1   **Long-term survey data reveals large predator and temperature effects on population**

2   **growth of multiple zooplankton species**

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15   **Running Head:** Predator effects on zooplankton populations

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Abstract

Predators can strongly affect prey communities, but their influence may be difficult to distinguish from bottom-up and other environmental effects. The problem of assessing predator impact is especially difficult in large systems that do not allow for comparisons across multiple units (e.g., small lakes) that have varying predator density. For instance, the invasion of the predatory zooplankter, *Bythotrephes longimanus*, into the Laurentian Great Lakes contributed to the nearly complete disappearance of several zooplankton species, but current effects on extant zooplankton are not well understood. We used generalized additive models (GAMs) applied to long-term data time series (1994-2012) to examine *B. longimanus* effects on zooplankton species in Lake Michigan. Because *B. longimanus* abundance varied over time, our approach allowed assessment of predator effects from field data while accounting for other factors, including food resources, temperature and seasonality. Results suggest that *B. longimanus* substantially reduces some zooplankton population growth rates, with the largest effects on species that *B. longimanus* affected more strongly in experiments. For example, at maximum *B. longimanus* abundance, *Daphnia mendotae*, *Bosmina longirostris*, and *Diacyclops thomasi* population growth rates were estimated to be reduced by 17%, 30%, and 21%, respectively, compared to no effect on calanoid copepods. Results further indicated positive temperature effects on population growth that differed by species. Our study thus provides field-based evidence for ongoing impacts of invasive species and temperature on zooplankton production and composition, with potential consequences for planktivorous fish, and exemplifies how GAMs can be used to determine predator effects from time series data.

Introduction

Predation can fundamentally shape population dynamics and community structure through effects on demographic rates. Such effects arise from both consumption, which may differentially affect species (Holt 1977), as well as induced changes in prey traits (e.g., habitat use or growth rates, Peacor et al. 2012; Lagrue et al. 2015). Short-term experiments or surveys can suggest differences among species in both types of predator effects but may provide only limited insights into longer-term dynamical consequences of predator effects in the field. Complementary analyses of long-term, field dynamical data are necessary to assess the extent and consequences of predator effects on prey population growth rates at field-relevant spatial and temporal scales.

Despite the clear need for such analyses for management and conservation, studies of field-scale effects of predators on prey population growth are surprisingly rare except in relatively tightly coupled predator-prey systems (e.g., cycles, Gilg et al. 2003; Krebs 2011) or for cases in which there are multiple units (e.g., lakes or islands) in which the system can be compared in predator absence and presence (e.g., Boudreau and Yan 2003; Blackburn et al. 2004; Peckarsky et al. 2008; Gallardo et al. 2016). A number of systems, however, include persistent prey and predator populations and do not exhibit tight predator-prey coupling yet likely experience chronic effects of predation on population growth. Predator effects in such systems need to be assessed while also accounting for other factors (e.g., temperature, food resources) that may simultaneously influence population growth. One limitation is that although long-term monitoring data do exist (as in Lake Washington, Edmondson et al. 1956; Lake Constance, Straile 2015), such data are relatively rare in studies of ecological communities.

64 Nevertheless, using long-term data to quantify predator effects will be vital to predict population

65 and community dynamics in important ecosystems.

66   For instance, the non-native predatory zooplankter, the spiny water flea (*Bythotrephes*

67 *longimanus*), has received attention for its impact on the zooplankton community in the Great

68 Lakes and other systems (e.g., Barbiero and Tuchman 2004; Kerfoot et al. 2016). For example,

69 comparisons between invaded and non-invaded sites in Canadian lakes (Boudreau and Yan 2003;

70 Strecker et al. 2011) or pre- and post-invasion in a large, Boundary Water lake complex (Kerfoot

71 et al. 2016) reveal large effects of *B. longimanus* on zooplankton communities. Similarly,

72 following its introduction into Lake Michigan during the 1980s, *B. longimanus* was associated

73 with near extinction of the native zooplankton species, *Daphnia pulicaria* and *D. retrocurva*

74 (Lehman and Caceres 1993). Much research since has evaluated effects on common extant

75 zooplankton species in the Great Lakes (e.g., Pangle et al. 2007; Bunnell et al. 2011; Bourdeau et

76 al. 2015). Consumptive effects (CEs) of *B. longimanus* are hypothesized to occur based on

77 experiments that have shown that *B. longimanus* preys upon common zooplankton species

78 (Vanderploeg et al. 1993; Pangle and Peacor 2009), and estimates of *B. longimanus* consumptive

79 requirements using a bioenergetics model suggest that predation is high at or shortly after times

80 when production of some prey species is also high based on egg ratios (Pothoven and

81 Vanderploeg 2018, 2019). In addition, field and laboratory experiments suggest that *B.*

82 *longimanus* can have nonconsumptive effects (NCEs) through effects on traits that lead to

83 reduced growth rates of some species (Pangle and Peacor 2006; Bourdeau et al. 2011). The

84 NCEs occur because zooplankton move from the warmer epilimnion to colder, deeper water to

85 avoid *B. longimanus*, which are typically restricted to the epilimnion, resulting in reduced growth

86 rates. Further, field data on vertical distributions of zooplankton suggest that zooplankton species

87   may differ in realized impacts of both CEs and NCEs, as species differ in spatial overlap with *B.*

88   *longimanus* and the extent of a behavioral response (Bourdeau et al. 2015; Nowicki et al. 2017).

89   Thus, previous studies indicate which zooplankton may serve as preferred prey of *B. longimanus*,

90   that *B. longimanus* occur at high enough densities to consume substantial densities of prey, and

91   that that *B. longimanus* likely affects the population growth rate of some zooplankton species

92   through NCEs. However, previous work has not quantified how *B. longimanus* is contributing to

93   realized changes in prey population growth rates and abundances in the field.

94   Existing time series data for zooplankton offer the opportunity to assess effects of *B.*

95   *longimanus* on community structure and zooplankton production in the field. In particular, time

96   series data can be used to evaluate changes in population growth rates of potential prey species in

97   response to *B. longimanus*, provided there is temporal variation in the abundance of *B.*

98   *longimanus*. A challenge is that other environmental factors, such as temperature and time of

99   year, may be correlated with *B. longimanus*, so it is important to account for a potential

100   confounding effect of such factors in assessing *B. longimanus* effects. An approach is needed

101   that can evaluate multiple predictors simultaneously, including nonlinear terms like seasonality

102   (i.e., change in growth rate with time of year) for which an a priori functional form may be

103   lacking.

104   Here we use such an approach, generalized additive models (GAMs), to address two

105   hypotheses regarding effects of *B. longimanus* on native zooplankton in Lake Michigan. First, *B.*

106   *longimanus* reduces zooplankton population growth rates in Lake Michigan. Second, *B.*

107   *longimanus* has a stronger negative effect on more vulnerable zooplankton species (as

108   determined from laboratory studies).

109

Methods

Data

Data are from a long-term NOAA Great Lakes Environmental Research Laboratory survey of offshore Lake Michigan zooplankton populations. Zooplankton were collected at a site near Muskegon, MI (depth = 110m; 43° 11.99', 086° 34.19'; located about 20 km offshore) via whole water column vertical net tows 7-16 times per year during 1994-2003 and 2007-2012 for a total of 175 collection dates. This date range includes major transitions in Lake Michigan including declines in planktivorous fish that likely reduced predation pressure on *B. longimanus* (Vanderploeg et al. 2012) and major shifts in dreissenid mussel impacts associated with the expansion of quagga mussels (*Dreissena rostriformis bugensis*) into deeper waters after 2004 (Madenjian et al. 2015). Areal densities of different taxa and life stages were calculated for each survey date from counts of subsamples of collected zooplankton. Details on sample collection and processing are described by Vanderploeg et al. (2012).

Estimated population growth rate calculation

We estimated population growth rate for fifteen zooplankton groups that were collected in net tows on a majority of sample dates. The groups included two cladocerans (*Daphnia mendotae* and *Bosmina longirostris*), two adult cyclopoid copepods (*Diacyclops thomasi* and *Tropocyclops prasinus mexicanus*), six adult calanoid copepods (*Leptodiaptomus ashlandi*, *Leptodiaptomus minutus*, *Leptodiaptomus sicilis*, *Limnocalanus macrurus*, *Epischura lacustris,* and *Skistodiaptomus oregensis*), and five groups of earlier copepod life stages (cyclopoid copepodite, diaptomid copepodite, *L. macrurus* copepodite, *E. lacustris* copepodite, and nauplii).

132   We note that the nauplii collected were probably calanoid nauplii, since cyclopoid nauplii are

133   smaller and likely passed through the net (153 μm mesh).

134   Estimated population growth rate (r_t) for each species or life stage group (i) at each time

135   point (t) was calculated (modified from Wetzel 2001):

$$r_{i,t} = \frac{\ln(Z_{i,t+1}) - \ln(Z_{i,t})}{I} \tag{1}$$

136

137   Where $Z_{i,t}$ is the density of an individual group of zooplankton at each time point. I is the time

138   interval between times t and t+1. We note that herein "growth rate" refers to the rate of change in

139   the density of a given species or life history stage and does not necessarily represent total

140   population growth rate, given that individual stages are examined and some groups include

141   multiple species (e.g., nauplii); the specific biological processes reflected in this estimated

142   growth rate may vary between species and life stages. For example, for cladocerans r_t represents

143   population growth rate, but for adult copepods, r_t represents the difference between recruitment

144   from copepodites and mortality. For nauplii and copepodites, r_t represents gains via births (for

145   nauplii) or recruitment from nauplii (for copepodites), with losses from mortality or recruitment

146   to the next developmental stage (copepodite or adult, respectively). This approach contrasts with

147   the egg ratio technique (Edmondson 1968), which allows explicit estimates for birth rates and

148   has been used to examine *D. mendotae* and *B. longirostris* dynamics in Lake Michigan for a

149   subset of years when egg ratio data were available (Pothoven and Vanderploeg 2018).

150   We focus on species densities rather than biomass because the data originated from

151   counts of individuals, which most directly correspond to species densities, while conversions to

152   biomass require additional manipulation that may not be accurate given imperfect knowledge of

153   average size of each species on each date.

154   We selected data to include in the analysis based on the time interval between data points

155   and using a minimum threshold density. The mean ± SD interval between data points within a

156   year was 24 ± 14 days (range: 5-92 days). A 45-day cutoff as the maximum interval between

157   data points was selected to include most points (86%) and as a realistic time window for

158   population change based on known life history parameters for zooplankton (Wetzel 2001). A

159   much longer interval between data points could lead to a less accurate estimate for growth rate.

160   Further, estimates calculated from data points that were based on only a few or no individuals in

161   the sample could also lead to inaccurate estimates for growth rate. At small sample sizes, even a

162   small change in the number of individuals in a net tow due to measurement error could have a

163   large effect on the estimated population growth rate. We therefore limited our analyses to growth

164   rates estimated based on data points where observed density was at least 1400 individuals/m^2

165   (i.e., based on a count of approximately at least 10 individuals per sample), which we expected

166   would reduce the influence of measurement error while allowing for sufficient power (enough

167   data points) to test for predicted effects. The number of growth rate data points for each analyzed

168   species is given in Table 1. Tests using alternative cutoffs for time interval between data points

169   (40 or 50 instead of 45 days) and minimum density (700 or 2800 instead of 1400 individuals/m^2)

170   were also performed to assess the influence of cutoff on our analysis; results were generally

171   consistent regardless of the cutoff used (see Appendix).

172

173   *GAM Analysis*

174   Our goal was to test how the population growth rates of each zooplankton group

175   depended on five factors: group density (i.e., conspecific density for cladocerans or density of

176   individuals belonging to the same zooplankton group for copepods), *B. longimanus* density (Fig.

177   S1a), chlorophyll *a* concentration (Fig. S1b), near-surface (0.5 m depth) water temperature (Fig.

178   S1c), and time of year. Group density could influence population growth rates due to density

179   dependence resulting, e.g., from resource competition. *B. longimanus* density was included to

180   assess its effects as a predator, given previous evidence of its importance in Lake Michigan.

181   Whole water column chlorophyll *a* concentrations were included as a proxy for zooplankton

182   food resources (either phytoplankton or microzooplankton that may track algal resources).

183   Interspecific competition could also have an effect on population growth; however, we expected

184   that interspecific competitive effects may be subsumed by the chlorophyll term, and tests

185   including total zooplankton biomass density as a predictor of growth rates did not indicate an

186   effect on any species. Temperature was included as it is known to affect zooplankton

187   reproduction and other vital rates; we used surface temperature for our analysis, as measurements

188   were available for more dates than other temperature measurements, and surface temperature

189   correlates with epilimnion temperatures, which can influence zooplankton vertical position and

190   potentially therefore also somatic growth and reproduction (Stich and Lampert 1984).

191   Finally, time of year may correlate with many factors that affect growth rate, such as day

192   length, water column structure, and light intensity. Further, zooplankton phenotype (e.g.

193   behavior, life history strategy, morphology) may change as a function of time of year as an

194   adaptive response to seasonal changes in factors such as temperature (e.g., cyclomorphosis,

195   Hutchinson 1957). For this reason, we consider a factor, which we term "seasonality," that

196   captures these many potential seasonal varying factors. A challenge is that while zooplankton

197 growth rate can vary seasonally (Scheffer et al. 1997; Bunnell et al. 2012), the shape of the

198 seasonal function may be more complex than some parametric approximations (e.g., a sinusoidal

199 function). To allow for greater flexibility in the shape of the seasonal growth rate function,

200 GAMs can represent a seasonal effect using a nonparametric function determined using

201 penalized regression splines (Crawley 2013). The other factors for which a reasonable a priori

202 hypothesized functional relationship may be expected (group density, *B. longimanus* density,

203 chlorophyll *a*, and temperature) can be included in a GAM included as parametric (i.e., linear)

204 terms, which allows more straightforward interpretation and comparison with other systems than

205 if those factors were treated as nonparametric terms. All models were fit using the gamm

206 function in the R mgcv package (Wood, 2017a).

207 First, we performed a separate analysis for each zooplankton group for which at least 30

208 data points over the threshold density were available. The following GAM was fit for the growth

209 rate ($r_{i,t}$) of each species i at time t:

$$r_{i,t} = \beta_{0,i} + \beta_{1,i}\ln(Z_{i,t}) + \beta_{2,i}\ln(B_t + 1.27) + \beta_{3,i}\ln(C_t) + \beta_{4,i}T + f_i(DOY)$$
$$+ A_{t,i} + \varepsilon_{t,i}$$

(2)

210 B_t is the density of *B. longimanus* (1.27 is ½ the lowest non-zero observed density, included to

211 account for data points when density is 0), C_t is whole water column chlorophyll *a* concentration,

212 *T* is surface water temperature, and DOY is day of year. $f_i(DOY)$ is a smooth nonparametric

213 function representing seasonality for species i. A_i describes yearly differences in growth rate due

214 to factors not included in the analysis (i.e., a year-specific random effect to account for non-

215 independence of data points from within the same year). For example, another predator in the

216 system for which we do not have data at the same temporal resolution as *B. longimanus*, such as

10

217 planktivorous fish or other predatory invertebrates (e.g., *Leptodora*, *Mysis*), could lead to

218 negative A_i in years when that predator occurs at high density. $\varepsilon_{t,i}$ is a normal error term

219 representing variation unexplained by other model terms. $\ln(Z_{i,t})$ is included to represent density

220 dependence. Group density and *B. longimanus* density were ln-transformed to improve normality

221 and homoscedasticity to meet statistical assumptions (Sokal and Rohlf 2012). An AR1 error

222 structure was also included in the model to account for non-independence of consecutive data

223 points, as consecutive data points may be expected to be correlated due to factors not included in

224 the model (Wood, 2017b), such as phytoplankton composition. The βs are comparable to linear

225 regression coefficients, which indicate how estimated population growth rate changes associated

226 with each factor. We tested for multicollinearity of predictors in the GAM for each species using

227 variance inflation factors (Sheather 2009).

228   Second, we fit a GAM including multiple species in a single model, to test whether

229 effects of each predictor differed among species, corresponding to our second hypothesis. This

230 multi-species GAM followed the general format as for the single species GAM, with population

231 growth rate as the response variable and included group density, *B. longimanus*, chlorophyll *a*,

232 and temperature as predictors. However, the multi-species model also included additional

233 predictors for species identity and interactive effects of each predictor and species identity (i.e.,

234 species x group density, species x *B. longimanus*, species x chlorophyll *a*, and species x

235 temperature). A significant species x predictor interaction would suggest differential effects of

236 each predictor on each species. Further, the multi-species GAM also included species-specific

237 smoothing functions allowing for species-specific seasonal variation in growth rate. Different

238 smoothing functions are fit for each species because seasonal changes in growth rate are

239 expected to be different for each zooplankton group. The analysis included cladocerans and adult

240   copepods (i.e., excluding nauplii and copepodites) of the 7 species for which we had at least 50

241   data points for estimated population growth rate (*D. mendotae*, *B. longirostris*, *D. thomasi*, L.

242   *sicilis*, *L. minutus*, *L. ashlandi*, and *L. macrurus*). A higher cutoff (50 data points) was used for

243   the multi-species analysis than the single-species analysis (30 data points) because we wanted to

244   maximize our power to detect species differences in the multi-species analysis, while we sought

245   to examine as many groups as possible for the single species analysis.

246   Values for predictors used in the analysis were measurements contemporaneous with the

247   first of the two data points for zooplankton density used for each calculated growth rate (i.e.,

248   measured at time t), in line with similar analyses of estimated growth rates in other systems

249   (Sibly and Hone 2002). An alternative would be to use an average value for each predictor

250   calculated across multiple data points (e.g., averaged across time t and t+1), although caution

251   would be necessary to avoid inferring an effect of a predictor based on data points that occurred

252   subsequent to the measured response variable, as growth rate at time t logically cannot depend on

253   data points at time t+1. Further, tests that we performed indicated that using a geometric mean

254   for predictors across times t and t+1 resulted in no improvement and frequently substantially

255   poorer model performance for each species based on the Akaike Information Criterion, a

256   measure of model quality (i.e., ability to fit the data relative to the number of parameters),

257   compared to using measurements contemporaneous with the first data point. For example, using

258   the geometric mean of predictors in the GAM for *D. mendotae* growth rate increased AIC by

259   44.4 units, which indicates a large drop in model performance.

260   Surface temperature data were not available for 2 dates and chlorophyll *a* data were not

261   available for 33 dates. For chlorophyll *a*, the first data point in 1994 and last data point in 2012

262   were included in the missing data, so we assumed that those values were equal to those measured

263   during the second and penultimate sampling dates, respectively. Other missing data points for

264   chlorophyll *a* and all missing data points for temperature were interpolated linearly from the

265   nearest data points in the time series data for each variable.

266   Another important consideration is that whereas an effect of density on growth rate

267   detected by our analysis could result from biological density dependence (e.g., to conspecific

268   competition for food resources), it could also result from a confounding effect of measurement

269   error. Quantifying density dependence from time series data can be challenging in the presence

270   of measurement error (Dennis and Taper 1994; Freckleton et al. 2006). For instance, in a

271   population with actual growth rate = 0, when the observed density (Z_t) happens to be higher than

272   the actual density due to measurement error, the next data point (Z_{t+1}) would most likely be

273   lower than the (Z_t), assuming measurement errors on different dates are independent.

274   Consequently, a bias of lower estimated growth rate increases with increasing observed densities

275   (i.e., regression to the mean, Kelly and Price 2005). As measurement error is inevitably present

276   in field data collection, an estimated effect of density here may thus partly reflect an artifact of

277   measurement error.

278

279   **Results**

280   To visualize how estimated population growth rate was calculated, we present *D.*

281   *mendotae* and *B. longimanus* density data and the corresponding estimated *D. mendotae* growth

282   rate (using Eq. 1) for an example year (2002; Fig. 1). In this example, estimated growth rate

283   peaks early in the growing season corresponding to the largest observed change in log-scale

284   density. We then show the relationship between estimated growth rate and *B. longimanus* density

285   (Fig. 2) for a subset of zooplankton groups for which a significant effect of *B. longimanus* was

13

286 found in the GAM analysis (see below). Although a negative relationship between each species

287 growth rate and *B. longimanus* density may be suggested for the species shown in these plots, a

288 large amount of noise is present that may be explained by potential confounding factors. The

289 following GAM analysis accounts for these potentially confounding factors and thereby better

290 isolates the *B. longimanus* effect.

291   The GAM analyses for each zooplankton group provided estimates for how each factor

292 affected each zooplankton group. In particular, population growth rates of two cladocerans (*D.*

293 *mendotae* and *B. longirostris*) and one adult cyclopoid copepod (*D. thomasi*) were negatively

294 associated with *B. longimanus* density (Table 1; Fig. 3), while other zooplankton groups were

295 not significantly associated with *B. longimanus*. Estimates for β_2 indicate the magnitude of the

296 *B. longimanus* effect (Table 1). Based on the estimates for β_2, an increase in *B. longimanus*

297 density from 0 to its peak (2247 *B. longimanus*/m^2) would reduce population growth rate by 17%

298 for *D. mendotae*, 30% for *B. longirostris*, and 21% for *D. thomasi* from maximum estimated

299 population growth rates; the mean *B. longimanus* density across dates that were included in the

300 analysis for each species (i.e., excluding points that did not meet the minimum density threshold)

301 would result in a 10% reduction for *D. mendotae*, 15% for *B. longirostris*, and 10% for *D.*

302 *thomasi*. Estimated growth rates of zooplankton groups were also affected by the other factors

303 included in our analysis. Estimated growth rates of 13 of the 15 zooplankton groups were

304 negatively associated with the density of their group (Table 1). For chlorophyll *a*, only growth

305 rates of *L. minutus* increased with whole water column chlorophyll *a* concentration, while no

306 significant effect was observed for other species (Table 1). Estimated growth rate also increased

307 with surface temperature for three zooplankton groups, with increases in maximum growth rate

308 of 3.1%, 1.6%, and 0.88% per 1 ˚C increase in temperature for *D. mendotae*, *D. thomasi*, and *L.*

309   *sicilis*, respectively (Table 1; Fig. 4). Finally, six groups showed significant seasonal variation in

310   population growth rate (Table 1; Fig. 5), with responses varying from linear increases (*L. sicilis*)

311   or decreases (*D. mendotae*) with day of year, or more complex, nonlinear relationships (e.g., *L.*

312   *ashlandi*, *L. minutus*, *L. macrurus* copepodites, and *E. lacustris* copepodites).

313   Variance inflation factors (VIFs) were used test for multicollinearity in our analyses. VIF

314   > 5 indicates potential problems in coefficient estimation due to multicollinearity (Sheather

315   2009), which was the case for only 3 predictors (surface temperature for *L. minutus* and *L.*

316   *ashlandi* and *B. longimanus* for *L. macrurus* copepodids) of 60 total predictors across the 15

317   groups. None of these 3 predictors significantly affected estimated growth rate when included in

318   the model (Table 1), and removing these terms from the GAM for each species did not

319   substantially affect the results for other predictors. Consequently, and because VIFs for the other

320   predictors were relatively low (VIF < 5, Sheather 2009), multicollinearity therefore unlikely

321   influenced our results

322   Finally, the multi-species analysis indicated that species differed in estimated effects of

323   *B. longimanus*, group density, and temperature, but not chlorophyll *a* (interaction terms in Table

324   2).

325

326   **Discussion**

327   Our results suggest that the population growth rates of major zooplankton groups in Lake

328   Michigan differentially depend on *B. longimanus* density and other environmental factors and

329   that *B. longimanus* has negatively affected several common species. In particular, the lower *D.*

330   *mendotae*, *B. longirostris*, and *D. thomasi* population growth rates associated with higher *B.*

331   *longimanus* density indicate that these species likely experience consumptive or nonconsumptive

332   effects. These findings build upon previous studies that showed major effects of *B. longimanus*

333   on the zooplankton community immediately after its introduction into Lake Michigan (Lehman

334   and Caceres 1993), other Great Lakes (Barbiero and Tuchman 2004; Barbiero et al. 2019), and

335   inland lakes (Boudreau and Yan 2003; Strecker et al. 2011; Kerfoot et al. 2016). However, our

336   results are distinct from previous studies because we address the current effects on population

337   growth rates rather than comparing different systems with and without *B. longimanus*, comparing

338   the same system before and after the invasion of *B. longimanus*, or using egg ratio methods to

339   probe *B. longimanus* effects on birth rates. Our analysis further exemplifies the utility of using

340   GAMs to examine how factors such as predators affect population dynamics by evaluating

341   chronic effects of a predator in a single large system, while also quantifying the effects of other

342   key factors, which may be generally useful in other systems (e.g., marine systems) with ongoing

343   long-term monitoring efforts.The estimated reductions in population growth rate caused by *B.*

344   *longimanus* are expected to cause substantial reductions in population density. For example,

345   excluding the influence of other factors, we can calculate the expected population density for

346   each species after a month of population growth in absence and presence of *B. longimanus*. If we

347   assume the growth rate equals the average growth rate across the time series, we can apply our

348   estimate for β_2 from the GAM analysis for the reduction of growth rate due to B. *longimanus*.

349   This exercise yields that *D. mendotae, B. longirostris*, and *D. thomasi* densities would

350   respectively be reduced by 52%, 80%, and 65% at mean *Bythotrephes longimanus* densities

351   (averaged across dates when each species occurs above the threshold density) and 71%, 96%,

352   and 90% at maximum *B. longimanus* densities over 30 days. Clearly, these are very large

353   predicted reductions in zooplankton densities that would be expected to affect zooplankton

354   composition and influence other organisms (e.g., fish) that prey on zooplankton. Effects of *B.*

355 *longimanus* may be particularly large, as defenses may be stronger against native predators (e.g.,

356 *E. lacustris*, *Leptodora kindtii*, and *L. macrurus*) than exotics like *B. longimanus* (Kerfoot and

357 Savage 2016). Variation in *B. longimanus* densities over time (e.g., due to declines in predation

358 on *B. longimanus* from planktivorous fish after the quagga mussel expansion, Vanderploeg et al.

359 2012) may thus have large consequences for other components of the food web.

360   Our analyses focus on effects of *B. longimanus* after it had already invaded and become

361 established in the lake and thus do not examine the initial impacts of *B. longimanus* that led to

362 the near extirpation of *D. pulicaria* and *D. rectrocurva* (Lehman and Caceres 1993). Comparing

363 a system before and after the invasion of a predator yields insight into both these initial impacts

364 and continued effects of the predator, as the sustained low densities of the rare species are likely

365 due to continued effects of the predator. Our analyses did not address effects on the rare, nearly

366 extirpated species, and thus do not represent the total effects of *B. longimanus* on the

367 zooplankton community. Our results, rather, suggest strong, ongoing *B. longimanus* effects on

368 species that persist at relatively higher densities in its presence.

369   The differences among *B. longimanus* effects on zooplankton groups observed here are

370 generally consistent with previous studies. In addition, prior work has indicated that the 3 species

371 that experienced strong, negative effects of *B. longimanus* here (*D. mendotae*, *B. longirostris*,

372 and *D. thomasi*) are likely to experience *B. longimanus* consumptive or nonconsumptive effects.

373 Direct consumptive effects of *B. longimanus* on *Daphnia* spp. and *Bosmina* are expected since

374 they are favored prey of *B. longimanus* (Vanderploeg et al. 1993; Schulz and Yurista 1998). *D.*

375 *mendotae* has been shown to be susceptible to predation by *B. longimanus* (Pangle and Peacor

376 2009) and also likely experiences nonconsumptive effects (Pangle et al. 2007). Further,

377 predation requirements of *B. longimanus* are likely high and coincide with peaks in *D. mendotae*

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378   and *B. longirostris* production based on egg ratios (Pothoven and Vanderploeg 2018, 2019). *B.*

379   *longirostris* is also a favored prey item for *B. longimanus* (Vanderploeg et al. 1993) and both *B.*

380   *longirostris* and *D. thomasi* occur deeper in the water column when *B. longimanus* is more

381   abundant, which may lead to NCEs (Bourdeau et al. 2015). In contrast to these three species, the

382   analysis did not detect an effect of *B. longimanus* on other groups for which an effect would not

383   be expected. For example, we found no effect of *B. longimanus* on copepod nauplii, which are

384   not a favored prey item (Vanderploeg et al. 1993) and show no detectable migration associated

385   with *B. longimanus* (Bourdeau et al. 2015). Similarly, other species for which our results did not

386   detect a significant effect of *B. longimanus* would be less expected to be affected by *B.*

387   *longimanus* predation due to body size and habitat (e.g., *L. macrurus*, a large predatory

388   zooplankter which primarily occurs in the hypolimnion).

389   Despite congruence between expected and observed *B. longimanus* effects for several

390   groups, however, *B. longimanus* effects on other groups are still uncertain. For example, some

391   calanoid species (e.g., *L. ashlandi*) have been observed to respond behaviorally to *B. longimanus*

392   for which we did not detect an effect (although $P = 0.085$ in this case). A potential explanation is

393   that calanoids exhibit more effective escape reactions to *B. longimanus* than other zooplankton

394   (Vanderploeg et al 1993; Pichlová-Ptáčníková and Vanderploeg 2011). In addition, for some

395   species, a small sample size of data points for which we were able to calculate population growth

396   rates may have limited out ability to detect an effect (e.g., *T. prasinus mexicanus*). We also note

397   that *B. longimanus* effects were detected for adult *D. thomasi* but not cyclopoid copepodids,

398   which may suggest differences in susceptibility at different life stages that could be explored in

399   future studies. Notably, the estimated effect of *B. longimanus* (β_2) was negative for all but one of

400   the zooplankton groups analyzed (Table 1), although only significant for 3 species. The mostly

401   negative estimates for β_2 indicate that *B. longimanus* may have a weak effect on most species

402   through CEs, NCEs, or competition (in the case of predatory species). However, *B. longimanus*

403   effects on some species may not be strong enough to be clearly detectable from the noisy time

404   series here, or other effects not included in the analysis (e.g., fish predation) overwhelm a *B.*

405   *longimanus* effect.

406   Our analyses provide information on the net effects of *B. longimanus*, but there are

407   multiple mechanisms that could be responsible that the analyses cannot differentiate. For

408   example, our results do not distinguish between the relative contributions of *B. longimanus* CEs

409   and NCEs to changes in estimated growth rate, although estimates for both *B. longimanus*

410   consumption requirements (Pothoven and Vanderploeg 2018) and reductions in population

411   growth due to NCEs (Pangle et al. 2007) suggest that both mechanisms may contribute. These

412   findings should therefore motivate and inform future work using approaches (e.g., state-space

413   models, Marino et al. 2019) that allow for explicit tests of hypothesized mechanisms (e.g.,

414   differential effects of water column temperature structure on CEs and NCEs) underlying effects

415   found here.

416   Our results also motivate additional future work assessing potential long-term

417   consequences of *B. longimanus* effects. For instance, an important next step will be to predict the

418   consequences of estimated effects of *B. longimanus* for future changes in community

419   composition (e.g., increased dominance by calanoid copepods, Barbiero et al. 2019) and whether

420   the currently most impacted species are likely to continue to persist or face extinction in light of

421   long-term suppression by *B. longimanus*. Further, future work should explore mechanisms that

422   have allowed for the continued persistence of these species (e.g., limited spatial or temporal

423   overlap between predators and prey or potential indirect dynamic feedbacks when *B. longimanus*

424   suppresses its preferred prey species).

425   For 13 of 15 zooplankton groups, density strongly and negatively corresponded to

426   estimated population growth. Density dependence may occur within these groups potentially due

427   to conspecific resource competition. Predator-prey dynamic feedbacks may also occur between

428   *B. longimanus* and major prey species that could also contribute to density effects. However, as

429   presented in the Methods section, the presence of measurement error can confound estimates of

430   density effects and lead to bias in our estimates of population growth (Dennis and Taper 1994;

431   Freckleton et al. 2006). We think this confounding factor is likely responsible for a large part of

432   the negative effect of density, as is highlighted by the fact that an effect of density was observed

433   even for several species that occur at relatively low densities (e.g., *S. oregensis*). Other

434   approaches that can explicitly account for the influence of measurement error (e.g., state-space

435   models, Newman et al. 2014; Marino et al. 2019) as well as other factors not considered here

436   (e.g., stage-structure, water column structure, interspecific competition, predator-prey feedbacks,

437   multiple predators), should be useful to more directly and mechanistically assess the impact of

438   density and other factors on dynamics.

439   Whole water column chlorophyll *a* was a poor predictor of population growth rate for

440   most groups, with the exception of *L. minutus*, which may benefit from increased food

441   availability associated with increased phytoplankton densities. The lack of an effect is surprising

442   given major changes in primary production during the survey duration associated with quagga

443   mussel effects (Yousef et al. 2014; Rowe et al. 2015). We note that tests using surface layer

444   chlorophyll a concentrations in analyses instead of whole water column concentrations did not

445   produce substantially different results. No effect of chlorophyll a is consistent with earlier work

446   in Lake Michigan (e.g., Lehman 1988) but contrasts with other studies that have shown effects of

447   phytoplankton resources on zooplankton populations elsewhere (e.g., Walsh et al. 2016). An

448   explanation for the widespread lack of a chlorophyll effect is that whole water column

449   chlorophyll *a* may be a poor proxy for food availability for those groups. Even for primarily

450   herbivorous species (e.g., *D. mendotae* or *B. longirostris*), phytoplankton communities of similar

451   chlorophyll *a* concentrations may vary substantially in size structure or quality as a food resource

452   (Vanderploeg 1994; MullerNavarra and Lampert 1996), so that changes in phytoplankton

453   composition may be more important than chlorophyll a concentrations. Many groups examined

454   are omnivorous or carnivorous (i.e., the copepods), so any effect of increased phytoplankton

455   resources would be indirect, if detected (e.g., through increased biomass of microzooplankton

456   that zooplankton consume). In addition, our analyses did not take into account vertical overlap of

457   zooplankton and chlorophyll *a*, as spatial data for zooplankton were not available for most dates.

458   A more refined analysis taking into account spatial overlap as well as phytoplankton composition

459   and variation among species in diet would likely offer further insights into the contribution of

460   food resources to Lake Michigan zooplankton dynamics. Nevertheless, our findings provide

461   evidence that either whole water column chlorophyll *a* concentrations are not an appropriate

462   proxy for zooplankton resource density or food resource effects are overwhelmed by other

463   factors affecting these populations.

464   Our results also indicate the influence of temperature on zooplankton population growth.

465   In particular, surface temperature, which we used in our analysis, is most similar to the

466   temperature in the epilimnion. As most groups analyzed typically occupy the epilimnion a

467   substantial portion of the time (except three species that typically occupy deeper water: *L.*

468   *ashlandi*, *L. sicilis*, and *L. macrurus*, Vanderploeg et al. 2012), we expected to detect an effect of

469   temperature on most groups. However, only three groups showed a change in growth rate

470   associated with surface temperature, with *D. mendotae, D. thomasi,* and *L. sicilis* having higher

471   growth rates at higher surface temperatures. Notably, *D. mendotae* and *D. thomasi* often occur in

472   the epilimnion, which would be consistent with our a priori prediction. The weaker but still

473   significant estimated effect of surface temperature on *L. sicilis* is surprising, as *L. sicilis*

474   primarily occurs in the hypolimnion; surface temperature may be a proxy for some other factor

475   (e.g., epilimnion depth, food resources) that affects *L. sicilis*. In contrast, there was no significant

476   effect of surface temperature on *L. macrurus*, which also occurs primarily in the hypolimnion

477   and would be expected to experience colder and less variable temperatures than at the surface.

478   Nevertheless, growth rates for other species that do often occur in the epilimnion (e.g., *B.*

479   *longirostris*) did not significantly change associated with temperature. One explanation is that

480   much variation in temperature may be captured by the seasonal function, which could reflect

481   seasonal variation in temperature but also other factors (e.g., water column thermal structure,

482   light levels, fish abundance and behavior, and food availability). The seasonal function may

483   provide more explanatory power than temperature because, e.g., in late spring and early fall,

484   temperatures are similar but zooplankton are in different population phases during each of those

485   times, reducing the role of temperature.

486   Six of the zooplankton groups examined showed clear seasonal variation in growth, with

487   differences likely attributable to variation in life history, habitat use, and other traits of these

488   species. For instance, estimated population growth rates for adults of the three *Leptodiaptomus*

489   species peak in late fall. A potential explanation for the late peak in *Leptodiaptomus spp.*

490   population growth is that positive population growth depends on recruitment from the copepodite

491   stage, which typically peaks in biomass in mid-year (Vanderploeg et al. 2012). In contrast, early

492 season peaks in population growth for *D. mendotae*, *L. macrurus* copepodites, and *E. lacustris*

493 copepodites may partly originate from early season recruitment from resting eggs for *D.*

494 *mendotae* or from nauplii for the copepods, while late-season declines may result, e.g., from

495 shifting resource allocation to resting egg production. The seasonality terms here are largely

496 phenomenological, potentially representing a combination of factors that repeatedly impact

497 zooplankton each year. In fact, the seasonality function may also include a contribution of *B.*

498 *longimanus* as well, so that our estimate for *B. longimanus* effects may be overly conservative.

499   Estimated changes in zooplankton production and composition resulting from *B.*

500 *longimanus* and other factors likely have important implications for other components of the

501 Great Lakes food web. Planktivorous fish, which constitute an important food resource for

502 valued fisheries (Jacobs et al. 2013), rely on zooplankton for food resources (Bunnell et al.

503 2015), so that changes in zooplankton production and composition may impact fisheries. Further,

504 mesozooplankton can have important effects on phytoplankton and microzooplankton production

505 (Bundy et al. 2005; Carrick et al. 2015), with potential consequences for nutrient cycling and

506 energy transfer (Lehman 1988; Walsh et al. 2016). In addition, although the focus of our study

507 was Lake Michigan, similar impacts of *B. longimanus* can be expected in other Great Lakes

508 (Huron, Erie, Ontario) where *B. longimanus* reaches high densities (Pothoven and Höök 2014;

509 Rudstam et al. 2015). Understanding the ongoing, dynamical effects of non-native predators,

510 temperature variation, and other factors will be vital in confronting ongoing and future

511 challenges to freshwater systems, including new species introductions and climate change.

512   Finally, our results demonstrate the utility of collecting and using long-term time series

513 data for quantifying long-term predator impacts at ecologically realistic temporal and spatial

514 scales. The mechanism underlying (e.g., NCE vs. CE) predator effects on prey growth rate can

515   be elucidated from laboratory and mesocosm studies and prey growth rate can be estimated from

516   theoretical considerations based on laboratory or mesocosm experiments of predator-prey

517   interactions (as done for *B. longimanus*-prey interactions, Vanderploeg et al. 1993; Pangle and

518   Peacor 2009), egg ratios and estimated birth rates (Pothoven and Vanderploeg 2018), or

519   bioenergetic requirements of predators (e.g., Yurista et al. 2010). However, complementary

520   studies that probe the actual influence of predators in the field, as we have done here, are critical

521   to estimate the realized impacts of these predators on prey populations. Our approach should thus

522   motivate the collection of time series data more broadly and provide a broadly applicable

523   example on how to use such data to assess the importance of predation and other factors for

524   changes in population growth across a range of systems.

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532

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Table 1: Results of generalized additive mixed model analysis for each zooplankton group, including βs (model coefficients) and number of data points (n). Predictors included group density, *Bythotrephes longimanus* density (*B. long*.), chlorophyll *a* concentration (Chl. *a*), surface temperature (Surf. T), and a smooth function of day of year (f(DOY)). ‡*P* < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001. Significant terms are bold.

		β_1	β_2	β_3	β_4	
	n	**Density**	***B. long.***	**Chl. *a***	**Surf. T**	**f(DOY)**
Daphnia mendotae	76	**-0.033**	**-0.0053***	-0.0064	**0.0075*****	***
Bosmina longirostris	78	-0.0040	**-0.014****	0.015	0.0016	*P* > 0.1
Diacyclops thomasi	127	**-0.036*****	**-0.013****	-0.0062	**0.0033****	*P* > 0.1
Tropocyclops p. mexicanus	30	-0.026‡	-0.00042	-0.0084	0.0011	*P* > 0.1
Leptodiaptomus sicilis	145	**-0.021*****	-0.0036	-0.0072‡	**0.0013***	*
Leptodiaptomus ashlandi	148	**-0.015****	-0.0038‡	-0.0014	0.0015	***
Leptodiaptomus minutus	140	**-0.027*****	-0.009	**0.013***	0.0027‡	***
Limnocalanus macrurus	115	**-0.30*****	-0.00041	0.0036	-0.00044	*P* > 0.1
Epischura lacustris	40	**-0.045*****	-0.0061	-0.0061	0.0013	*P* > 0.1
Skistodiaptomus oregensis	43	**-0.37****	-0.0046	-0.090	-0.00061	*P* > 0.1
Cyclopoid C1-C5	133	**-0.010****	-0.0023	-0.0086	0.00012	‡
Diaptomid C1-C5	148	**-0.0170*****	-0.0033‡	-0.0041	-0.00010	*P* > 0.1
Limnocalanus C1-C5	33	**-0.022***	0.020‡	0.012	-0.0017	**
Epischura C1-C5	57	**-0.047*****	-0.00051	-0.0180	0.0054‡	*
Nauplii	148	**-0.029*****	-0.00083	0.014‡	-0.0012	*P* > 0.1

703 **Table 2:** Results of generalized additive mixed model analysis of estimated population growth

704 rate, including 7 most common species (>50 data points per species). Significant terms are bold.

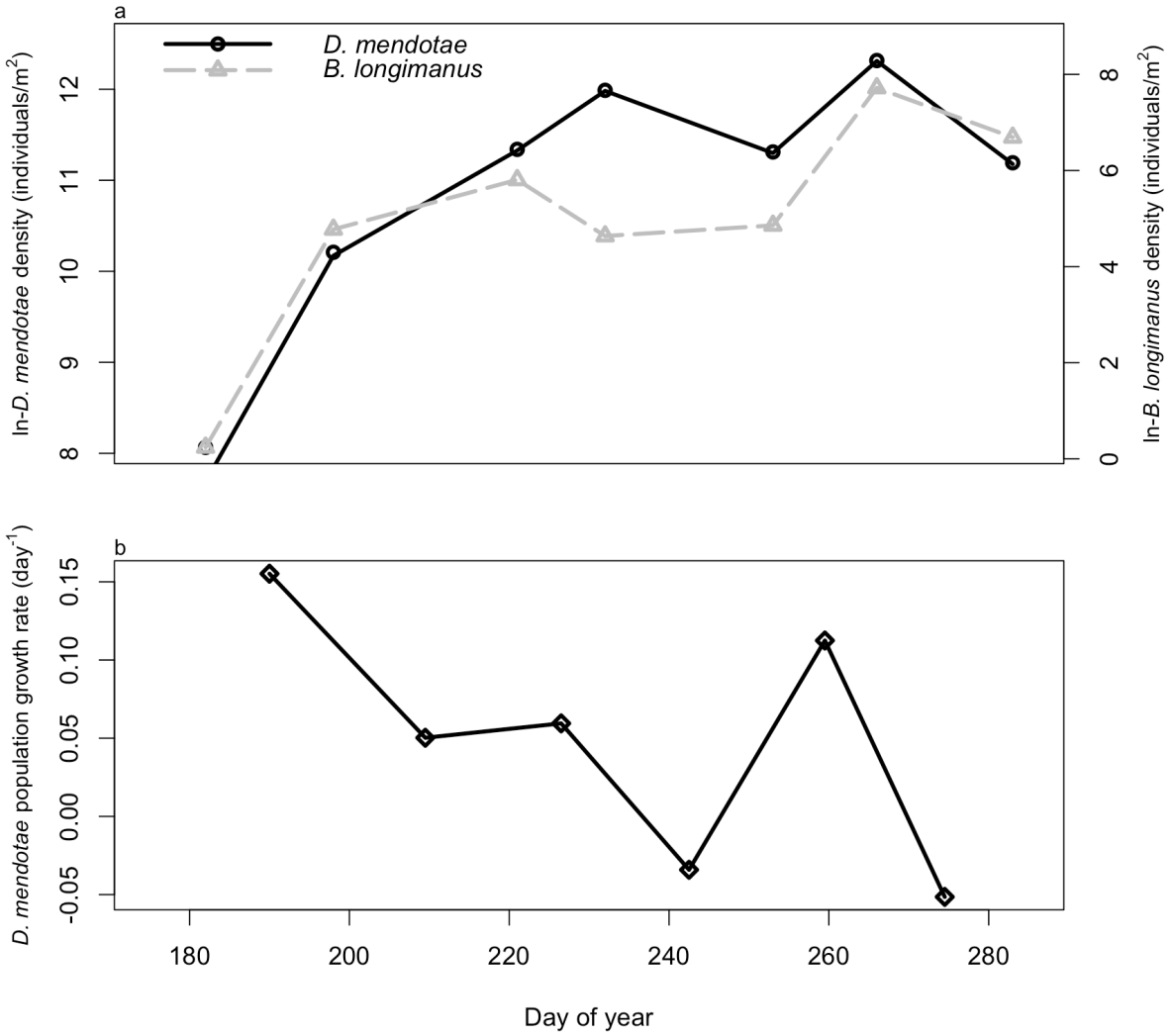|	F	df	P
Species	2.50	6	**0.021**
Bythotrephes longimanus	14.01	1	**<0.001**
Group Density	9.87	1	**0.0017**
Chlorophyll *a*	0.51	1	0.48
Surface Temperature	0.71	1	0.40
Species x *B. longimanus*	2.12	6	**0.049**
Species x Density	3.37	6	**0.0027**
Species x Chlorophyll	1.49	6	0.18
Species x Temp	4.00	6	**<0.001**

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Figure 1: Example data and estimated growth rate: a) *Daphnia mendotae* (black line) and

Bythotrephes longimanus (gray line) densities (ln-transformed) vs. day of year in 2002. b)

Estimated *D. mendotae* population growth rate (r) calculated based on densities in (a) vs. day of

year according to Eq. 1.

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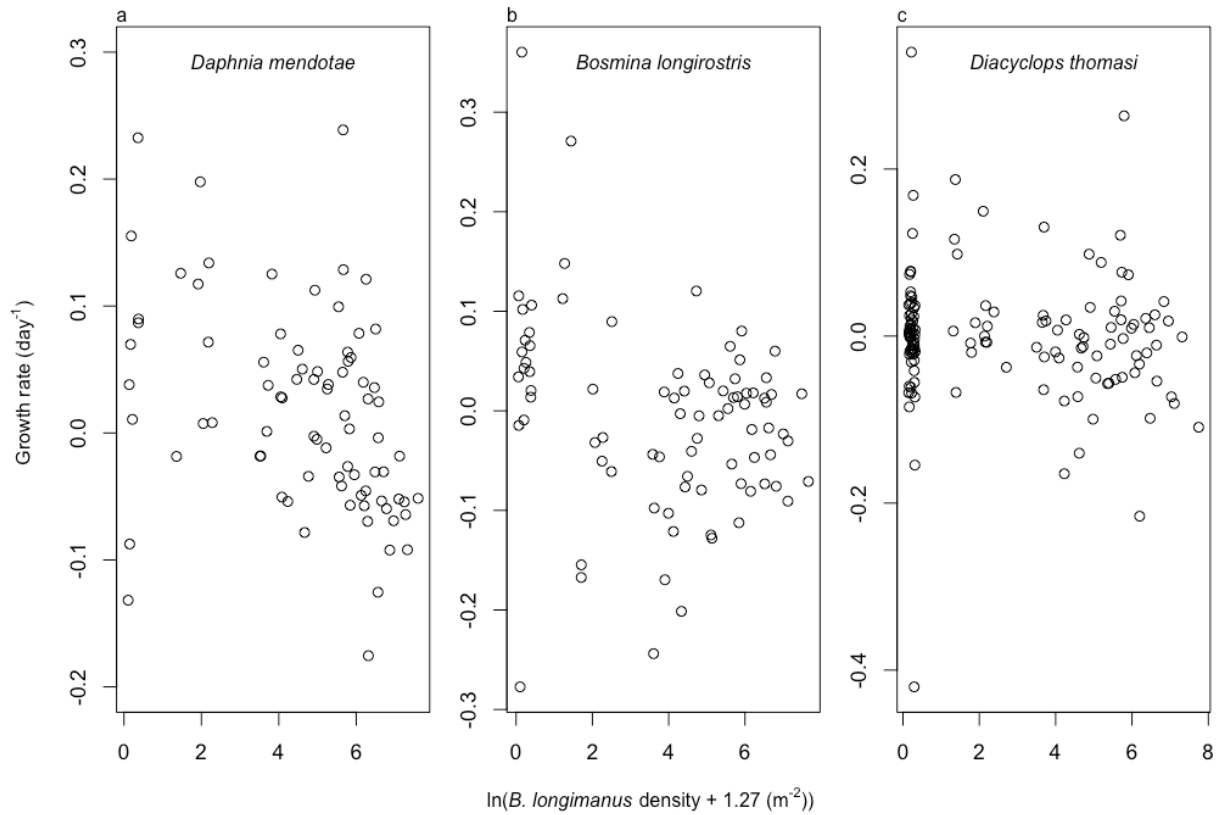
Figure 2: Estimated population growth rate vs. ln (*Bythotrephes longimanus* density + 1.27 /m^2)

for a) *Daphnia mendotae*, b) *Bosmina longirostris,* and c) *Diacyclops thomasi.* Points have been

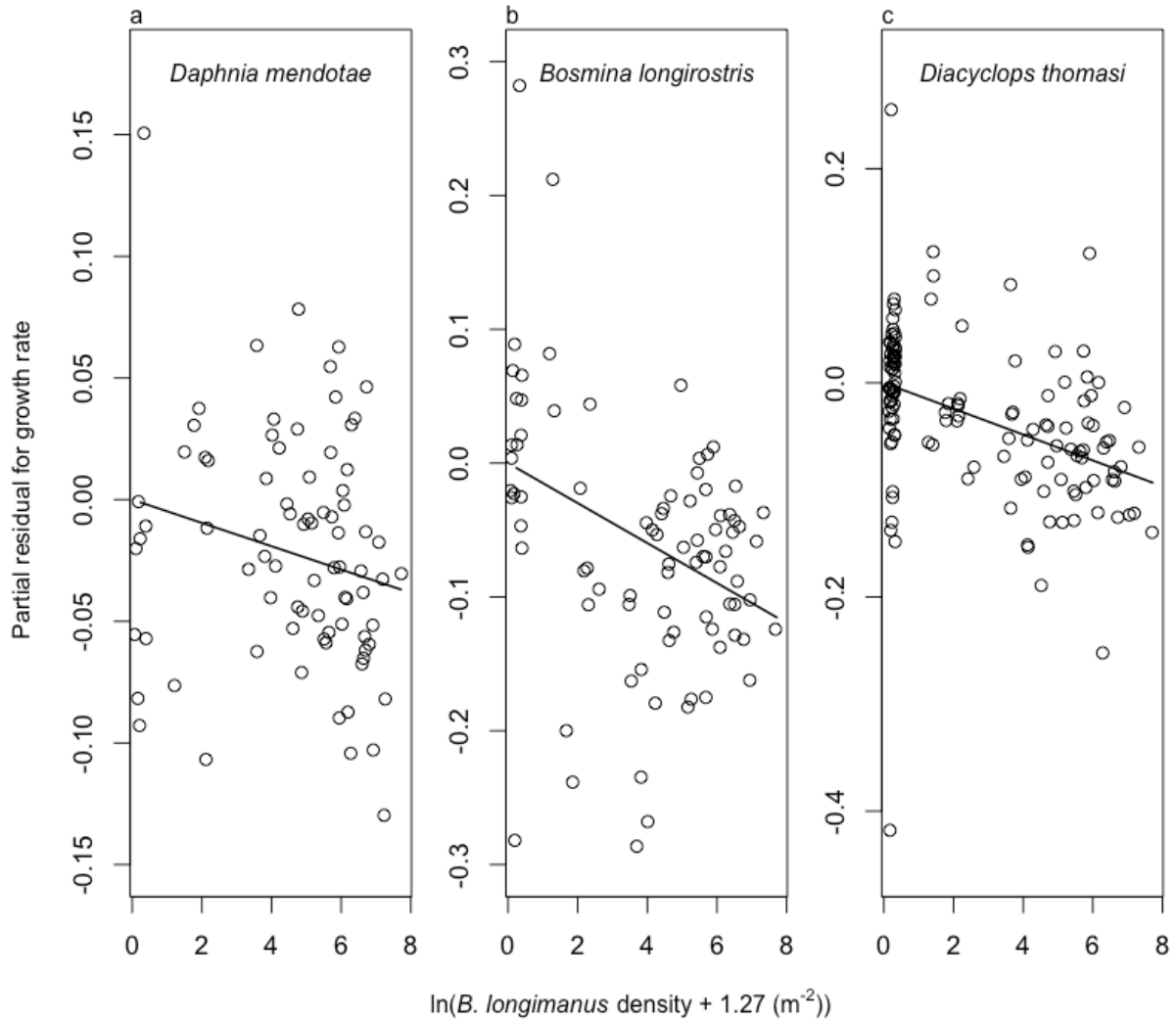horizontally offset by adding noise to make overlapping points visible.

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Figure 3: Partial residuals of generalized additive mixed models (excluding effect of *Bythotrephes longimanus*) vs. ln (*B. longimanus* density + 1.27 /m^3) for a) *Daphnia mendotae*, b) *Bosmina longirostris*, and c) *Diacyclops thomasi*. Points have been horizontally offset by adding noise to make overlapping points visible.
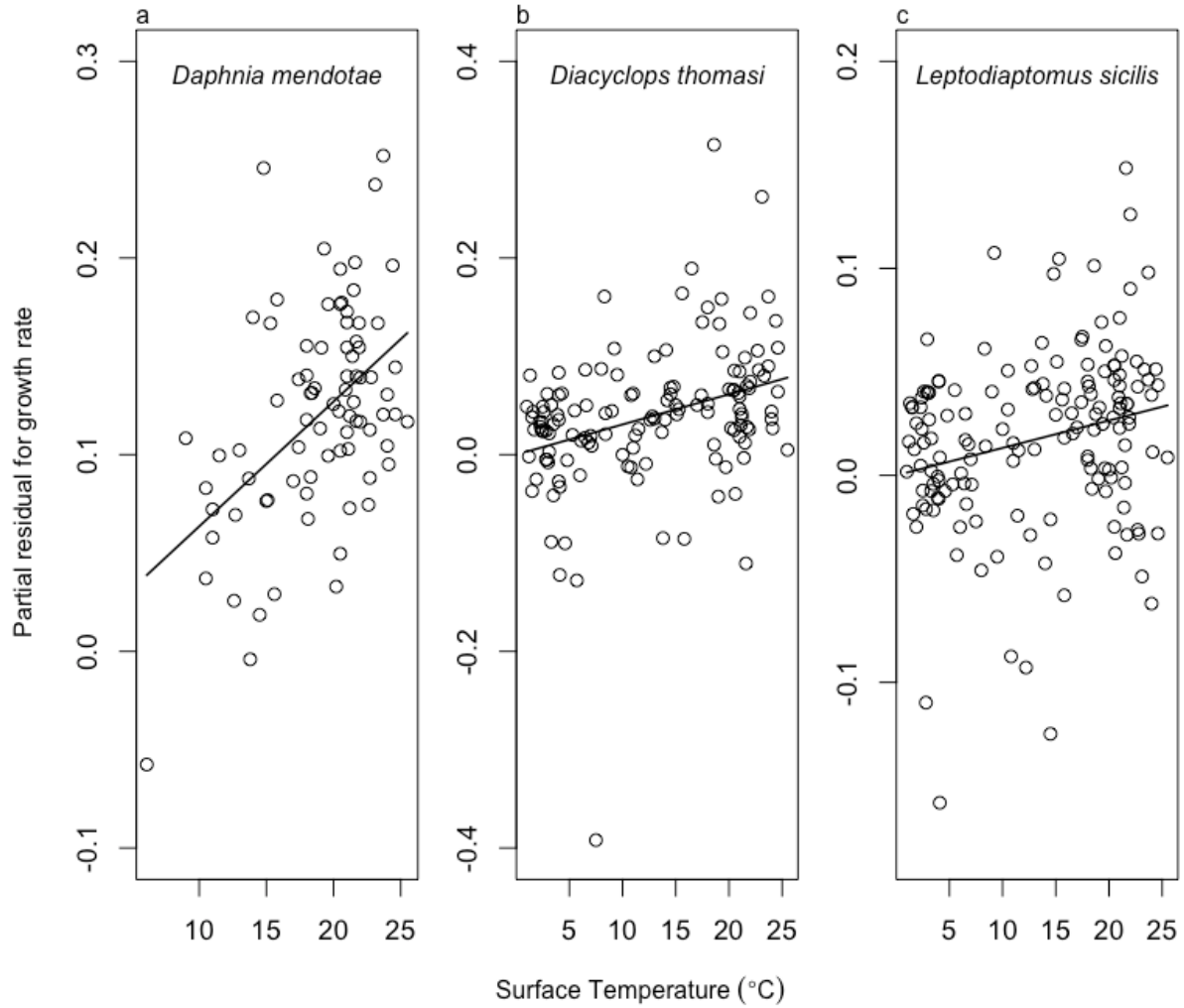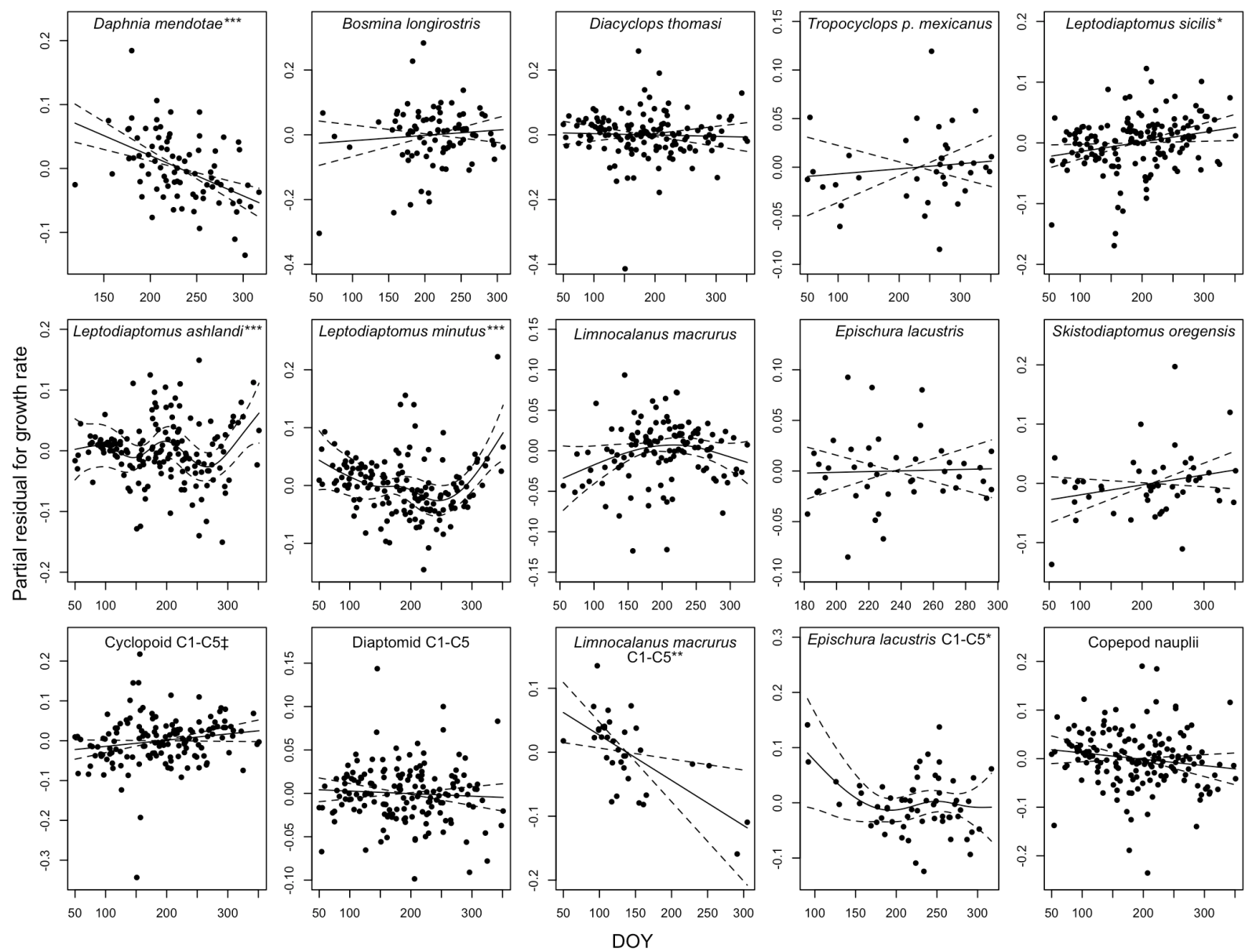
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Figure 4: Partial residuals of generalized additive mixed models (excluding effect of

temperature) vs. surface temperature for a) *Daphnia mendotae*, b) *Diacyclops thomasi*, and c)

Leptodiaptomus sicilis.

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Figure: Partial residual for growth rate plotted against DOY for multiple zooplankton taxa: *Daphnia mendotae****, *Bosmina longirostris*, *Diacyclops thomasi*, *Tropocyclops p. mexicanus*, *Leptodiaptomus sicilis**, *Leptodiaptomus ashlandi****, *Leptodiaptomus minutus****, *Limnocalanus macrurus*, *Epischura lacustris*, *Skistodiaptomus oregensis*, Cyclopoid C1-C5‡, Diaptomid C1-C5, *Limnocalanus macrurus* C1-C5**, *Epischura lacustris* C1-C5*, Copepod nauplii.

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729 **Figure 5:** Partial residuals and seasonal functions from fitted generalized additive mixed model showing estimated growth rate

730 function vs. day of year (DOY) for each zooplankton group. The solid line indicates the smoothing function f(DOY), dashed lines

731 indicate 95% confidence bands, and points show partial residuals (excluding effect of DOY). Symbols next to species names indicate

732 significance for f(DOY): $^{\ddagger}P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.