700-, and 800-mm length categories, the distributions  
510 of weights in the 2010s were also approximately 10% lower than they were in the 1990s, but  
511 were equivalent or slightly greater in the 2010s compared to the 1980s. Why lake whitefish  
512 condition in the 1990s was so much greater than the other time periods across all evaluated  
513 length categories is unclear. *Diporeia* densities in Lake Superior were approximately 7 times  
514 greater in the 1994 than in 1973 and approximately 5 times greater in the region from the  
515 Keweenaw Peninsula to Grand Island (Scharold et al., 2004), suggesting that higher condition

516 could have stemmed from an abundance of a preferred food resource. Improvements in water  
517 quality in Lake Superior stemming from enactment of the Great Lakes Water Quality Agreement  
518 in the early 1970s (Bellinger et al., 2016; Jeremisaon et al., 1994; Scharold et al., 2004) also  
519 could have contributed to the high condition of fish in the 1990s.

520 The factors contributing to the decline in condition for lake whitefish in the 400- and  
521 500-mm length categories in the Keweenaw Peninsula region of Lake Superior are uncertain.  
522 Several hypotheses are possible, including intra- or inter-specific competition caused by fish  
523 abundance changes or declines in availability of energetically-profitable prey, environmental  
524 changes (e.g., warming water temperature), or condition-dependent selective predation to name a  
525 few. Based on catch-per-effort statistics for commercial gillnet fisheries operating in the  
526 Keweenaw Peninsula region of Lake Superior, relative abundance of lake whitefish in the region  
527 has declined since the mid- to late-2000s (Mattes, 2019). Consequently, intra-specific  
528 competition caused by increasing lake whitefish abundance is likely not contributing to changes  
529 in fish condition. *Diporeia* density in the region extending from the Keweenaw Peninsula to  
530 Grand Island in Lake Superior declined from 1,697/m<sup>2</sup> (SE = 228/m<sup>2</sup>) in 1994 to 1,268/m<sup>2</sup> (SE =  
531 208/m<sup>2</sup>) in 2000 (Scharold et al., 2004). In this same general region of Lake Superior, *Diporeia*  
532 densities ranged from 619 to 1,200/m<sup>2</sup> in the 2000s (Auer et al., 2013). While these studies  
533 provide some empirical support that an important food resources for lake whitefish in this region  
534 of Lake Superior may have declined from the 1990s to 2000s, changes in prey density alone does  
535 not prove that resources were sufficiently limiting to lead to competition for resources and/or  
536 declines in condition. If intra- or interspecific competition for *Diporeia* or *Mysis* were  
537 contributing to declines in lake whitefish condition, the reason for the decline to be limited to  
538 just certain sizes of lake whitefish is not clear. In northern and central Lake Michigan, condition  
539 of lake whitefish larger than 650 mm did not differ between pre- and post-*Dreissena* invasion  
540 time period even though condition of fish less than 650 mm was significantly lower during the  
541 post-*Dreissena* time period when lake whitefish were likely competing for food resources  
542 (DeBruyne et al., 2008). Thus, the recent declines in condition in subsets of lake whitefish length  
543 categories we observed could indicate competition or limited prey availability. The warming  
544 water temperatures of Lake Superior also could be a factor contributing to declines in condition  
545 (Rennie et al., 2010; Rennie, 2013). In a study evaluating lake whitefish populations across  
546 multiple lakes within Ontario, fish condition was found to decline in populations in northwest

547 Ontario where temperatures had warmed considerably whereas condition was more stable in  
548 southern Ontario where warming had not been as dramatic (Rennie et al., 2010). As with the  
549 hypothesis that intra- or interspecific competition could be contributing to declines in condition,  
550 why warming temperatures would only affect condition in certain length categories rather than  
551 across all evaluated lengths is uncertain. Condition-selected mortality due to natural (i.e.,  
552 predation) or fishery-related causes, where fish in the best condition and a limited length range  
553 are targeted, could also be a factor contributing to lower condition by exerting selection pressure  
554 towards individuals with lower than expected weights in the 400- and 500-mm length categories  
555 (Uusi-Heikkilä et al., 2016; Wang and Höök, 2009). Based on the relationship for maximum  
556 consumable prey length versus predator length presented in Stockwell et al. (2010), lake trout  
557 would need to be between 750 and 1,125 mm to prey on lake whitefish between 400 and 600 mm  
558 in length, which suggests if condition-selected mortality stemming from predation was a factor  
559 than it would be caused by predation from the largest segments of the lake trout populations.  
560 According to Ebener et al. (2008), commercial fisheries for lake whitefish in the Great Lakes  
561 region may also be selective for fish in better condition because processors pay higher prices per  
562 unit weight for larger fish, which also could result in some selection pressure on lake whitefish  
563 populations in this Lake Superior region.

564 While the mechanisms that are contributing to declining condition in some sizes of lake  
565 whitefish off the Keweenaw Peninsula region of Lake Superior are not known, the occurrence of  
566 these declines, in combination with declines in condition and growth that have been observed in  
567 other parts of Lake Superior (Rennie, 2013), have potentially important management  
568 consequences. Declines in condition and growth, similar to what we observed here for the 400-  
569 and 500-mm length categories, preceded declines in lake whitefish recruitment in Lakes Ontario  
570 (Hoyle et al., 1999, 2005), Huron (Mohr and Ebener, 2005), and Michigan (Nalepa et al., 2005a;  
571 Pothoven et al., 2001). Reduced recruitment levels have led to declines in abundances and  
572 commercial catch rates and yields in Lakes Huron and Michigan (Great Lakes Fishery Trust and  
573 Great Lakes Fishery Commission, 2018); similar declines, if they were to occur on Lake  
574 Superior, could have major ramifications on commercial and tribal fisheries. We recommend  
575 expanded spatial and temporal assessment of prey resource availability, environmental  
576 conditions, and consumption by lake whitefish and potential competitor species to permit  
577 ongoing monitoring of conditions that could affect future recruitment levels in lake whitefish

578 populations. We also recommend expanded monitoring of fish growth, condition, and mortality  
579 levels for determining how stable lake whitefish population dynamics and demographics are in  
580 the system. Finally, we echo the recommendation from Rennie (2013) for expanded research,  
581 including cross-region and cross-lake analyses, to try and identify what stressors might be  
582 leading to changes in fish condition in Lake Superior to assist in determining what fishery  
583 management actions might help protect populations and fisheries.

584

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595

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875 Table 1. Categories used to describe lake whitefish diets and the description of the items  
 876 composing these categories. Diet categories are from a categorization system developed and  
 877 agreed upon by the Lake Superior Technical Committee (Lake Superior Technical Committee,  
 878 unpublished report).

Reporting Category	Description
Coregonid	<i>Coregonus</i> spp.
Burbot	<i>Lota lota</i>
Smelt	<i>Osmerus mordax</i>
Sculpin	Cottidae spp.
Stickleback	<i>Gasterosteus aculeatus</i>
<i>Mysis</i>	<i>Mysis diluviana</i>
<i>Diporeia</i>	<i>Diporeia</i> spp.
Terrestrial	Non-aquatic insects
Unknown Fish	Unidentifiable fish spp.
Eggs	Fish eggs
Sphaeriids	Sphaeriidae
Other	

879

880 Table 2. Schoener index values comparing diet similarities between seasons for lake whitefish  
881 collected off the Keweenaw Peninsula of Lake Superior. Values in parentheses are the lower and  
882 upper 95% confidence limits (CL).

Comparison	Diet Overlap Index
Spring vs Summer	0.631 (0.524 - 0.735)
Spring vs Fall	0.349 (0.258 - 0.435)
Spring vs Winter	0.486 (0.374-0.602)
Summer vs Fall	0.643 (0.521-0.783)
Summer vs Winter	0.426 (0.307-0.580)
Fall vs Winter	0.2667 (0.184-0.389)

883

884 Table 3. Mean Shannon diversity, richness, and individual specialization values overall and by  
 885 season for lake whitefish collected off the Keweenaw Peninsula of Lake Superior. Values in  
 886 parentheses are the lower and upper 95% confidence limits (CL).

Category	Shannon Diversity	Richness	Individual Specialization
Overall	0.285 (0.245 – 0.323)	2.068 (1.976 – 2.162)	0.694 (0.694 – 0.694)
Spring	0.262 (0.204 – 0.318)	2.007 (1.866 – 2.147)	0.650 (0.650 – 0.651)
Summer	0.332 (0.248 – 0.419)	2.201 (1.999 – 2.408)	0.582 (0.580 – 0.584)
Fall	0.217 (0.176 – 0.260)	1.544 (1.419 – 1.670)	0.525 (0.525 – 0.526)
Winter	0.321 (0.212 – 0.410)	2.088 (1.781 – 2.329)	0.557 (0.503 – 0.610)

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889 Table 4. Percentages of lake whitefish diets consisting of *Diporeia*, *Mysis*, sphaeriids, fish eggs,  
 890 and other items from this study and other diet studies from Lake Superior.

Study – Location, Year, and Season (n=number of stomachs with food contents)	<i>Diporeia</i>	<i>Mysis</i>	<i>Diporeia</i> + <i>Mysis</i>	Sphaeriid	Fish Eggs	Other
<b>Anderson and Smith (1971) - Western Lake Superior (1965-1968)</b>						
Dec.-Feb. (n=8)	78%	0%	78%	12%	3%	7%
May-Jul. (n=30)	34%	28%	62%	6%	0%	22%
Sep.-Nov. (n=13)	52%	6%	58%	14%	0%	28%
<b>Gamble et al. (2011)<sup>-1</sup> - Multiple Sites (2005)</b>						
May-Jun. (n=140*)	13%	87%	100%	<1%	0%	<1%
Jul.-Aug. (n=34*)	43%	47%	90%	10%	0%	<1%
Sep.-Nov. (n=48*)	30%	69%	99%	<1%	0%	<1%
<b>Stockwell et al. (2014) – Western Lake Superior (2010-2011)</b>						
Dec.-Jan. (n=31)	0%	0%	0%	NA <sup>-2</sup>	99%	1%
Mar.-Apr. (n=12)	12%	0%	12%	NA <sup>-2</sup>	16%	72%
<b>Rennie et al. (2012)<sup>-3</sup></b>						
Apostle Islands (2004; Summer) (n=NA)	32%	12%	44%	9%	0%	47%
Thunder Bay (2005; Summer) (n=NA)	54%	25%	79%	10%	0%	11%
<b>Present study – Keweenaw Peninsula (2015-2017)</b>						
Dec.-Feb. (n=116)	11%	25%	37%	30%	27%	7%
Mar.-May (n=379)	42%	16%	59%	30%	3%	8%
Jun.-Aug. (n=272)	27%	47%	74%	21%	0%	4%
Sep.-Nov. (n=122)	3%	48%	51%	22%	0%	27%

891 <sup>1</sup>-Percentage of lake whitefish diets consisting of *Diporeia* and *Mysis* for Gamble et al. (2011)  
 892 were reported in Stockwell et al. (2014). Estimated diet percentages for sphaeriids from Gamble  
 893 et al. (2011) were extracted from a published figure using WebPlotDigitizer software  
 894 (<https://automeris.io/WebPlotDigitizer/>)

895 <sup>2</sup>-Percentage of lake whitefish diet consisting of sphaeriids was not reported by Stockwell et al.  
 896 (2014) although it was noted that clams and leeches were included in the other category.

897 <sup>3</sup>- Percentages of lake whitefish diets from Rennie et al. (2012) were calculated excluding  
 898 inorganic material.

899 \* - Number of stomachs reported in Gamble et al. (2011) is the total number of stomachs  
 900 examined, including empty stomachs.

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Figure Captions

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- Figure 1. Locations off the Keweenaw Peninsula of Lake Superior where lake whitefish were collected by commercial fishing and assessment gillnets for diet characterization from 2015-2017. The small grid and accompanying labels are 10-minute grids commonly used in the Great Lakes to denote locations. The larger regions demarcate Lake Superior lake whitefish management units.
- Figure 2. Mean (averaged across years) prey-specific abundance plotted against mean (averaged across years) frequency of occurrence in the diet of lake whitefish collected off the Keweenaw Peninsula of Lake Superior, 2015-2017.
- Figure 3. Percentage by wet weight for each prey type in lake whitefish diets by season (spring: March to May; summer: June to August; fall: September to November; winter: December to February) for fish collected off the Keweenaw Peninsula of Lake Superior, 2015-2017.
- Figure 4. Mean (averaged across years) prey-specific abundance plotted against mean (averaged across years) frequency of occurrence seasonally for lake whitefish collected off the Keweenaw Peninsula of Lake Superior, 2015-2017.
- Figure 5. Predicted weights at 400-, 500-, 600-, 700-, and 800-mm reference lengths of lake whitefish collected off the Keweenaw Peninsula of Lake Superior from quantile regression models fits  $\log_{10}$ -weight versus  $\log_{10}$ -length relationships using decade as a categorical grouping factors. Regressions were fit to quantiles from 0.1 to 0.9 in 0.05 increments.