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Invasive Predator, Bythotrephes, has Varied Effects on Ecosystem Function in Freshwater Lakes

Angela L. Strecker

Portland State University, strecker@pdx.edu

Shelley E. Arnott

Queen's University - Kingston, Ontario

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1 RH: Invader effects on ecosystem function

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6 Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in
7 freshwater lakes

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10 *Angela L. Strecker^{1,2} and Shelley E. Arnott*

11 *Department of Biology, Queen's University, 116 Barrie St., Kingston, Ontario, Canada K7L 3N6*

12

13 ¹ *Corresponding author's email: astrecker@eeb.utoronto.ca*

14 ² *Current address: Department of Ecology & Evolutionary Biology, University of Toronto,*

15 *25 Harbord St., Toronto, Ontario, Canada M5S 3G5*

16 *Tel: (416) 946-7223*

17 *Fax: (416) 978-8532*

18

19 ABSTRACT

20 *Bythotrephes longimanus* is an invertebrate predator that has invaded the North American Great
21 Lakes and a number of inland lakes, where it preys on crustacean zooplankton. We examined the
22 effect of *Bythotrephes* on two measures of ecosystem function during a four month observational
23 study of freshwater lakes on the boreal shield. *Bythotrephes*-invaded lakes had significantly lower
24 epilimnetic zooplankton abundance and production compared to reference lakes. On average,
25 *Bythotrephes* consumed 34% of zooplankton production when it was present in lakes. There was
26 some evidence of changes in the timing of zooplankton production, as well as shifts to cooler, less
27 productive habitats, which may lessen the overall effect of the invader on the transfer of energy to
28 higher trophic levels. We experimentally demonstrated a weak trophic cascade where invader
29 predation reduced zooplankton biomass, and subsequently increased phytoplankton growth.
30 However, the response was small in magnitude and not biologically relevant at the whole lake-
31 scale. The most conspicuous effect of *Bythotrephes* that we measured was a diversion of energy
32 away from native predators at higher trophic levels.

33

34 Keywords: invasive species, ecosystem function, crustacean zooplankton, *Bythotrephes*,
35 freshwater lakes, secondary production, zooplankton grazing

36 INTRODUCTION

37 The introduction of non-indigenous species is expected to be one of the greatest threats to
38 species across all ecosystems (Wilcove and others 1998; Sala and others 2000) and the single most
39 important driver of biodiversity loss in freshwater lakes (Sala and others 2000). Although there is
40 evidence that invasive species can alter ecosystem function (Brooks and others 2004; Zhu and
41 others 2006), we currently lack understanding of how newly-introduced species may affect
42 ecosystem processes (Millenium Ecosystem Assessment 2005). Thus, the invasion of a non-
43 native species presents a unique opportunity to understand how complex ecosystems operate.

44 *Bythotrephes longimanus* (Crustacea, Branchiopoda, Onychopoda) is a parthenogenetic
45 invertebrate predator that has invaded all of the North American Great Lakes (Jin and Sprules
46 1990), and > 100 inland lakes in North America, including waterbodies in Ontario (N. Yan,
47 *unpublished data*), Minnesota (Branstrator and others 2006), and Michigan (Jarnagin and others
48 2000). Although studies have indicated that *Bythotrephes* prefers large, deep, low productivity
49 lakes in both its native Eurasia and in invaded regions (MacIsaac and others 2000), it has been
50 found in smaller shallow waterbodies and higher productivity lakes as well (Jarnagin and others
51 2000). *Bythotrephes* has the potential to invade many boreal shield and northern temperate lakes,
52 especially those visited by human vectors.

53 *Bythotrephes* can have substantial effects on the community structure of its primary prey,
54 crustacean zooplankton, and although there is some degree of among-lake variability in the
55 response to invasion, the general trend has been reductions in species richness (Yan and others
56 2002; Strecker and others 2006), total community biomass (Boudreau and Yan 2003; Strecker and
57 Arnott 2005), and total community abundance of zooplankton (Yan and others 2001; Strecker and
58 Arnott 2005; Strecker and others 2006). These trends follow from dramatic declines in cladoceran

59 zooplankton richness and abundance (Yan and others 2001; Boudreau and Yan 2003; Strecker and
60 others 2006).

61 Zooplankton are a central component in freshwater food webs, transferring energy to
62 young-of-year (YOY) and planktivorous fish via production of biomass, grazing on phytoplankton
63 biomass, and recycling dissolved nutrients to phytoplankton. Foraging success of juvenile fish can
64 be greatly influenced by variability in zooplankton populations in freshwater ecosystems (Chick
65 and van den Avyle 1999; Beauchamp and others 2004). In one study, it was observed that
66 *Bythotrephes* consumed large portions of zooplankton production in Harp Lake, Ontario during
67 summer (Dumitru and others 2001), potentially decreasing the amount of production available to
68 other components of the aquatic food web. Additionally, when *Bythotrephes* was present, total
69 consumption of the invertebrate predator guild increased by >300% (S. Foster, *pers. comm.*),
70 potentially reducing the efficiency of energy transfer to higher trophic levels (Sprules 1980).

71 The impact of zooplankton on phytoplankton is influenced by zooplankton biomass and
72 community composition – and is therefore potentially affected by *Bythotrephes* predation.
73 Zooplankton grazing and nutrient recycling can have a greater effect on phytoplankton biomass in
74 lakes than nutrient recycling of fish (Sarnelle and Knapp 2005), and grazing by large cladoceran
75 zooplankton can exert strong top-down control on phytoplankton (Elser and Goldman 1991).
76 Thus, zooplankton community structure in lakes can be a primary determinant of the flow of
77 energy and nutrients to all trophic levels; however, few studies have examined the effects of
78 invaders on nutrient and energy flow at multiple levels of organization in freshwater systems
79 (Simon and Townsend 2003).

80 The overall purpose of this study was to determine the effects of the invasive predator,
81 *Bythotrephes*, on ecosystem function in boreal lakes. Ecosystem function is commonly measured
82 as changes in rates of productivity, decomposition, nutrient cycling, and resistance and resilience

83 to perturbations (Loreau and others 2001). In our study we measured ecosystem function as
84 changes in rates of secondary productivity and the combined effects of zooplankton grazing and
85 nutrient cycling on phytoplankton. The two main objectives of our study were to examine: (1) the
86 effect of *Bythotrephes* on crustacean zooplankton production within each lake stratum and
87 throughout the ice-free season; and (2) if zooplankton impact on phytoplankton is influenced by
88 *Bythotrephes*-induced changes in community composition and biomass.

89 Based on reductions in zooplankton abundance observed in previous studies (Yan and
90 others 2001; Strecker and others 2006), we hypothesized that *Bythotrephes* would negatively
91 affect zooplankton production. *Bythotrephes* tends to be absent in lakes until middle-to-late June
92 (Yan and others 2001), creating a window of opportunity before this time period for zooplankton
93 to increase their reproduction. Therefore, we expect to see a less pronounced effect of
94 *Bythotrephes* on coarse measures of overall seasonal and whole water column production, but
95 differences in fine-scale temporal (biweekly) and spatial (variation between strata) patterns of
96 zooplankton production. Secondly, the effects of zooplankton grazing and nutrient recycling on
97 phytoplankton are significantly influenced by both community biomass and composition (Elser
98 and Goldman 1991; Cyr 1998; Elser and others 2000), thus, we would expect zooplankton
99 communities in invaded lakes to have a lessened impact on phytoplankton as a result of
100 *Bythotrephes*-induced reductions in total zooplankton biomass and selective predation on
101 cladocerans.

102

103 MATERIALS AND METHODS

104 *Study Site and Sampling*

105 Eight lakes in the Parry Sound and Muskoka districts of south-central Ontario were chosen
106 for our study (Table 1). The study lakes are located in mixed-forest catchments, have low

107 productivity (oligo-mesotrophic), and are circumneutral. Lakes are relatively deep, ranging from
108 23 – 59 m, and have surface areas ranging from 72 – 2058 ha (Table 1). Lakes were chosen based
109 on prior knowledge of the invasion of *Bythotrephes* (invaded lakes had *Bythotrephes* for at least 5
110 years), proximity, and similarity of chemical, physical, and morphometric characteristics. As well,
111 all of the lakes contained the glacial relict *Mysis relicta*, which is indicative of a similar post-
112 glacial history, and planktivorous fish communities, including yellow perch (*Perca flavescens*) and
113 a combination of cisco (*Coregonus artedi*), rainbow smelt (*Osmerus mordax*), and lake whitefish
114 (*Coregonus clupeaformis*) (Appendix 1).

115 Lakes were visited every two weeks from May to September 2003 (n = 9), and samples
116 were generally taken within a five-day time period. At a deep station in the lake, temperature,
117 dissolved oxygen, and Secchi depth were measured, and samples were taken for zooplankton,
118 *Bythotrephes*, and chlorophyll *a* (chl *a*). Four additional sample stations for *Bythotrephes*
119 collection were chosen along a transect, starting at the deep station and moving toward shore,
120 marking each station with a GPS to locate it on the next sampling date (see Strecker and others
121 2006 for sampling details). Logistical constraints prevented sampling at night so all samples were
122 taken during the day. Chl *a* samples were taken from the epilimnion using a 2.5-cm diameter
123 integrated tube sampler. The integrated tube sampler was also used to collect water from the
124 epilimnion on the week of 14 July 2003 for analysis of water chemistry variables.

125 Zooplankton were sampled with a 110- μ m mesh conical closing net that was 0.5 m in
126 diameter. Samples were taken in the epilimnion, metalimnion, and hypolimnion (from 5 m off the
127 lake bottom to the top of the hypolimnion) after thermal strata were determined from a
128 temperature profile taken at 1-m intervals. The top of the metalimnion was defined as a change of
129 $> 1^{\circ}\text{C}$ per meter, and the top of the hypolimnion by a change of $< 0.2^{\circ}\text{C}$ per meter. On the first
130 sampling date, stratification had not yet been achieved in Bernard Lake, so the depth of the entire

131 water column was roughly divided in 3 and samples were taken from those depths. Average
132 temperatures from each strata in Bernard Lake on the first date were consistent with other lakes,
133 thus, we do not believe that this method affected our results. The hypolimnion of Doe Lake could
134 not be sampled on seven dates because it was too shallow; therefore, this lake was excluded from
135 hypolimnetic abundance and production estimations. Samples for *Bythotrephes* were taken over
136 the entire water column, starting from 5 m off the lake bottom, using a 400- μ m mesh conical net
137 that was 0.5 m in diameter. *Bythotrephes* and zooplankton samples were anesthetized and
138 preserved in 5.5% sugared and buffered formalin.

139 Zooplankton samples were enumerated and measured on a Leica MZ12.5 dissecting
140 microscope using the semi-automated counting system ZEBRA2 (Allen and others 1994).
141 Subsamples of a known volume were taken and a minimum of 350 individuals were identified to
142 genus, with the exception of *Daphnia mendotae*, *Eubosmina (Neobosmina) tubicen*, *Eubosmina*
143 (*Eubosmina*) *coregoni*, *Eubosmina (Eubosmina) longispina*, and other species which are the only
144 representative of their genus in the area. Diaptomid calanoid copepods belonging to the genera
145 *Leptodiaptomus* and *Skistodiaptomus* were grouped simply as *Diaptomus* spp. To obtain a
146 representative enumeration of all zooplankton genera present, only 40-50 individuals of the
147 dominant taxa, 40-50 copepodids per order, and 20-30 nauplii per order were counted. Both loose
148 and attached eggs were counted in the subsamples, stopping either when the minimum number of
149 individuals was reached or > 700 loose eggs were counted. Loose eggs were designated as
150 cladoceran or copepod and apportioned to the number of adults present. *Bythotrephes* samples
151 containing < 32 individuals were counted in their entirety, while samples with greater numbers
152 were split with a Folsom plankton splitter and mixed to ensure that clumping did not occur. All
153 instars were enumerated and abundances were averaged across the five sampling stations.

154

155 *Zooplankton Production*

156 Although *Bythotrephes* (Pangle and Peacor 2006) and other visual predators (Lampert
157 1989) can induce diel vertical migration of zooplankton, we chose to sample during the day to
158 specifically examine the vertical distribution of productivity available to visually foraging
159 predators, such as cisco, which are daytime feeders (Milne and others 2005). Comparisons of day
160 and night vertically-stratified samples of zooplankton taken in 2007 in most of our study lakes
161 suggest that some zooplankton migrated downwards in invaded lakes during the day, while diel
162 migrations in non-invaded lakes tended to be small in magnitude (S. Arnott, *unpublished data*).
163 There was variability in the extent of migration in invaded lakes: on average 15% of total
164 zooplankton (range: -13 – 31%; negative value represents migration in the opposite direction)
165 moved from the metalimnion to the epilimnion at night, but migration of zooplankton away from
166 the hypolimnion to warmer temperatures at night was small (mean: 9%, range: -9 – 28%). We
167 acknowledge that as a result of these migrations, our calculations may underestimate metalimnetic
168 production in invaded lakes by including organisms that have spent nights at warmer temperatures.

169 Biweekly zooplankton production was calculated using two methods. For the calanoid
170 copepod species which do not carry their eggs in an egg sac (e.g., *Senecella calanoides*), the
171 cohort method was used (Downing 1984). For all other zooplankton, the egg-ratio method was
172 used (Borgmann and others 1984), following Paloheimo (1974). Temperature and species-specific
173 values for egg development time were determined from the literature (see Kuns and Sprules 2000),
174 and the mean temperature of each stratum was used. Mean dry weights for zooplankton were
175 calculated using length-weight regressions (McCauley 1984; Culver and others 1985; Yan and
176 Mackie 1987; Yan and Pawson 1997; W.G. Sprules, *unpublished data*). Areal biweekly
177 production was calculated by multiplying volumetric production by the depth of the stratum. All
178 of our production estimates were calculated at the genus level and then summed across all taxa to

179 obtain total crustacean zooplankton production. *Bythotrephes* production was calculated
180 separately from the crustacean zooplankton community, as we wanted to examine the effects of
181 *Bythotrephes* as a predator on zooplankton productivity, exclusive of its contribution to total
182 zooplankton productivity (for comparison, *Bythotrephes* production is displayed in Fig. 1).
183 Biweekly *Bythotrephes* consumption ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) was estimated by dividing *Bythotrephes*
184 biweekly production ($\text{mg m}^{-2} \text{ fortnight}^{-1}$; calculated by the egg-ratio method from whole water
185 column samples) by growth efficiency, which was estimated at 27% for a population of mixed
186 instars (Dumitru and others 2001). Consumption by *Bythotrephes* was contrasted with
187 zooplankton production from the epilimnion and metalimnion, as a concurrent study in a subset of
188 the lakes in our study suggests that this is where the invader is generally found (Young and Yan
189 2008).

190

191 *Impact of Zooplankton on Phytoplankton*

192 To assess the effects of *Bythotrephes* on trophic interactions between zooplankton and
193 phytoplankton, an *in situ* experiment was conducted three times in a subset of the study lakes: two
194 invaded and three reference lakes. Using a technique modified from Elser and Goldman (1991),
195 Cyr (1998), and Sommer and others (2001), we measured zooplankton impact on the
196 phytoplankton community, including direct grazing effects, but also indirect effects, such as
197 nutrient recycling, as no nutrients were added to the carboys. Four translucent 20-L carboys were
198 deployed for 72 hr in each lake, once during June, July, and August, approximately four weeks
199 apart. Water was taken from the region of the lake at which the carboys were incubated (~50%
200 light penetration), thus minimizing between-lake differences in light exposure. Water was filtered
201 through 80- μm mesh to remove zooplankton and added to each carboy. Zooplankton were added
202 to each of the carboys at several densities (0, 1, 2, and 3 \times ambient) by taking discrete hauls with a

203 closing net through each of the strata (epi-, meta-, and hypolimnion), thus compensating for any
204 diel vertical migration that may have been occurring, but also likely overestimating grazing due to
205 the presence of hypolimnetic taxa that would not be feeding in the epilimnion during the day. The
206 carboys were then sealed, weighted, and incubated for 72 hr. All predaceous macroinvertebrates,
207 e.g., *Bythotrephes*, were excluded from the carboys. By removing *Bythotrephes* from the carboys,
208 we are thus explicitly testing how zooplankton communities shaped by invasion will influence
209 algal community biomass in short term experiments in invaded and reference lakes. Although
210 initial differences in the composition of phytoplankton communities could influence zooplankton
211 grazing, the invaded and reference lakes in this study have similar proportions of edible
212 phytoplankton cells (B. Beisner, *unpublished data*), suggesting that conditions were relatively
213 comparable in invaded and reference lakes. Chl *a* samples from each carboy were taken at the
214 beginning and end of the experiment, concentrating water samples onto 1.2- μm glass fiber filters,
215 and measured using fluorometry. Following Cyr (1998), the realized algal growth rate per day for
216 the carboys that contain zooplankton (r) were calculated from

217 (1) $r = \ln(C_1 / C_0) / T$

218 where C_0 and C_1 are chl *a* concentrations ($\mu\text{g L}^{-1}$) at the beginning and end of the experiment, and
219 T is the length of time the experiment ran (days). Zooplankton impact was calculated as the slope
220 (b) of the equation

221 (2) $r = b(ZB) + a$

222 where ZB is the zooplankton biomass at 0, 1, 2 or 3 \times ambient biomass and a is the growth rate in
223 the absence of zooplankton. Zooplankton biomass was determined from the average of the two
224 survey sampling dates that surrounded the experiment. The coefficients of the equation were
225 estimated by linear regression. Percent change in algae (per day) was calculated as $(- (1 - e^b) \times$
226 100). Although this experiment and others upon which it was modeled (Elser and Goldman 1991;

227 Cyr 1998) are brief, our experiment was designed to provide insight into possible trophic
228 interactions that may result from changes in lake food webs and should be looked upon as a
229 simplified test of the interaction between zooplankton and phytoplankton without confounding
230 factors from higher trophic levels.

231

232 *Statistical Analyses*

233 One-way ANOVAs were used to examine differences in physical, chemical, and
234 morphological characteristics of study lakes. Repeated measures ANOVAs were used to test if
235 there were differences between invaded and reference lakes for chl *a*, secondary production,
236 zooplankton abundance, and egg ratio (eggs individual⁻¹). Because of non-normality and
237 heteroscedasticity in some of the above measures, all values were log (x+1)-transformed. The
238 Huynh-Feldt adjusted *p*-value was used in situations where the assumption of sphericity was not
239 met for repeated measures analyses. Although we would expect to observe seasonal changes in
240 zooplankton communities, independent of invasion status, it was not our intention to describe
241 these changes, therefore, we will not discuss time effect results unless there is an interaction with
242 invasion. A two-factor ANOVA was used to test for differences in zooplankton grazing impact
243 over all three experimental time periods in invaded and reference lakes, with time as a block
244 factor. Statistical analyses were performed using Statistica 6.0 (StatSoft 2001).

245

246 RESULTS

247 *Zooplankton Production*

248 Reference and invaded lakes were similar in surface area, maximum depth, and primary
249 productivity (chl *a* and total phosphorus) (Table 1), as well as thermal structure (epilimnetic

250 temperature: $F_{1,6} = 0.01, p = 0.98$). There was also no significant difference in concentrations of
251 calcium and dissolved organic carbon, pH, and conductivity between lake categories (Table 1).

252 Zooplankton production was significantly lower in the epilimnion of *Bythotrephes*-invaded
253 lakes throughout the summer, declining on average by $> 6000 \text{ mg m}^{-2} \text{ season}^{-1}$, or about 67% (Fig.
254 2, Table 2). There was no difference in metalimnetic or hypolimnetic production between invaded
255 and reference lakes (Fig. 2, Table 2), although the hypolimnions of two of the four invaded lakes,
256 Bernard and Harp, were 18 \times and 13 \times more productive than the average hypolimnetic productivity
257 of reference lakes (Fig. 1). When all of the strata were combined, there was no statistical
258 difference in whole-water column zooplankton production between invaded and reference lakes
259 (Fig. 1, 2, Table 2).

260 In the epilimnion, production of calanoid copepods, cyclopoid copepods, and small
261 cladocerans was significantly reduced in *Bythotrephes*-invaded lakes (Fig. 3, Table 3).
262 Epilimnetic production by large cladocerans tended to be reduced in *Bythotrephes*-invaded lakes,
263 though not significantly. There was a significant Time \times Invasion interaction for small
264 cladocerans, where production in invaded lakes was high early in the season, but declined
265 precipitously from an average of $442 \text{ mg m}^{-2} \text{ fortnight}^{-1}$ in May and early June to $< 2 \text{ mg m}^{-2}$
266 fortnight^{-1} over the remainder of the sampling dates (Fig. 3, Table 3). In the metalimnion,
267 production by cyclopoids, calanoids, and small cladocerans was similar in reference and invaded
268 lakes, while large cladoceran production was 90% lower in invaded lakes compared to reference
269 lakes, averaging $13 \text{ mg m}^{-2} \text{ fortnight}^{-1}$ over the season (Fig. 3, Table 3). In the hypolimnion,
270 cyclopoid copepods had higher production in invaded lakes early in the season, followed by a
271 decrease beginning in mid-June, and calanoid copepod production was significantly greater in
272 invaded lakes (Fig. 3, Table 3). There was no difference in large and small cladoceran
273 hypolimnetic production between lake groups (Fig. 3, Table 3).

274 The abundance of crustacean zooplankton in the epilimnion was significantly affected in
275 invaded lakes, with declines of $> 33\ 000$ individuals m^{-3} , on average (Fig. 4, Table 2). There was
276 also a significant Time \times Invasion interaction, such that abundances were similar in invaded and
277 reference lakes in May and early June, but showed significant declines in the invaded lakes after
278 this time. There was no difference between invaded and reference lake zooplankton abundance in
279 the metalimnion, hypolimnion, and when all strata are combined, nor were there any interactions
280 between invasion status and time (Fig. 4, Table 2).

281 *Bythotrephes*-invaded lakes had a marginally significant increase in numbers of eggs
282 produced per individual zooplankter in the hypolimnion, which was most noticeable early in the
283 summer (Fig. 5, Table 2). This peak was likely driven by extremely high egg production by
284 hypolimnetic cyclopoid copepods, who produced on average > 9000 eggs m^{-3} (A. Strecker,
285 *unpublished data*), far greater numbers than other zooplankton of a similar size, and had greater
286 numbers of eggs per individual in invaded lakes compared to reference lakes (Fig. 5, Table 4).
287 When all strata were combined, there was a marginally significant increase in eggs produced per
288 individual zooplankter in invaded lakes compared to reference lakes on the first sampling date
289 ($F_{1,6} = 3.82, p = 0.10$). This early season peak in number of eggs per individual in invaded lakes
290 came mostly from small cladoceran and cyclopoid functional groups (Fig. 5). There was no
291 significant effect of invasion on total or functional group eggs per individual in the epilimnion,
292 metalimnion, or when all strata were combined, nor were there any significant Time \times Invasion
293 interactions (Fig. 5, Table 2).

294 *Bythotrephes* consumed substantial portions of the total seasonal zooplankton production
295 in three of the four invaded lakes (Fig. 6), on average consuming > 1000 $mg\ m^{-2}\ season^{-1}$ or about
296 17% of secondary production from the middle of May to the middle of September. However,
297 *Bythotrephes* did not tend to appear until mid-June in our samples, thus zooplankton production

298 consumed after *Bythotrephes* starts reproducing is, on average, about 34% (Fig. 6). *Bythotrephes*
299 consumed > 100% of zooplankton production on two sampling dates in Bernard Lake and Harp
300 Lake, but its consumption never exceeded zooplankton production in Peninsula and Vernon lakes.
301 In general, *Bythotrephes* production was low, only comprising < 6% of total zooplankton
302 production, on average (Fig. 1).

303

304 *Impact of Zooplankton on Phytoplankton*

305 In each grazing experiment, algae decreased in reference lakes and increased in invaded
306 lakes (Fig. 7a). There was a significant effect of invasion on zooplankton impact on the algal
307 community (invasion: $F_{1,8} = 23.13$, $p < 0.01$, time: $F_{2,8} = 0.85$, $p = 0.46$), such that % change in
308 algae increased in the invaded lakes. However, this increase is likely not biologically meaningful
309 in the long term, as changes in chl *a* in the experimental carboys were typically < 1 $\mu\text{g L}^{-1}$.
310 Indeed, there was no significant difference in epilimnetic chl *a* concentrations between lakes with
311 and without *Bythotrephes* throughout the entire season in the entire subset of lakes sampled (Fig.
312 7b, Table 1).

313

314 DISCUSSION

315 We found that the invasive invertebrate predator, *Bythotrephes*, altered some measures of
316 ecosystem function in freshwater lakes, such as epilimnetic secondary production, but that other
317 measures were generally unchanged. There was some evidence for seasonal shifts in the
318 production of different functional groups and individual egg production in invaded lakes in May
319 and early June, but this was not great enough to balance production lost to *Bythotrephes*
320 consumption later in the season. The effects of *Bythotrephes* on whole lake productivity may be
321 moderated by behavioural shifts in zooplankton abundance to the cool dark waters of the

322 hypolimnion and/or increased abundance of hypolimnetic species, and consequently, increased
323 production in the hypolimnion of some lakes. *Bythotrephes* cannot compensate for the declines in
324 biomass production observed in invaded lakes, as it generated <6% of total zooplankton
325 production. Our study provides compelling evidence that *Bythotrephes* can alter the flow of
326 energy in parts of freshwater lakes, but may leave other measures of ecosystem function relatively
327 unaffected. Changes in energy flow will likely have implications for growth and reproduction of
328 other trophic levels in the food web, including macroinvertebrates, planktivorous fish, and young-
329 of-year piscivorous fish, since these organisms all rely on zooplankton as a major food source.

330

331 *Zooplankton Production*

332 There was a significant decrease in epilimnetic zooplankton production in lakes invaded by
333 *Bythotrephes*. This was likely the result of significant reductions in zooplankton abundance in the
334 epilimnion, as there was no difference in other factors that influence productivity, such as egg
335 production, chlorophyll *a*, and temperature, in invaded lakes compared to non-invaded lakes.
336 Although previous studies have observed declines in overall zooplankton abundance (Yan and
337 others 2001; Strecker and others 2006), this is the first study to detect negative effects of
338 *Bythotrephes* on epilimnetic zooplankton production in multiple lakes and reduced production in
339 several functional groups (calanoids, cyclopoids, and small cladocerans) within the epilimnion.
340 The substantial declines in epilimnetic production are likely the result of a combination of direct
341 predation on zooplankton by *Bythotrephes*, as well as behavioural shifts away from the epilimnion
342 to cooler darker habitat. Although we cannot determine the relative importance of predation
343 versus migration, what remains is that the epilimnion of lakes has dramatically changed following
344 the invasion of *Bythotrephes*, and that there is significantly less productivity available to foraging
345 species. Although few studies exist that compare secondary productivity across different

346 predatory regimes, our results are similar in magnitude to those observed in a fish biomanipulation
347 experiment, where the introduction of piscivores into a piscivore-free lake resulted in reductions in
348 planktivorous fish, increased biomass of the native invertebrate predator *Chaoborus*, and
349 significant declines in zooplankton productivity (Ramcharan and others 2001). This suggests that
350 the introduction of non-native species can act in an analogous fashion to the complete restructuring
351 of a lake food web by the introduction of a top predator.

352 We observed an increase in productivity in the hypolimnion in some invaded lakes, which
353 likely results from predator-induced habitat shifts. As discussed above, diel vertical migrations of
354 zooplankton can confound estimations of secondary productivity. However, it is unlikely that
355 these migrations influenced our estimates of epilimnetic or hypolimnetic production because we
356 have no evidence that zooplankton migrated downwards from the epilimnion at night, and
357 zooplankton migration upwards from the hypolimnion at night was minor (S. Arnott ,
358 *unpublished*). However, we may have underestimated metalimnetic production in invaded lakes,
359 as diel migrations from the warmer epilimnion at night to the cooler metalimnion during the day
360 may be a response of some zooplankton taxa to *Bythotrephes*. Dumitru and others (2001)
361 examined the effect of *Bythotrephes* on whole water column zooplankton production in a single
362 lake, and therefore did not consider the spatial distribution of production. Pangle and Peacor
363 (2006) and Pangle and others (2007) demonstrated that *Bythotrephes* can induce cladoceran taxa to
364 migrate into the hypolimnion to avoid predation, with significant costs as a result of exposure to
365 cooler temperatures: our results extend their findings to the entire zooplankton community over a
366 greater part of the ice-free season. The non-lethal costs of these migrations may be substantial.
367 Using Harp Lake as an example, we estimate that epilimnetic production would be about 44%
368 greater if ~50% of zooplankton (based on differences in hypolimnetic abundance between Harp

369 and reference lakes) in the hypolimnion of Harp Lake are epilimnetic species that have
370 behaviourally shifted habitats to avoid *Bythotrephes*.

371 There was considerable among-lake variability in response to the invasion of *Bythotrephes*.
372 Although the hypolimnion of some invaded lakes made substantial (> 25%) contributions to total
373 seasonal productivity, the hypolimnion contributed very little to overall productivity in other
374 invaded lakes (< 4%). This variability in invaded lakes may be partly due to differing planktivore
375 communities. Planktivores may influence the vertical distribution of *Bythotrephes*, which may, in
376 turn, influence the distribution of zooplankton. A concurrent study in two of our invaded lakes
377 revealed that *Bythotrephes* distribution is indeed related to the presence of the cold-water
378 planktivore, cisco (Young and Yan 2008), suggesting that other components of the food web may
379 mediate the effects of *Bythotrephes* on crustacean zooplankton.

380 In addition to spatial shifts in productivity, we observed seasonal shifts in invaded lakes
381 during periods when *Bythotrephes* was not present, i.e., in the spring before population growth
382 rates increase. In three of the four invaded lakes, there was a large pulse in small cladoceran
383 epilimnetic production early in the season, likely from above average egg production per
384 individual small cladoceran in two of the invaded lakes, in combination with greater abundances in
385 May and early June. This suggests that small cladocerans may alter their life history, at least in
386 some lakes, by shifting reproduction to earlier in the season to avoid the invader. This is in
387 agreement with another field study, where temporal shifts in copepod egg production were
388 observed as a result of the presence of a fish predator (Hairston Jr. and Walton 1986).

389 Increased production of other intermediate trophic levels may offset reduced epilimnetic
390 crustacean production. For instance, rotifers were more abundant in lakes invaded by
391 *Bythotrephes*, especially the colonial *Conochilus* (Hovius and others 2006), which has high
392 intrinsic rates of increase (Allan 1976) and is probably an inedible prey item for *Bythotrephes*.

393 However, rotifers likely do not substitute for crustacean zooplankton as prey for fish (Threlkeld
394 1988). In addition, Sherwood and others (2002) showed that the lack of large-bodied prey groups
395 could reduce the efficiency of energy transfer to fish in metal-polluted lakes with simplified food
396 webs, implying that the loss of typical prey in invaded lakes may prevent higher trophic levels
397 from reaching their normal body size.

398 The spatial, temporal, and taxonomic redistribution of secondary production in
399 *Bythotrephes*-invaded lakes will likely have important implications for aquatic food webs. Shifts
400 in zooplankton reproduction from the epilimnion to the hypolimnion may negatively affect
401 epilimnetic-feeding fish species that rely on zooplankton, such as larval cisco, which inhabit
402 surface waters (Oyadomari and Auer 2004), and are highly reliant on crustaceans as their prey
403 (Davis and Todd 1998). In addition, cold-water planktivores (i.e., adult cisco), would be unlikely
404 to benefit from this shift since they have reduced foraging success in poorly-lit waters (Milne and
405 others 2005) and tend to prefer temperatures around 12°C (Rudstam and Magnuson 1985), which
406 falls into the metalimnion in most of our lakes.

407

408 *Impact of Zooplankton on Phytoplankton*

409 Despite experimental results that were suggestive of reduced control of the algal
410 community by the zooplankton community, we did not observe the expected changes in
411 phytoplankton biomass (as measured by chlorophyll *a*) at the lake-level in *Bythotrephes*-invaded
412 lakes. Even though low productivity lakes, such as those in our study, are predicted to be
413 influenced more by bottom-up, rather than top-down, forces (Jeppeson and others 2003),
414 significant effects of zooplankton on phytoplankton biomass have been observed in other
415 oligotrophic lakes (Sarnelle and Knapp 2005). The weak overall effects of zooplankton on
416 phytoplankton echo the experimental results of Sommer and others (2001), where increased

417 abundance of zooplankton functional groups had no effect on total phytoplankton biomass. Pérez-
418 Fuentetaja and others (2000) also found that zooplankton had a weak influence on chlorophyll in
419 oligo- and meso-trophic lakes. Thus, it appears that the invasion of *Bythotrephes* will probably not
420 have a large cascading effect on phytoplankton biomass in lower productivity lakes, despite large
421 reductions in epilimnetic zooplankton biomass (>70%). However, more productive lakes may be
422 more likely to respond to top-down changes (Jeppesen and others 2003), and although
423 *Bythotrephes* seems to prefer oligotrophic lakes, it has been found in some mesotrophic systems
424 (Jarnagin and others 2000), suggesting that the invader may have the potential to instigate
425 increases in algal biomass in lakes of moderate productivity.

426

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577

578 APPENDIX 1. Planktivorous fish and *Mysis relicta* categorical abundance in study lakes. Fish data
 579 provided by Ontario Ministry of Natural Resources (*unpublished*) and *Mysis* data from Nordin
 580 (2005). Lakes sorted by increasing *Bythotrephes* abundance.

Lake	Cisco (<i>Coregonus</i> <i>artedi</i>)	Rainbow smelt (<i>Osmerus</i> <i>mordax</i>)	Lake whitefish (<i>Coregonus</i> <i>clupeaformis</i>)	Yellow perch (<i>Perca</i> <i>flavescens</i>)	<i>Mysis</i> <i>relicta</i>
Not Invaded					
Buck	A/P	A	A	P	H
Doe	L	A	L	P	L
Pickerel	L	A/P	A	P	H
Sand	L	H	A	P	L
Invaded					
Harp	H	A	A	P	M
Vernon	A	M	A	P	L
Bernard	A/P	L/M	H	P	L
Peninsula	A	M	A	P	M

581 A = absent
 582 A/P = absent, but detected in past
 583 P = present
 584 L = low
 M = medium
 H = high

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590

591

592

593 FIGURE CAPTIONS

594
595 Figure 1. Total secondary production ($\text{mg m}^{-2} \text{ season}^{-1}$) of *Bythotrephes* (■) and zooplankton in
596 the epilimnion (□), metalimnion (■), and hypolimnion (■) of invaded and reference lakes. For
597 the purposes of our study, we define the season as the middle of May to the middle of September.

598
599 Figure 2. On the left axis, average secondary production of zooplankton of invaded (□) and
600 reference (■) lakes ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) and on the right axis, average seasonal production (mg m^{-2}
601 season^{-1}) of invaded (□) and reference (■) lakes in the (a) epilimnion, (b) metalimnion, and (c)
602 hypolimnion ($n = 4$, except reference lake hypolimnion where $n = 3$). Production is calculated
603 from two adjacent sampling dates, so the value shown represents that of the following two-week
604 interval, i.e. the value from the middle of May represents the sampling period from then until early
605 June. Sampling occurred approximately fortnightly (mean: 13.5 days) and we define the season as
606 the middle of May to the middle of September. Error bars are ± 1 standard error.

607
608 Figure 3. Average biweekly secondary production ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) in calanoids (a-c),
609 cyclopoids (d-f), large cladocerans (g-i), and small cladocerans (j-l) in the epi-, meta-, and
610 hypolimnion of invaded (□) and reference (■) lakes ($n = 4$, except reference lake hypolimnion
611 where $n = 3$). Sampling occurred approximately fortnightly (mean: 13.5 days). Error bars are ± 1
612 standard error.

613
614 Figure 4. Average abundance of small cladocerans, large cladocerans, cyclopoids, and calanoids
615 (individuals L^{-1}) in the epilimnion (a-b), metalimnion (c-d), and hypolimnion (e-f) of invaded and
616 reference lakes.

617 Figure 5. Average number of eggs individual⁻¹ of entire zooplankton community in each strata in
618 invaded (□) and reference (■) lakes (left column: a,d,g) and for each functional group in the
619 epilimnion (b,c), metalimnion (e,f), and hypolimnion (h,i) of invaded and reference lakes (n = 4,
620 except reference lake hypolimnion where n = 3). Error bars are ±1 standard error. Note that the
621 ratio of eggs to individuals for separate functional groups does not sum to equal the average of the
622 entire community as a result of different densities of zooplankton in each group.

623
624 Figure 6. Epi- and metalimnetic zooplankton production (◆; mg m⁻² fortnight⁻¹) and *Bythotrephes*
625 consumption (■; mg m⁻² fortnight⁻¹) in invaded lakes, contrasted with *Bythotrephes* abundance
626 (△; individuals m⁻³) on the right axis. In each panel, the top bracketed value is the percent of total
627 seasonal zooplankton production consumed by *Bythotrephes*, and the bottom bracketed value is
628 the percent of seasonal production consumed by *Bythotrephes* starting in the middle of June.
629 Asterisk (✱) indicates the dates on which *Bythotrephes* consumption exceeded zooplankton
630 production. Sampling occurred approximately fortnightly (mean: 13.5 days).

631
632 Figure 7. (a) Percent change in algae during zooplankton impact experiment in invaded (□; n = 2)
633 and reference lakes (■; n = 3). Positive values indicate that phytoplankton increased during the
634 experiment, while negative numbers indicate a decrease in algae. (b) Total chlorophyll *a* (μg L⁻¹)
635 of all invaded (□) and reference (■) lakes (n = 4). Error bars are ±1 standard error.

636

637 TABLE CAPTIONS

638 Table 1. Morphometric, physical, chemical, and biotic characteristics of study lakes. A one-way
639 ANOVA was performed on parameters ($n = 4$, treatment $df = 1$, error $df = 6$). Lakes sorted by
640 increasing *Bythotrephes* abundance. Lat = latitude, long = longitude, Z_{\max} = maximum depth, Ca =
641 calcium, DOC = dissolved organic carbon, Cond = conductivity, TP = total phosphorus, chl a =
642 chlorophyll a .

643
644 Table 2. Repeated measures ANOVAs on stratified and whole water column zooplankton
645 secondary production, total zooplankton abundance, and eggs individual⁻¹. The mean effect size of
646 production is calculated by summing all the sampling dates and then averaging between lakes in
647 each category. The mean effect size of abundance and eggs individual⁻¹ is calculated by averaging
648 all of the lakes in each category on all dates.

649
650 Table 3. Repeated measures ANOVAs on zooplankton secondary production for each functional
651 group. The mean effect size of production is calculated by summing all the sampling dates and
652 then averaging between lakes in each category.

653
654 Table 4. Repeated measures ANOVAs on zooplankton egg production per individual for each
655 functional group. The mean effect size is calculated by averaging all of the lakes in each category
656 on all dates

657 TABLE 1.

Lake	Lat Long	Z _{max} (m)	Area (ha)	Ca (mg L ⁻¹)	DOC (mg L ⁻¹)	Cond (µmhos cm ⁻¹)	pH	TP (µg L ⁻¹)	Mean total chl <i>a</i> (µg L ⁻¹)
Reference									
Buck*	45°25'N, 79°23'W	23.0	656.0	2.6	10.7	25.6	6.3	13.3	2.8
Doe*	45°32'N, 79°25'W	23.0	1187.0	3.6	7.0	46.0	7.1	12.0	3.4
Pickerel*	45°41'N, 79°18'W	38.0	513.0	2.8	6.7	32.4	6.8	8.1	4.4
Sand	45°37'N, 79°10'W	59.0	568.2	3.5	6.0	37.2	6.8	7.1	2.0
Mean		35.8	731.1	3.1	7.6	35.3	6.8	10.1	3.1
Invaded									
Harp*	45°23'N, 79°07'W	37.5	71.7	3.0	6.7	38.0	7.0	7.2	1.7
Vernon*	45°20'N, 79°17'W	37.2	1505.1	3.0	7.1	36.8	6.8	7.9	2.8
Bernard	45°45'N, 79°23'W	47.9	2057.7	4.1	3.4	65.2	7.1	9.6	2.8
Peninsula	45°20'N, 79°06'W	34.1	864.8	4.4	6.1	70.6	7.1	9.0	2.6
Mean		39.2	1124.8	3.6	5.8	52.7	7.0	8.4	2.5
<i>F</i> -ratio		0.14	0.75	1.04	1.74	3.10	1.96	1.16	1.51
<i>p</i> -value		0.72	0.42	0.35	0.23	0.13	0.21	0.32	0.27

658 * lakes included in grazing experiment

659

660 TABLE 2.

Measure	Stratum	Invasion		Time		Time × Invasion		Mean effect size
		$F_{1,6}$	p	$F_{7,42}^a$	p	$F_{7,42}^a$	p	
Secondary production	Epilimnion	9.68	0.02*	2.13	0.11	1.31	0.29	-67%
	Metalimnion	0.03	0.87	5.19	<0.01*	0.58	0.75	+15%
	Hypolimnion‡	3.46	0.12	1.77	0.13	0.43	0.88	+766%
	All strata	1.24	0.31	1.85	0.14	0.64	0.65	-35%
Total abundance	Epilimnion	16.91	<0.01*	17.48	<0.01*	6.55	<0.01*	-59%
	Metalimnion	0.80	0.40	8.08	<0.01*	0.80	0.56	+55%
	Hypolimnion‡	1.78	0.24	4.02	<0.01*	0.50	0.85	+137%
	All strata	0.42	0.54	12.03	<0.01*	0.80	0.61	-17%
Eggs individual ⁻¹	Epilimnion	1.90	0.22	1.56	0.19	1.06	0.41	-17%
	Metalimnion	0.01	0.91	2.86	0.08†	0.19	0.88	+10%
	Hypolimnion‡	6.04	0.06†	4.70	0.02*	1.63	0.23	+213%
	All strata	1.74	0.24	3.58	<0.01*	1.52	0.20	-20%

661 * $p < 0.05$, † $p < 0.10$ 662 ‡ Invasion error df = 5, Time × Invasion error df = 35; total abundance Time × Invasion
663 error df = 40664 ^a total abundance: $F_{8,48}$

665 TABLE 3.

Stratum	Functional group	Invasion		Time		Time × Invasion		Mean effect size
		$F_{1,6}$	p	$F_{7,42}$	p	$F_{7,42}$	p	
Epilimnion	calanoids	10.50	0.02*	3.95	<0.01*	0.77	0.62	-90%
	cyclopoids	54.02	<0.01*	4.10	<0.01*	1.64	0.17	-57%
	large cladocerans	2.48	0.17	1.62	0.21	0.14	0.95	-61%
	small cladocerans	24.97	<0.01*	3.45	0.02*	5.45	<0.01*	-17%
Metalimnion	calanoids	2.71	0.15	3.79	0.02*	0.53	0.71	+250%
	cyclopoids	0.05	0.83	4.61	0.01*	0.56	0.65	+45%
	large cladocerans	2.07	0.20	4.01	<0.01*	2.12	0.07†	-90%
	small cladocerans	0.04	0.85	1.64	0.19	1.47	0.24	+96%
Hypolimnion‡	calanoids	9.70	0.03*	1.15	0.36	0.43	0.81	+61%
	cyclopoids	0.35	0.58	5.48	<0.01*	1.97	0.09†	+964%
	large cladocerans	0.57	0.48	2.08	0.17	0.52	0.61	+6188%
	small cladocerans	0.03	0.88	1.77	0.18	0.79	0.53	-4%

666 * $p < 0.05$, † $p < 0.10$

667 ‡ Invasion error df = 5, Time × Invasion error df = 35

668

669 TABLE 4.

Stratum	Functional group	Invasion		Time		Time × Invasion		Mean effect size
		$F_{1,6}$	p	$F_{7,42}$	p	$F_{7,42}$	p	
Epilimnion	calanoids	3.15	0.13	1.16	0.35	1.01	0.40	-72%
	cyclopoids	0.01	0.92	0.95	0.40	1.37	0.29	7%
	large cladocerans	0.65	0.45	2.42	0.09†	0.67	0.59	75%
	small cladocerans	0.02	0.89	2.58	0.05*	0.41	0.82	-4%
Metalimnion	calanoids	3.02	0.13	0.61	0.54	0.71	0.49	295%
	cyclopoids	0.09	0.77	2.59	0.12	0.08	0.92	-17%
	large cladocerans	1.90	0.22	1.26	0.32	0.40	0.77	-54%
	small cladocerans	0.07	0.80	3.01	0.05*	1.55	0.23	11%
Hypolimnion‡	calanoids	2.54	0.17	0.95	0.44	0.51	0.69	253%
	cyclopoids	4.04	0.10†	4.92	0.03*	3.44	0.07†	157%
	large cladocerans	0.01	0.99	1.20	0.34	1.26	0.33	-2%
	small cladocerans	1.20	0.32	3.12	0.08†	1.06	0.39	67%

670 * $p < 0.05$, † $p < 0.10$

671 ‡ Invasion error df = 5, Time × Invasion error df = 35

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673

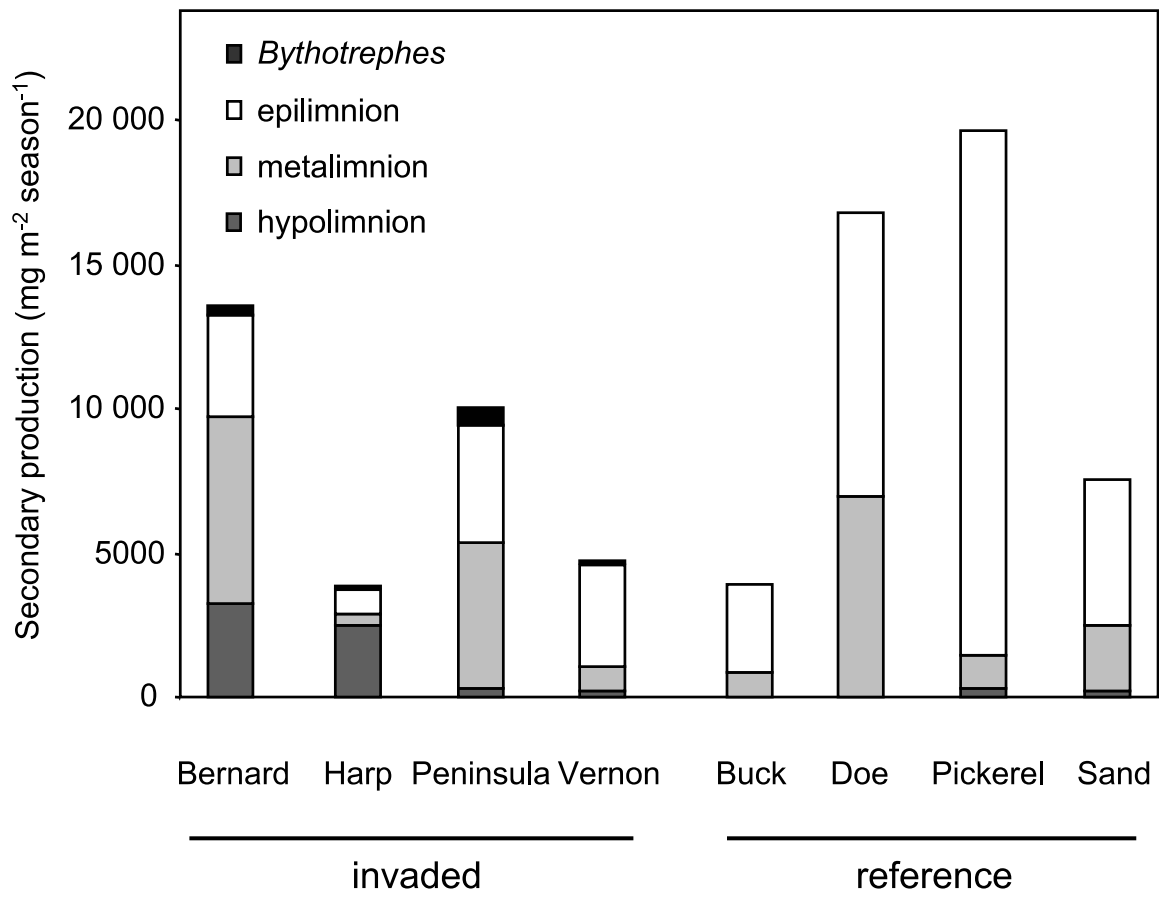


Fig. 1

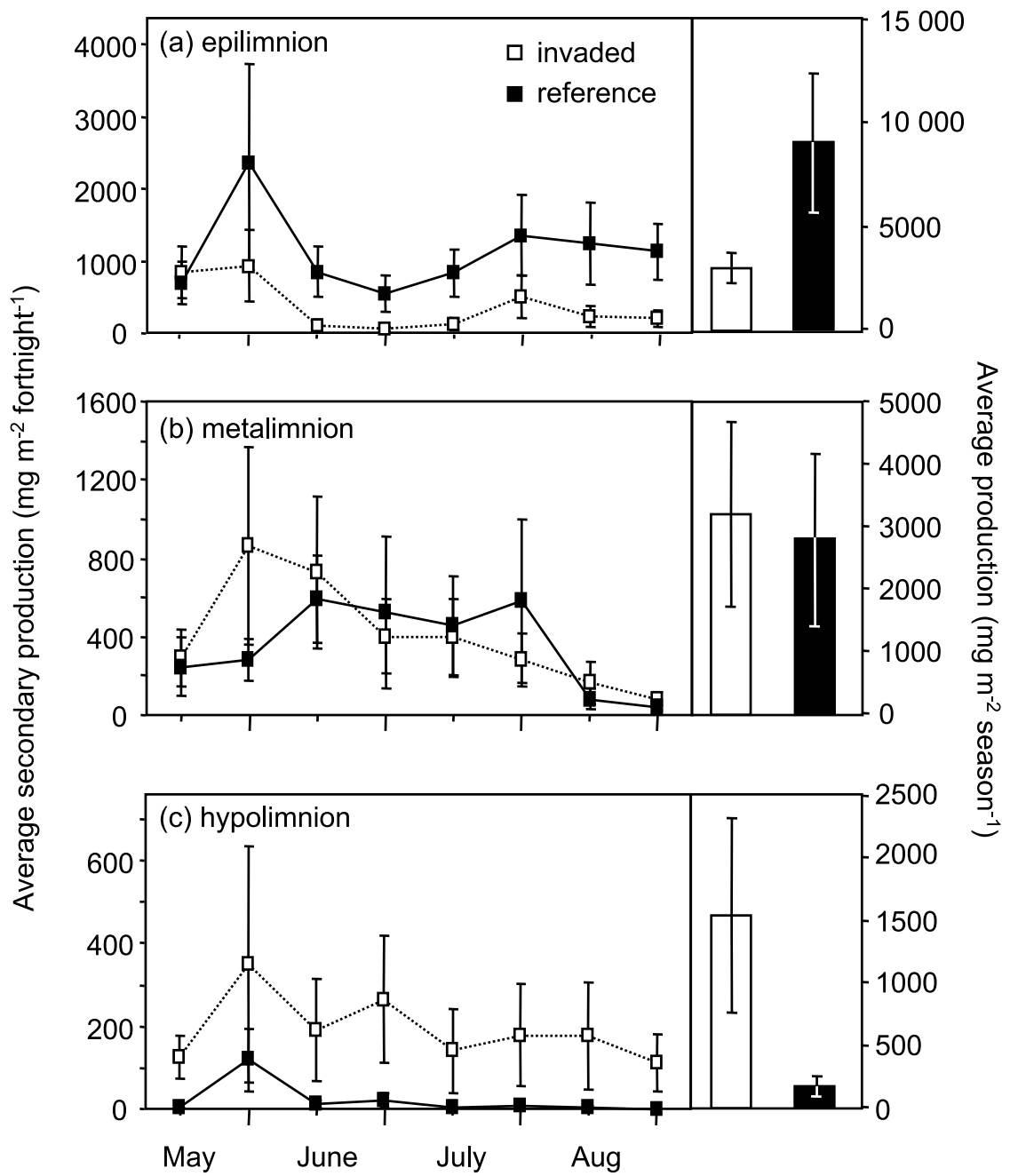


Fig. 2

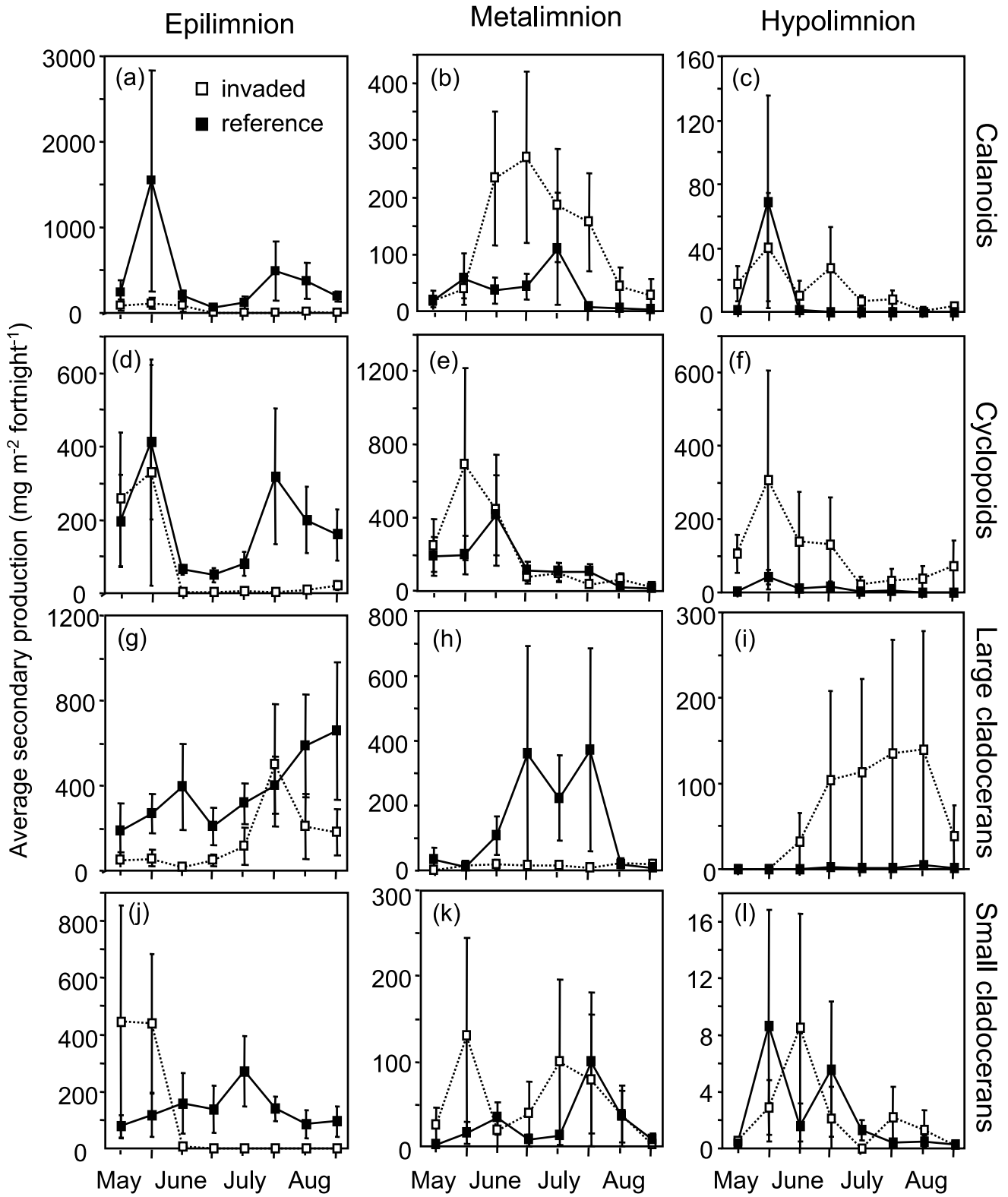


Fig. 3

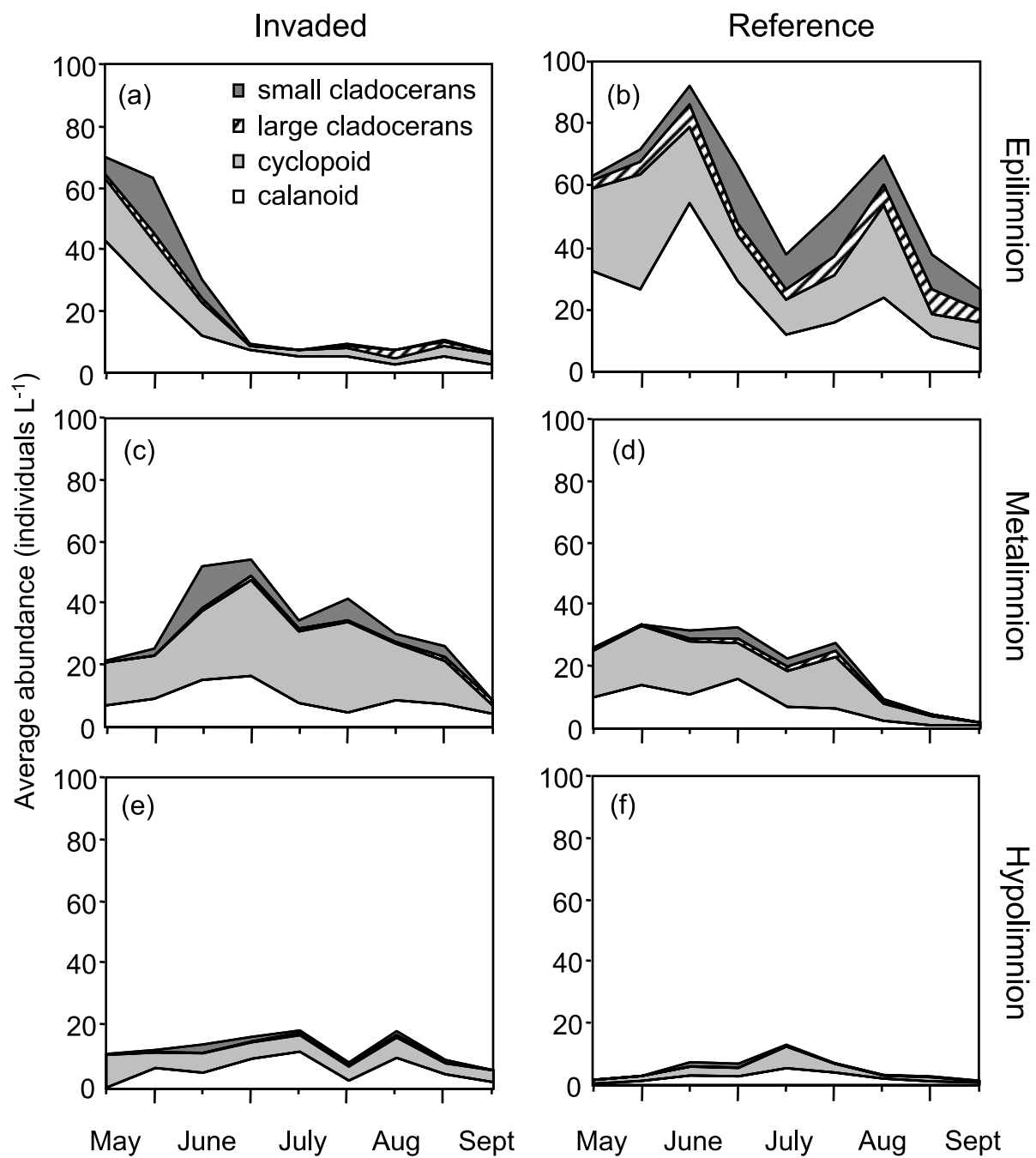


Fig. 4

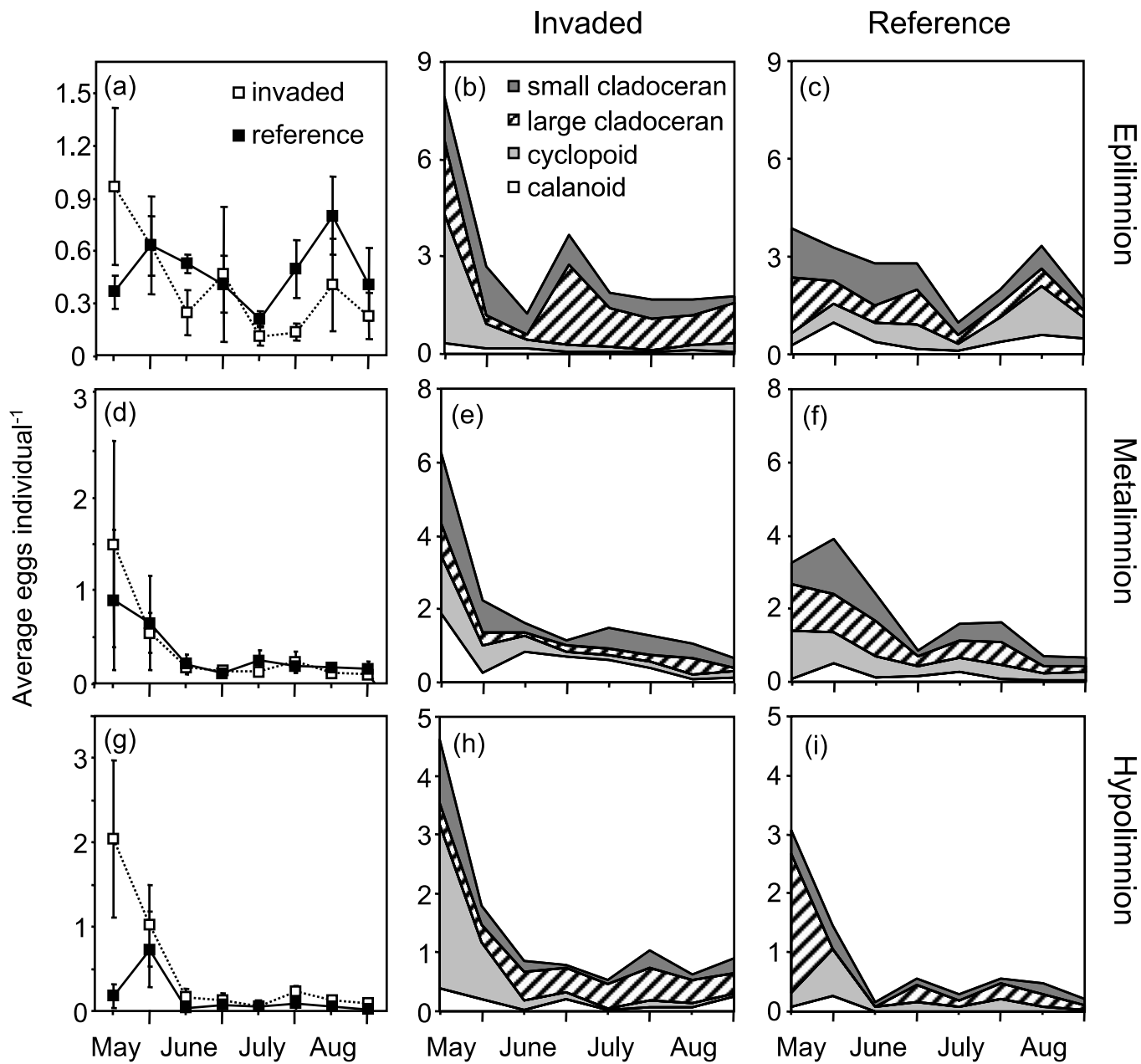


Fig. 5

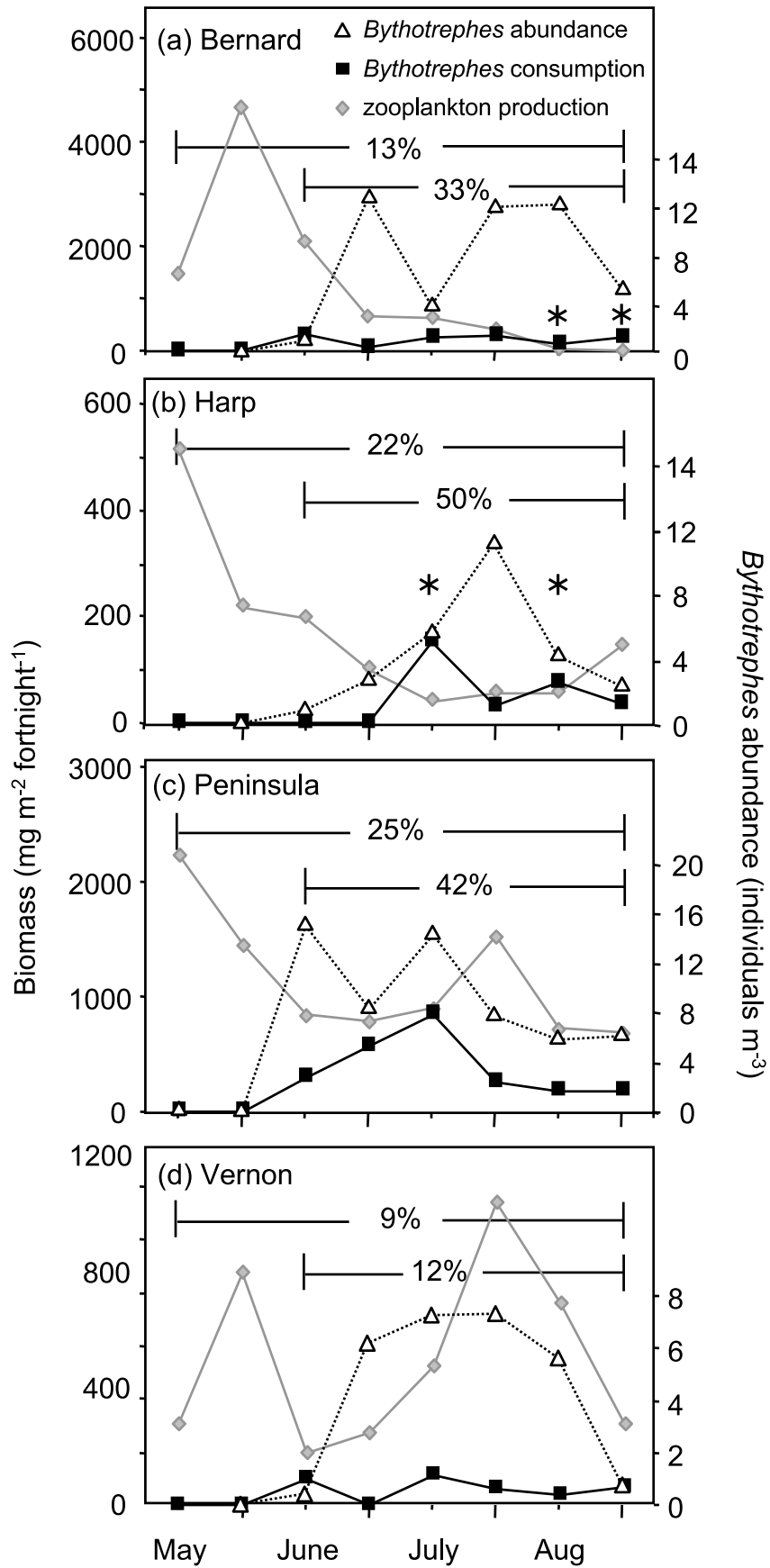


Fig. 6

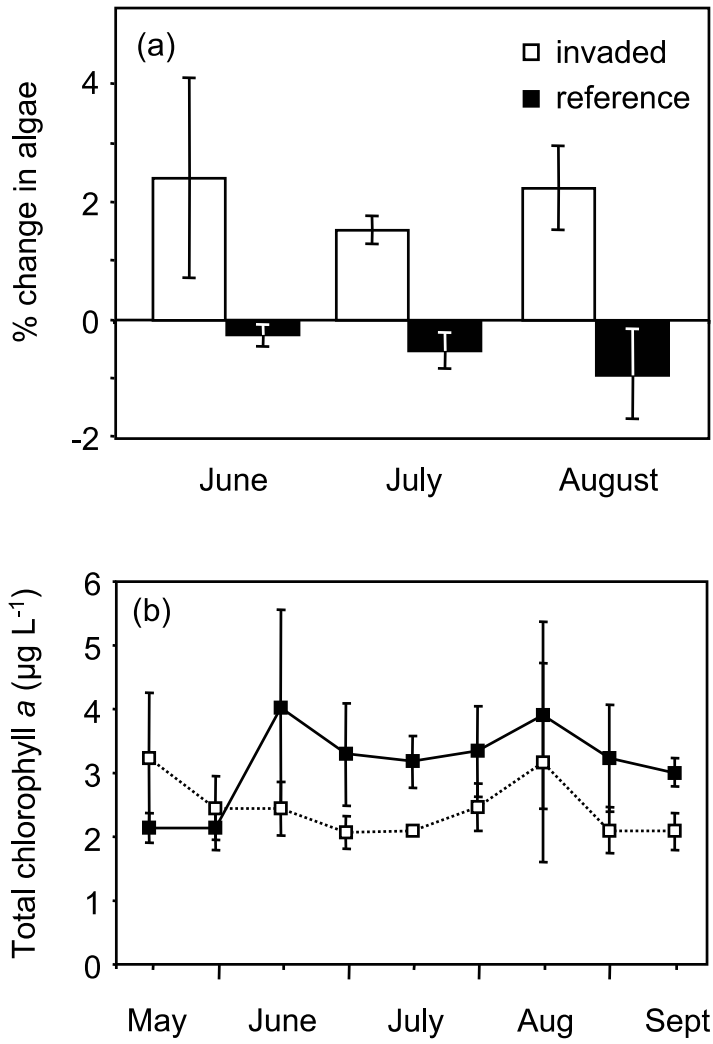


Fig. 7