

1 Do intraspecific or interspecific interactions determine responses to
2 predators feeding on a shared size-structured prey community?

3

4 Hanna ten Brink^{1,2}, Abul Kalam Azad Mazumdar¹, Joseph Huddart^{1,3}, Lennart Persson¹ &
5 Tom C. Cameron*^{1,4}

6

7 ¹Ecology & Environmental Sciences, Umeå University, Umeå, Sweden, 90742

8 ² present address Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam,
9 P.O. Box 94248, 1090 GB Amsterdam, The Netherlands

10 ³ present address Department of Life Sciences, Imperial College London, Ascot, UK, SL5 7PY

11 ⁴School of Biological Sciences, University of Essex, Colchester, UK, CO4 3SQ

12

13 * tcameron@essex.ac.uk

14

15

16 Keywords: *Bythotrephes*, Competition, Complexity, Emergent Facilitation, *Holopedium*, Invasive
17 Predator, Intraguild Predation, Ontogenetic Asymmetry, Predator Mediated Coexistence, Perch

18

19 Running Title: Experimental field test of Emergent Facilitation

20 No. of References: 69

21 No of Figures: 5

22 No of Tables: 1

23 This submission includes Supplementary online material

24

25 Statement of Authorship:

26 The field experiments were designed by TCC and LP, and undertaken and the data analysed by TCC
27 and HTB. AKAM, JH and TCC undertook the attack rate experiments. TCC, HTB and LP wrote the
28 manuscript.

29

30 **Abstract**

- 31 1. Coexistence of predators that share the same prey is common. This is still the case in
32 size structured predator communities where predators consume prey species of
33 different sizes (interspecific prey responses) or consume different size classes of the
34 same species of prey (intraspecific prey responses).
- 35 2. A mechanism has recently been proposed to explain coexistence between predators
36 that differ in size but share the same prey species, *emergent facilitation*, which is
37 dependent on strong intraspecific responses from one or more prey species. Under
38 emergent facilitation predators can depend on each other for invasion, persistence or
39 success in a size structured prey community.
- 40 3. Experimental evidence for intraspecific size-structured responses in prey populations
41 remain rare and further questions remain about direct interactions between predators
42 that could prevent or limit any positive effects between predators (e.g. intraguild
43 predation).
- 44 4. Here we provide a community wide experiment on emergent facilitation including
45 natural predators. We investigate both the direct interaction between two predators
46 that differ in body size (fish vs. invertebrate predator) and the indirect interaction
47 between them via their shared prey community (zooplankton).
- 48 5. Our evidence supports the most likely expectation of interactions between differently
49 sized predators, that intraguild predation rates are high and interspecific interactions
50 in the shared prey community dominate the response to predation (i.e. predator-
51 mediated competition). The question of whether emergent facilitation occurs
52 frequently in nature requires more empirical and theoretical attention, specifically to
53 address the likelihood that its pre-conditions may co-occur with high rates of
54 intraguild predation.

55

56

57

58

59

60

61 **Introduction**

62 Effects of predation on a diverse range of prey communities are often highly size-specific
63 where predators, depending on life history characteristics, can drive the prey communities
64 towards smaller or larger sizes (Zaret 1980; Kerfoot & Sih 1987; Hildrew, Raffaelli &
65 Edmonds-Brown 2007). In doing so predators induce an interspecific response in prey
66 communities by altering the abundance and coexistence patterns among differently sized prey
67 species (Sprules 1972; Milbrink & Bengtsson 1991; Gurevitch, Morrison & Hedges 2000;
68 Chase *et al.* 2002). Moreover, shifts in the size structure across prey communities may
69 feedback on predator performance and affect interactions between predators feeding on
70 differently sized prey species, an interspecific feedback (Dodson 1970). An alternative route
71 by which predator coexistence may be promoted by size selective predation is when predators
72 feed on different sizes/stages of the same prey species (De Roos *et al.* 2008).

73 Positive interactions between predators could occur via plastic responses of prey
74 species to one predator, a non-consumptive predation effect, which results in increased prey
75 availability to other predator species due to the a change in prey behaviour (Touchon *et al.*
76 2013). These multiple-predation-effects (MPEs) on prey survival however, are often found to
77 be non-additive which results in either negative or no effect of one predators actions on the
78 other (Vonesh & Osenberg 2003; Vonesh 2005; Touchon *et al.* 2013). Consumptive effects
79 of predators have also been predicted to lead to positive interactions between predators
80 through predator induced changes in prey population demography. Reduction in prey density
81 by one predator can reduce confusion effects or increase efficiency of a second predator
82 depending on the shape of its functional response (Vonesh & Osenberg 2003; McCoy *et al.*
83 2011). A less well appreciated effect of size-specific predation is reduction of prey density in
84 one stage or size class leading to increased densities of other size classes of prey (i.e. through
85 release of density and stage dependent vital rates (De Roos *et al.* 2007)). Stage-structured
86 biomass overcompensation is an intraspecific prey response to mortality demonstrated in
87 experimental systems e.g. (Nicholson 1957; Cameron & Benton 2004; Schroder, Persson &
88 de Roos 2009), and is predicted to occur wherever there are differences between life history
89 stages in their net response to increasing resource availability, leading to ontogenetic
90 asymmetry (Persson *et al.* 1998; De Roos, Metz & Persson 2013; Persson & de Roos 2013).
91 Shifts in prey biomass caused by one predator could lead to facilitation between predators that

92 specialise on different sizes of the same prey species. This phenomenon, emergent facilitation,
93 was identified in the analysis of stage structured predator-prey models (De Roos *et al.* 2008).

94 De Roos *et al.* (2008) and De Roos & Persson (2013) discussed several systems where
95 the occurrence of an intraspecific prey response to predation could lead to emergent
96 facilitation (e.g. terrestrial invertebrates (Nicholson 1957; Cameron & Benton 2004), aquatic
97 invertebrates (Murdoch & Scott 1984; Leibold & Tessier 1991), aquatic vertebrates (Olson,
98 Green & Rudstam 2001; Zimmerman 2006)). While intuitively emergent facilitation should
99 be possible in other stage or size-structured systems such as parasitoid-host communities or
100 estuarine and marine food webs, clear empirical evidence of such intraspecific responses
101 within prey giving rise to emergent facilitation is absent. It is clear that for emergent
102 facilitation to occur, the responses of prey communities to mortality should be dominated by
103 strong intraspecific interactions (in one or more species) such that competition leads to an
104 increase in biomass production in one or other stage/class in response to mortality.

105 We therefore present an experimental study of the interaction between two differently
106 sized predators that share the same prey community, and more specifically we test for the role
107 of intraspecific or interspecific responses of prey species to size-selective predation. One
108 predator, European perch (*Perca fluviatilis*) has a large average size and feeds on large or
109 adult zooplankton and macroinvertebrates (Bystrom, Huss & Persson 2012; Nunn, Tewson &
110 Cowx 2012). The other predator, the invertebrate *Bythotrephes longimanus*, is small and
111 largely feeds on small or juvenile zooplankton prey (Vanderploeg, Liebig & Omair 1993; Yan
112 & Pawson 1997; Wahlström & Westman 1999; Yurista *et al.* 2010). This is a suitable system
113 to study as Huss and Nilsson provided evidence that emergent facilitation between perch and
114 *Bythotrephes* could occur due to positive size-selective predation on the large cladoceran;
115 *Holopedium gibbernum* (2011). However this study did not take into account predation by
116 perch on *Bythotrephes* in addition to their sharing of prey. Therefore, despite the theoretically
117 and empirically demonstrated potential of an intraspecific response of prey to predation (De
118 Roos *et al.* 2008; Huss & Nilsson 2011), empirical evidence including all major ecological
119 feedbacks are still missing (e.g. intraguild predation, continuous predator presence).

120 We undertook a large scale lake enclosure experiment where we tested the effects of
121 *Bythotrephes*, Young-of-Year perch (YOY, 12-30mm) and larger One-Year-Old juvenile
122 perch (OYO, 80-100mm) in isolation or in combination on the abundance of each other and

123 on the abundance and size structure of their shared zooplankton prey community. We have
124 combined this with laboratory and field experiments to estimate size-dependent attack rates of
125 perch and *Bythotrephes* feeding on zooplankton or of perch feeding on *Bythotrephes* (i.e.
126 IGP). Our objectives were to **(1)** characterise the different size-selective effects of predators
127 on prey species/communities (e.g. YOY, OYO and *Bythotrephes*); **(2)** determine which of
128 any predators undergoes significant shift in predation effect through the season (e.g. as a
129 consequences of growth); **(3)** to determine whether *Holopedium* undergoes compensatory
130 shifts in absolute biomass of smaller individuals in response to predation (e.g. intraspecific
131 response or emergent facilitation) and **(4)** to characterise the net interaction between the
132 vertebrate predator, perch, and the invertebrate predator *Bythotrephes*. Our results support that
133 predation on zooplankton results in shifting prey community species composition, perch and
134 *Bythotrephes* largely avoid competition through niche separation and intraguild predation
135 (IGP) by perch on *Bythotrephes* is comparatively high.

136

137 **Materials and Method**

138 *Site description*

139 The enclosure experiments, and field collection for feeding trials, were conducted at an
140 Experimental Lake Research Area in central Sweden (64°477'N, 19°429'E). Further
141 particulars about the site are published (Persson *et al.* 1996).

142 *Enclosure experiment: description of enclosures*

143 Enclosure experiments were conducted in 32 transparent mesocosm enclosures in Lake
144 Abborrtjärn 3 (AT3) in the summer of 2012. The enclosures had a diameter of 1.6 meter and
145 were 6.5 meter deep; the volume was 13 m³. Each enclosure was attached to a floating
146 wooden frame. The frames were placed in two sets each with two rows of eight mesocosms.
147 There were three pontoons between two of these rows. The distance between the two sets of
148 pontoons and their attached enclosures was approximately 8 m. Both pontoons were placed in
149 an east-west position. We used 16 of the 32 enclosures for this experiment, of which 12 were
150 attached to the first set of pontoons and 4 to the second.

151 *Inoculation of enclosures*

152 In the last week of May (29-31st May) the enclosures were filled with lake water. The
153 enclosures were assigned to one of 4 treatments with 4 replicates each. As the primary
154 question of interest was the fate of and effect of predators in different predator-predator
155 interactions, the treatments were *Bythotrephes* only (control), YOY perch only, both
156 *Bythotrephes* and YOY perch or both *Bythotrephes* and 1 year old perch (hereafter OYO
157 perch). To prevent inoculation of *Bythotrephes* in the enclosures that were assigned to the
158 YOY perch only treatment, the lake water was filtered through 50 μm -mesh nylon net. On the
159 4th of June zooplankton was collected from the lake with a 0.5-mm mesh zooplankton net
160 (diameter 0.6 m). The zooplankton were inspected for *Bythotrephes*, and any removed, before
161 adding to the four enclosures that were assigned to the YOY perch only treatment. This
162 ensured that the species composition in this treatment was the same as in others other than
163 receiving no *Bythotrephes*. One week later (11-12th June) the enclosures were inoculated with
164 12 YOY perch individuals (YOY perch treatment), 50 *Bythotrephes* individuals (*Bythotrephes*
165 only treatment), both (*Bythotrephes* and YOY treatment) or 50 *Bythotrephes* individuals and
166 two OYO perch (*Bythotrephes* + OYO treatment). The densities used correspond to 0.9 YOY
167 perch per m^3 , 0.15 OYO perch per m^3 and 3.8 *Bythotrephes* per m^3 . Two weeks later (26-27th
168 June) all enclosures containing *Bythotrephes* were inoculated with an additional 100
169 *Bythotrephes* individuals such that the density was 11.5 per m^3 corresponding to average
170 natural densities in Lake AT3 at this time of year ($12.6 \pm 3.3\text{s.e.}$). Because survival of YOY
171 perch in the mesocosms is substantially higher than in the lakes, we used a lower initial
172 density than the average natural density around this time of year (mean $2.7 \pm 0.67\text{s.e.}$) to
173 capture the average density over the experimental period. Densities of OYO perch were
174 higher than in the lake, but allowed for death of any one fish of the two per mesocosm.

175 *Sampling enclosures*

176 The first sampling of zooplankton was taken one week after the initial inoculation of perch
177 and *Bythotrephes* (on 3-4th July). Thereafter samples were taken once a week for a period of 7
178 weeks. *Bythotrephes* were sampled once a week for a period of five weeks starting three
179 weeks after the inoculation, this was because *Bythotrephes* densities were too low at the start
180 of the experiment. At each sampling occasion the position of the thermocline was determined
181 with a thermistor. Zooplankton samples were taken separately from the epilimnion and
182 hypolimnion. Because ours and previous experiments showed that epilimnetic and
183 hypolimnetic samples were qualitatively similar (Wahlström & Westman 1999), we present

184 only the epilimnetic data. Zooplankton were sampled with vertical hauls using a 100- μ m
185 mesh net (diameter 0.25 m). Samples were first put in carbonated water 10 seconds to
186 anaesthetise the zooplankton. This prevents the zooplankton from releasing eggs in response to
187 preservative fluid. After this the zooplankton samples were preserved in Lugol's solution. In
188 the laboratory the zooplankton was classified under an Olympus inverted microscope
189 (magnification 2X). All *Holopedium* individuals were counted and measured. For each other
190 taxon a subsample (~1/10 of the sample) was counted and the body length of at least 10
191 individuals (all, if fewer) was measured. The lengths were transformed to biomass using
192 length to weight regressions (Bottrell et al. 1976). Total biomass was calculated per species
193 and for different size classes. Five size classes were used (1: up to 0.4 mm, 2: 0.4-0.6 mm, 3:
194 0.6-0.8 mm, 4: 0.8-1.0 mm, 5: >1 mm). The number of eggs per female was counted for
195 *Holopedium*. From week three, the full depths of the enclosures were sampled weekly for
196 *Bythotrephes* with a 0.5-mm mesh net (diameter 0.6 m). *Bythotrephes* were counted in the
197 field and then preserved in Lugol's solution. At the termination of the experiment (31 July)
198 the full depth of the enclosures was sampled for YOY perch with a 0.5-mm mesh net
199 (diameter 1.6 m) to get an estimate about the number of fish that survived. Because only a few
200 fish were caught this way, one week later (7 August) the enclosures were inspected for 15
201 minutes each and any fish were caught with a hand net.

202 As an estimate of phytoplankton biomass chlorophyll-a content was measured halfway
203 through (week 4) and at the end (week 7) of the experiment in half of the mesocosm
204 enclosures. Samples were taken at the thermocline with a Ruttner water sampler after mixing
205 the water column. From each sample 100 ml was filtered through Whatman GF/C filters. The
206 filters were dried and frozen until further analyses. The algae on the filters were extracted in
207 ethanol for 24 hours and the absorbance at 433 and 673 nm was measured in a
208 spectrophotometer.

209 *Statistical analyses*

210 One of the enclosures (*Bythotrephes* only treatment) looked less full than the others. During
211 the experiment we also observed a YOY perch in this enclosure. Based on these two
212 observations we concluded that there was a hole in the mesocosm. Because of this the data
213 from this enclosure were removed from the analyses. There were thus 3 replicates for the
214 treatment with *Bythotrephes* only and 4 replicates for the other three treatments.

215 To investigate whether there was a positive effect of perch on *Bythotrephes* due to
216 emergent facilitation, we tested the effects of treatment and time on the densities of
217 *Bythotrephes*, the biomass of juvenile and adult *Holopedium* individuals and the proportion of
218 fecund *Holopedium* individuals. Generalized linear mixed models (GLMM's) with mesocosm
219 as the random intercept were used. The data were poisson distributed and therefore log-link
220 functions, or binomial and ratios, were used. Models were tested for overdispersion and if
221 needed fitted using a quasi-distribution to account for this. Based on the experimental design,
222 a series of apriori candidate models were selected based on the explanatory variables and their
223 interactions (e.g. holopedium biomass ~ week, ~ predator treatment, ~ week + predator
224 treatment, etc). Each candidate model was fitted using maximum likelihood estimation using
225 the Laplacian approximation. To determine the best predictive model we calculated the
226 Akaike Information Criteria score for each model, using the best practice for GLMM (e.g.
227 AIC) (Burnham & Anderson 2002). The best model(s) was selected based on its Akaike
228 weight relative to all models in the candidate set (Burnham & Anderson 2002). The
229 significance of effects in the selected best model(s) was then determined with a likelihood
230 ratio test. A Wald Z-test was used to evaluate the properties of individual coefficients. The
231 biomass of *Holopedium* after week 5 of the experiment was very low and therefore week 6
232 and 7 were not included in the models that tested the effect of treatment on *Holopedium*
233 biomass and fecundity. A breakdown of model weights and the selection of the best model(s)
234 for each analysis are listed in Tables S1 and S2 in the supplementary material. In figures we
235 present the weekly mean or final number of predators and zooplankton biomass, with bias
236 corrected and adjusted bootstrapped estimates of treatment confidence intervals based on
237 1000 resamples.

238 Multivariate analysis was used to investigate the effects of different predators on the
239 species and size composition of the zooplankton prey community. This was done with
240 redundancy analysis (RDA). RDA is an ordination method that is comparable with principal
241 component analysis (PCA) (ter Braak. 1995). The ordination axes in RDA are, however,
242 constrained to be linear combinations of the environmental variables (predator treatments).
243 The axes in RDA thus only reflect the variation that can be explained by the different
244 treatments. RDA were performed on the biomasses of the most abundant zooplankton species
245 (*Holopedium*, *Bosmina*, *Ceriodaphnia*, *Calanoid copepods*, *Cyclopoid copepods*) and on both
246 the biomasses of the species and of the size classes for week 4 (halfway through the

247 experiment). The results were qualitatively the same in week 2 and week 4. Monte Carlo
248 permutations (n=1000) were used to assess significance of predator treatments.

249 All statistical analyses were carried out using R 2.15.1 (R Core Team. 2012).
250 GLMM's were fitted in the package glmmADMB version 0.7.2.12 (Skaug et al. 2012).
251 Redundancy analyses were conducted using the package vegan version 2.0-5 (Oksanen et al.
252 2012).

253 *Instantaneous attack rates of Predators on Prey*

254 Maximum Instantaneous attack rates were estimated by examining the relationship between
255 prey consumption and prey density by estimating the best fit parameters from the data to
256 describe a type II Hollings functional response equation (Hjelm & Persson 2001). The
257 functional response equation for perch feeding on *Holopedium* was formulated to estimate the
258 maximum instantaneous attack rate a for each predator size class. No account was made for
259 prey depletion as *Holopedium* densities were very high and only the data from the first 5 prey
260 items were used. Model parameters were estimated using non-linear regression. For the
261 functional response equation for perch feeding on *Bythotrephes*, prey densities are low and
262 depletion is likely. Therefore the Rogers random-predator equation was used to estimate
263 attack rate, a , in L/s; predator and prey densities are per unit Litre (Bolker 2008). Model
264 parameters were estimated using a maximum likelihood function (R function "mle2" in
265 package "bbmle" version 2.12.2). All model fitting exercises were carried out using R 2.15.1
266 (R Core Team. 2012).

267 Attack rates of *Bythotrephes* on zooplankton were measured insitu lake AT3 in 2011-2013
268 using two Paired-Schinder Patalis plankton chambers (Aquatic Research Instruments, Hope,
269 ID, USA) (Vanderploeg, Liebig & Omair 1993). An average per capita capture rate (L/s) of
270 *Bythotrephes* on the five most common zooplankton species was calculated by estimating the
271 per capita reduction in zooplankton abundance per unit time in the chamber where
272 *Bythotrephes* were released compared to the predator free paired control. The experiments ran
273 between 4 and 20 hours between early June and late August in each year at a range of
274 predator densities as appropriate for that time of year in lake AT3 (0.16-0.66 *Bythotrephes*/L)
275 at natural prey densities.

276

277 **Results**

278 *Predator – Predator interactions*

279 *Bythotrephes* densities were highest in the *Bythotrephes* alone treatment, first
 280 increasing to 9.1 individuals per m³ in week 5 (95% CI=6.5-10.9, GLMM Wald Z=3.36,
 281 $P=0.0008$) before the densities decreased. In the YOY perch + *Bythotrephes* treatment,
 282 *Bythotrephes* decreased from 4.7 individuals per m³ in week 3 (95% CI=4.1-5.6) to only 1.5
 283 individuals per m³ (95% CI=0.3-3.1 GLMM Wald Z=-3.35, $P=0.0008$) in week 6. In the
 284 treatment with OYO Perch and *Bythotrephes*, excluding one outlier, there was no significant
 285 increase/change in *Bythotrephes* density in the OYO perch treatment from week 3-6 (2.4
 286 individuals per m³ over the same period GLMM Wald Z=-0.06, $P=0.95$, Figure 1).

287 At the end of the experiment the number of YOY perch that were caught back was
 288 significantly lower in the treatment with *Bythotrephes* than in the YOY perch alone treatment
 289 (ANOVA, $F_{1,6}=10.57$, $P<0.02$, YOY perch alone on average 3.5 fish (± 1 standard deviation
 290 (sd)), YOY perch + *Bythotrephes* on average 1.25 fish (± 0.96 sd) per mesocosm).

291 Maximum attack rates of perch on *Bythotrephes* estimated from individual based experiments
 292 peaked with 55mm sized perch at 0.6L/s (Table 1).

293 *Size-dependent predator effects on prey community*

294 There was a clear seasonal change in the size composition of the zooplankton communities in
 295 the YOY perch treatment as the fish grew, and also in the *Bythotrephes* alone treatment as
 296 their densities increased (ANOVA, $F_{7,97}=12.53$, $P<0.001$, Figure 2a and b). At the start of the
 297 experiment in the YOY alone treatment there was a dominance of large prey biomass
 298 (0.76 ± 0.2 sd mm) and overall large biomasses ($104 \text{ ug L}^{-1} \pm 63$ sd, week 2). By week 4
 299 overall numbers of zooplankton were reduced ($27 \text{ ug L}^{-1} \pm 11$ sd), particularly the biomass of
 300 large individuals, and the biomass of small individuals (≤ 0.75 mm) became dominant
 301 (0.46 ± 0.17 s.d. mm, week 4). In the *Bythotrephes* only treatment there was a maintained or
 302 increasing predation pressure on small individuals (0.72 ± 0.3 sd mm at week 2, 0.81 ± 0.2 sd
 303 mm at week 4, Figure 2), zooplankton were heavily suppressed ($62 \text{ ug L}^{-1} \pm 5.6$ sd at week 2,
 304 $25 \text{ ug L}^{-1} \pm 5.6$ sd at week 4), and the large individuals dominated the biomass (Figure 2b).
 305 There was no significant difference in the total biomass of large or small individuals in any

306 week in the OYO + *Bythotrephes* treatment (ANOVA, OYO:week interaction, $t_{3,6} = 1.224$,
 307 $P > 0.22$, Figure 2b).

308

309 *Emergent facilitation*

310 Adult *Holopedium* biomass decreased after the second week of the experiment (Figure
 311 3a). In the YOY perch only treatment the biomass was more than 3.3 times higher than in
 312 other treatments at that point (95% CI of difference = 0.97 – 11.46, GLMM Wald $Z = 1.92$,
 313 $P = 0.055$). After the third week the biomass of adult *Holopedium* continued to decrease in the
 314 OYO perch, the YOY perch only and the *Bythotrephes* + YOY perch treatments.

315 After an initial increase in the biomass of juvenile *Holopedium*, biomass decreased rapidly in
 316 all treatments (Figure 3b). In the second and third week of the experiment the juvenile
 317 *Holopedium* biomass was 2.7 times higher in the YOY perch only treatment compared to the
 318 other treatments (95% CI = 1.69 – 4.44, GLMM Wald $Z = 4.1$, $P < 0.001$). The biomass of
 319 *Holopedium* juveniles consistently decreased from week 2 onwards in all mesocosms and
 320 disappeared completely after the fifth week of the experiment.

321 In the invertebrate predator treatment (*Bythotrephes* only) adult and juvenile
 322 *Holopedium* biomass was significantly reduced at the onset of the experiment (i.e. Figure 3,
 323 week 1), despite total zooplankton biomass being similar across all treatments (ANOVA on
 324 total zooplankton at week 1, $F_{2,11} = 2.007$, $P > 0.15$, Figure S3). The *Bythotrephes* only
 325 *Holopedium* biomass recovered to levels seen in other treatments containing *Bythotrephes* in
 326 week 2 (ANOVA, $F = 1.629$, $P > 0.2$), and thereafter declines as in all other treatments.

327 In all treatments the proportion of fecund *Holopedium* decreased after the second
 328 week, on average by 60% (95% CI = 33% - 77%, GLMM Wald $Z = -3.44$, $P < 0.001$). In the
 329 YOY perch only treatment and the OYO perch treatment the proportion fecund females were
 330 lower compared to the *Bythotrephes* only treatment (85% lower in the YOY perch only
 331 treatment (95 % CI = 70 – 92%, GLMM Wald $Z = -5.46$, $P < 0.001$), 45% lower in the perch
 332 80+ treatment (95% CI = 16 – 65%, GLMM Wald $Z = -2.74$, $P = 0.006$) compared to
 333 *Bythotrephes* alone in week 2). In the fourth week there were no fecund individuals in the
 334 YOY perch only and the OYO perch treatment. There was a significant difference in the
 335 number of eggs per fecund female between predator treatments, but only for *Holopedium* in

336 the YOY alone treatment where we found lower fecundity than all other treatments at week 2
 337 (Linear mixed effects model with poisson error: #Eggs/female per predator treatment;
 338 $\chi^2=31.28_{2,5}$, $P<0.001$). This difference in fecundity was not sustained from week 3 and
 339 onwards.

340 Maximum attack rates (Litres of lake water cleared per second) of perch on adult *Holopedium*
 341 were not affected by predator body size above a threshold of 25mm (ANOVA: L/s ~body
 342 length; $F=1.13_{1,397}$, $P>0.25$). Juvenile perch <25mm could not consume adult *Holopedium*.
 343 Perch attack rates on *Holopedium* peaked at 0.1L/s at a 100mm body size (Table 1).
 344 Maximum *Bythotrephes* attack rates on all zooplankton were 0.007 L/s (Table 1), with attack
 345 rates on *Bosmina*, *Holopedium* and copepods being 0.008, 0.005 and 0.004 L/s respectively
 346 (Table 1).

347 *Community effects*

348 The species composition changed over the course of the experiment and was different among
 349 different predator treatments (Figure 5). There were some clear seasonal patterns across all
 350 treatments. *Holopedium* was abundant in all treatments near the beginning of the experiment,
 351 especially in the YOY perch only treatment. In the second half of the experiment, however, it
 352 disappeared from the mesocosms. *Ceriodaphnia quadrangula*, in contrast, was almost absent
 353 early in the experiment but was highly abundant at the end. Overall there were contrasting
 354 effects of either YOY perch or *Bythotrephes* as predators (MANOVA on cladoceran vs
 355 copepod biomass in *Bythotrephes* alone vs. YOY alone; appx. $F=33.42_{1,52}$, $P<0.0001$). In the
 356 treatment with only YOY perch there were relatively many cladocerans (pink, orange and
 357 yellow in Figure 4) and relatively few copepods (blue and green bars in Figure 4). In contrast,
 358 when *Bythotrephes* was present there were relatively many copepods and few cladocerans in
 359 the mesocosms. The MANOVA demonstrates that any shift in the proportion of copepods in
 360 the zooplankton communities is driven by changes in cladoceran biomass (MANOVA output
 361 on response of total copepod biomass to predator*week; appx. $F=1.07_{3,104}$, $P>0.3$).

362 An RDA ordination of week 4 zooplankton species biomasses (halfway through the
 363 experiment, results were qualitatively similar in weeks 2-4 when *Holopedium* densities
 364 remained high) showed that 80% of the variance in the species composition could be
 365 explained by predator treatment (Figure 5a). Considered separately, the first axis of the
 366 species-based RDA plot explained 60% of the variance (RCA1), the second axis 15%

367 (RCA2). The first axis was mainly related to *Bosmina longirostis*, *Ceriodaphnia* and the
368 copepods while the second axis was mainly related to *Holopedium* biomass. Predator
369 treatment was highly significant (Monte Carlo permutation test $P=0.001$). The species
370 composition of the YOY perch only treatment was dominated by *Ceriodaphnia* and *Bosmina*.
371 In contrast, the species composition in all the treatments with *Bythotrephes* present was
372 dominated by calanoid and cyclopoid copepods. The *Bythotrephes* only treatment had a
373 relatively high abundance of *Holopedium* and calanoid copepods and the RDA plot shows that
374 these are negatively correlated with *Bosmina* biomasses. The combined YOY perch and
375 *Bythotrephes* treatment was more similar to the *Bythotrephes* alone treatment on the RCA1
376 axis (Figure 5a).

377 An RDA ordination of zooplankton species and size class biomasses in week 4 showed that
378 predator treatment explained 78% of the variance in size and species composition (Figure 5b),
379 and was highly significant (Monte Carlo permutation test $P=0.001$). Considered separately,
380 the first axis of the RDA ordination plot explained 56% of the variance (RCA1); the second
381 axis explained 16% (RCA2). *Holopedium* was correlated with the largest size class, while
382 *Bosmina* was correlated with the two smallest size classes. The YOY perch only treatment
383 was dominated by *Bosmina* and small individuals while the *Bythotrephes* only treatment was
384 dominated by *Holopedium* and large individuals. The other two treatments were dominated by
385 calanoid copepods and individuals of average size.

386 *Phytoplankton in Mesocosm Experiments*

387 There was no significant difference between the chlorophyll-a content between the different
388 predator treatments ($F_{3,12}=0.9206$, $p=0.46$, mean=0.88, std=0.31).

389 *Results summary*

390 Our main result was that YOY perch switched from negative to positive size selective
391 predation as they grow while *Bythotrephes* negatively size selected for smaller prey. The
392 effects of OYO perch were unclear. Increased juvenile or total biomass of *Holopedium* in
393 response to predation was not found, and we saw no competitive release of female fecundity.
394 Our community analysis demonstrated how the predation generated changes in prey
395 community size structure were largely caused by species specific changes in the community
396 composition. Perch, once greater than 25mm length, were formidable predators of
397 *Bythotrephes*.

398 Discussion

399 *Bythotrephes* and YOY perch fed on differently sized prey, a necessary condition for
400 positive effects between them via intraspecific or interspecific processes. However, a main
401 result is that despite this the population growth of *Bythotrephes* was highest when on its own
402 without perch. There was also a lower number of YOY perch in the YOY + *Bythotrephes*
403 mesocosms at the end of the experiment than the YOY alone. The effect of the two predator
404 species on the species composition of their prey communities was markedly different. We
405 shall discuss these results firstly in light of intraspecific or interspecific responses of the prey
406 communities to predation and the interactions between differently sized predators, and
407 secondly what these results say about the likelihood for emergent facilitation across animal
408 communities in general.

409

410 *Exploring intraspecific responses of prey communities to multiple predation*

411 While Huss and Nilsson (2011) found that positive size-selective mortality of a
412 zooplankton community using a size-selective net increased the biomass of juvenile
413 *Holopedium*, leading to increased *Bythotrephes* population growth rate, we did not. There are
414 several reasons why we can expect different results with live predators: (1) a single net
415 predation event occurred at the beginning instead of continuous predation, (2) the net was
416 constrained to cause high mortality on large *Holopedium* and (3) netting was carried out once
417 the prey population growth rate was limited by high densities. We shall discuss each of these
418 points that lead us to refute that responses of the prey community to perch predation were
419 dominated by intraspecific responses in *Holopedium*.

420 First, the intensity of fish predation on zooplankton generally changes over season as a
421 result of the dynamics of recruiting YOY cohorts (Gliwicz & Pijanowska 1989), but is always
422 present to some extent. Moreover, strong between year variation in predation on zooplankton
423 may be present as a result of variation in mortality rates of YOY fish. For example, YOY
424 perch mortality in the studied lakes may vary as much as 50 times between years as a result of
425 variation in cannibalism (Persson *et al.* 2004). Although a single pulsed net predation event
426 represents an extreme form of mortality, we suggest that such a mortality event captures the
427 situation only in years with very high YOY fish mortality, and hence that the extent to which
428 intraspecific overcompensation is present in the system may vary between years. The

429 continuous predation in the current experiment may prevent or reduce the effects of any
430 intraspecific response that might occur in a pulsed experiment.

431 Second, while our estimated attack rates of perch on *Holopedium* were lower than those
432 estimated on *Bosmina* or *Daphnia* by 50-100mm perch (e.g. 0.06-0.1L/s vs. 0.24-0.45L/s),
433 they were similar to attack rates on copepods where clear ecological responses of predation
434 are well documented (Persson 1987; Persson & Greenberg 1990; Bystrom & Garcia-Berthou
435 1999). However, the net was a less efficient predator of other zooplankton prey species and
436 indeed Huss and Nilsson found no evidence of zooplankton community composition changes
437 in their study (n.b. excluding rotifers (Huss & Nilsson 2011)). Live predators are not
438 constrained to feed only on large adult *Holopedium* and as we discuss in later sections, have
439 significant effects on prey community structure as a consequence.

440 Third, in the experiment by Huss & Nilsson (2011), the *Holopedium* populations grew
441 without predation for several weeks and the net predation occurred once the *Holopedium*
442 population densities were high. This is in contrast to our experiment where prey and predators
443 were introduced to the mesocosms almost simultaneously, similar to how they emerge
444 seasonally in nature. While adult *Holopedium* biomasses peaked at similar densities in the two
445 experiments, it was only after the net predator had invaded the community to remove large
446 *Holopedium* that *Bythotrephes* was added. We suggest that the constant presence of predators
447 in our experiment, whether they affect *Holopedium* directly or not, leads to transient dynamics
448 in the *Holopedium* population structure with juvenile biomasses of up to 50% of the adult
449 population. This suggests that *Holopedium* females were not resource limited during this
450 period. More explicitly, we found no evidence of increased per capita or proportion of
451 population fecundity in *Holopedium* populations from any treatment in response to time
452 exposed to predation. We similarly found no increase in juvenile:adult ratio of other
453 zooplankton species exposed to predation by perch. Therefore the mechanism that was
454 proposed to lead to overcompensatory biomass responses of zooplankton to predation,
455 through release of adults from competition and a subsequent increase in individual and
456 population fecundity, did not occur in any of the perch treatments.

457

458 *Interspecific community responses – community compensation*

459 We have established that there are significant shifts in the size structure of
460 zooplankton prey communities caused by size-selective predation, as evidenced by the
461 shifting dominance of biomass to large or small individuals. We also established that the size
462 structured changes observed are not likely to have been caused by intraspecific compensatory
463 responses within individual prey species. Instead, predation effects on size distributions of
464 prey are more parsimoniously explained by shifts in the competitive dominance of differently
465 sized zooplankton species (Paine 1966; Dodson 1974), or through the interaction of predation
466 effects and seasonal succession as also identified in phytoplankton communities (Hansson,
467 Bergman & Cronberg 1998). Including individual body sizes of prey did not improve on a
468 model that contained only species labels due to the high correlation between them. Prey body
469 mass is often said to be an important factor determining susceptibility of a prey to a certain
470 predator, e.g. (Brose *et al.* 2006). We do not refute this, but we found that prey body size
471 variation was largely reflected in species variation.

472 On their own, *Bythotrephes* and YOY perch had markedly different effects on the prey
473 species composition. *Bythotrephes* selected against small cladocerans, *Bosmina* in particular.
474 We see this in both the species composition RDA and the size frequency histograms where
475 there is a selection against 0.5-0.6mm zooplankton corresponding to these small cladocerans.
476 That the seasonal switch of late-season dominance to small cladocerans is entirely driven by
477 *Ceriodaphnia* in the presence of *Bythotrephes*, but otherwise by both *Bosmina* and
478 *Ceriodaphnia*, is further evidence of this. Our attack rate estimates from in situ chambers
479 supports *Bosmina* as a preferred prey for *Bythotrephes* in our study lakes. In its North
480 American invasive range the consensus is that *Bythotrephes* causes large reductions in mainly
481 small cladoceran zooplankton as we found here (Vanderploeg, Liebig & Omair 1993;
482 Dumitru, Sprules & Yan 2001). In this mesocosm study YOY perch largely select against
483 copepods. At the smaller YOY sizes examined, and certainly in systems where larger
484 *Daphnia* spp. are not common, copepods are found to be an important food source for YOY
485 European and Yellow perch (*Perca flavescens*) (Wang & Appenzeller 1998; Bystrom &
486 Garcia-Berthou 1999; Persson *et al.* 2000).

487 The species composition of YOY perch + *Bythotrephes* treatment and larger juvenile
488 OYO perch + *Bythotrephes* treatment were very similar halfway through the experiment at
489 weeks 4 and 5 (delineated together in the RDA plots), which suggests that both larger YOY
490 and OYO perch had a similar effect on the zooplankton community. From other experiments

491 it is known that juvenile perch predate larger copepods and cladocerans in addition to more
492 preferred prey (Persson 1987; Persson & Greenberg 1990; Nunn, Tewson & Cowx 2012). The
493 juvenile OYO perch + *Bythotrephes* treatment has the strongest negative correlations with
494 *Bosmina* and *Holopedium* and positive correlations with copepods. We interpret this as OYO
495 perch not being such efficient predators on copepods as YOY perch. However, without an
496 adequate control it is difficult to quantify the effects OYO perch have on the zooplankton prey
497 community that is different from YOY perch.

498 We found a clear predation effect of YOY perch on copepods when *Bythotrephes* was
499 not present. However, copepod biomasses were higher in treatments with *Bythotrephes* (up to
500 x25 greater calanoid copepod biomass in the two multiple predator treatments). It appears that
501 the predation effect of perch on copepods was much smaller in the presence of *Bythotrephes*.
502 The most parsimonious explanation for the high density of copepods despite perch predation
503 is competitive release in the presence of *Bythotrephes*. Because of the lower densities of
504 cladocerans due to strong predation by *Bythotrephes*, especially of *Bosmina* (e.g. in week 5
505 *Bosmina* densities were 12.15 µg/L (5.7 std) in the YOY only treatment, compared to 0.39
506 µg/L (0.4 std) in the treatment with YOY Perch and *Bythotrephes*) this is likely to increase the
507 growth, survival and fecundity of the copepods (Vanni 1986; Sommer *et al.* 2001).

508 Our results highlight the importance of taking into account invertebrate predator
509 effects in aquatic community structure (Brooks & Dodson 1965; Dodson 1970; Dodson
510 1974). It is often assumed that the structure of aquatic prey communities are determined by
511 fish predation, but here we have shown that while fish predation always reduced the mean
512 size of zooplankton, the species composition that led to those size distributions differed when
513 invertebrate predators were present (Lane 1979; Hoffman, Smith & Lehman 2001; Gal *et al.*
514 2006; Bunnell *et al.* 2011). While individual consumption rates by YOY perch are 6 times
515 that of *Bythotrephes* (0.05 vs. 0.008 L/s), *Bythotrephes* are 6 times more abundant on average
516 than the highest observed YOY perch density across our study lakes (19.7 vs. 3.49 /m³). This
517 results in a high population level predation effect and is evident from the higher suppression
518 of zooplankton densities in the *Bythotrephes* alone treatment. Unlike vertebrate predators,
519 *Bythotrephes* has very high investment in large clutches of large offspring (c.70% adult size at
520 birth) and consume up to 40% of their lifetime prey consumption during their pre-adult stages
521 with each individual killing 60-300 small cladocerans per day (Yurista & Schulz 1995).

522

523 *Predator-predator interactions and the likelihood of emergent facilitation in animal*
524 *communities*

525 This study presents the first estimates of natural consumption rates of *Bythotrephes* by
526 juvenile fish from native European lakes. The most parsimonious explanation for reduced
527 invertebrate predators, IGP, is likely given our estimated attack rates of 20-100mm perch on
528 *Bythotrephes*. At average lake densities of 5-10 *Bythotrephes*/m³, juvenile perch can clear the
529 epilimnion volume of one mesocosm of *Bythotrephes* in 72 hours (N.B. assuming no
530 alternative prey). On its own this is not evidence that interspecific facilitative interactions via
531 shared prey could not operate. But it is evidence that in natural systems where such
532 facilitative mechanisms were operating, IGP could cancel any positive effect on the growth,
533 survival and fecundity of smaller predators. As we only have a simple measure of YOY
534 success we cannot easily distinguish between YOY mortality caused by competition or other
535 interactions with *Bythotrephes*. Competition between *Bythotrephes* and juvenile fish is a
536 major concern where it has invaded non-native habitats in North America (Hoffman, Smith &
537 Lehman 2001; Yurista *et al.* 2010); but we instead propose the question of why such complex
538 fish communities as in the North American great lakes do not reduce *Bythotrephes* densities
539 via the high IGP predation rates we observed in this study?

540

541 The role of IGP on the likelihood of emergent facilitation to occur across animal communities
542 remains unexplored in theoretical approaches that otherwise predict the importance of
543 emergent facilitation in predator coexistence and extinction cascades in top predators. Body
544 size ratios between size at birth and maturation of prey species, and between predators and
545 prey can be used to ascertain the likelihood of conditions promoting emergent facilitation and
546 IGP occurring simultaneously. A crude consideration of this based on parameters summarised
547 by Peters (Peters 1983) and confirmed by later reviews and analyses (Brose *et al.* 2006;
548 Barnes *et al.* 2010; De Roos & Persson 2013) suggests where prey neonate-maturation body
549 mass ratio's vary from 0.08-0.0001 and average predator-prey body mass ratios vary from
550 0.1-0.02 across a wide variety of taxa, predators on immature prey will always be vulnerable
551 to predators large enough to consume adult prey as they will fall within 10-0.1% of the mass
552 of large predators. Emergent facilitation therefore is more likely to be found where gape size

553 is less important or feeding mechanisms are highly specialist. We suggest two systems that fit
554 these criteria where research into emergent facilitation could be undertaken. Firstly in insect
555 communities with strong intraspecific interactions between prey stages and where natural
556 enemies are often highly specialist in their mode of feeding (e.g. parasitoids vs. *Anthocordids*)
557 (Cameron *et al.* 2007a; Cameron *et al.* 2007b). Here parasitoids of eggs or juvenile prey can
558 facilitate predators of later stages without direct interactions between predators. Secondly
559 negative density dependent effects on growth, reproduction, and post-settlement survival is
560 widespread in intertidal bivalve beds (Kristensen 1957; Jensen 1992; Jensen 1993). Predation
561 by birds on bivalves is often size-selective with specialists on large adults or small juveniles
562 (Sutherland 1982; Zwarts & Blomert 1992) and effects of food limitation on winter survival
563 and breeding success of bivalve feeding shore birds is well recorded (Atkinson *et al.* 2003).
564 IGP will not occur between different shorebird species, indeed while feeding occurs on the
565 same bivalve beds it can be seasonally separated, so facilitative interactions could well have
566 positive population scale effects.

567

568 *Conclusion*

569 Our research shows that the interaction between juvenile perch and *Bythotrephes* is
570 negative and can be explained by IGP. Although we found that the two predators prefer
571 different prey sizes, we found no evidence of intraspecific responses of prey through size-
572 selective predation by perch on *Holopedium*. Instead our results support predators having
573 species specific prey preferences, and that these preferences have clear effects on the seasonal
574 succession of prey community composition. The interaction between two predators that share
575 the same prey community can be complicated by IGP and complex interspecific responses.
576 We look to communities where IGP is less likely to occur between predators of large and
577 small prey as systems where emergent facilitation could occur.

578

579 **Acknowledgements**

580 This work was funded by a Marie Curie Intra-European Fellowship to TCC (FANTI-SIZE,
581 275873), Erasmus travel grants (HTB, JH) and by Umeå University (LP, MAKKA). HTB, JH
582 and MAKKA undertook this research as part of their study for Masters Degrees in Ecology.

583 **Data Accessibility**

584 Individual zooplankton measurements per mesocosm and functional response experimental
 585 data from field chambers and laboratory experiments: DRYAD entry doi:10.5061/dryad.qg372
 586 (ten Brink *et al.* 2014).

587 **References**

- 588 Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A. & Ireland, P.L. (2003) Changes in
 589 commercially fished shellfish stocks and shorebird populations in the wash, England.
 590 *Biological Conservation*, **114**, 127-141.
- 591 Barnes, C., Maxwell, D., Reuman, D.C. & Jennings, S. (2010) Global patterns in predator-prey size
 592 relationships reveal size dependency of trophic transfer efficiency. *Ecology*, **91**, 222-232.
- 593 Bolker, B.M. (2008) *Ecological models and data in R* Princeton University Press, Princeton.
- 594 Brooks, J.L. & Dodson, S.I. (1965) Predation body size and composition of plankton. *Science*, **150**, 28.
- 595 Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J.L.,
 596 Brey, T., Carpenter, S.R., Blandenier, M.-F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F.,
 597 Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K.,
 598 Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J.,
 599 Woodward, G. & Cohen, J.E. (2006) Consumer-resource body-size relationships in natural
 600 food webs. *Ecology*, **87**, 2411-2417.
- 601 Bunnell, D.B., Davis, B.M., Warner, D.M., Chriscinske, M.A. & Roseman, E.F. (2011) Planktivory in the
 602 changing Lake Huron zooplankton community: *Bythotrephes* consumption exceeds that of
 603 mysis and fish. *Freshwater Biology*, **56**, 1281-1296.
- 604 Bystrom, P. & Garcia-Berthou, E. (1999) Density dependent growth and size specific competitive
 605 interactions in young fish. *Oikos*, **86**, 217-232.
- 606 Bystrom, P., Huss, M. & Persson, L. (2012) Ontogenetic constraints and diet shifts in perch (*Perca*
 607 *fluviatilis*): Mechanisms and consequences for intra-cohort cannibalism. *Freshwater Biology*,
 608 **57**, 847-857.
- 609 Cameron, T.C. & Benton, T.G. (2004) Stage-structured harvesting and its effects: An empirical
 610 investigation using soil mites. *Journal of Animal Ecology*, **73**, 996-1006.
- 611 Cameron, T.C., Metcalfe, D., Beckerman, A.P. & Sait, S.M. (2007a) Intraspecific competition: The role
 612 of lags between attack and death in host-parasitoid interactions. *Ecology*, **88**, 1225-1231.
- 613 Cameron, T.C., Wearing, H.J., Rohani, P. & Sait, S.M. (2007b) Two-species asymmetric competition:
 614 Effects of age structure on intra- and interspecific interactions. *Journal of Animal Ecology*, **76**,
 615 83-93.
- 616 Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M. &
 617 Case, T.J. (2002) The interaction between predation and competition: A review and synthesis.
 618 *Ecology Letters*, **5**, 302-315.
- 619 De Roos, A.M., Metz, J.A.J. & Persson, L. (2013) Ontogenetic symmetry and asymmetry in energetics.
 620 *Journal of Mathematical Biology*, **66**, 889-914.
- 621 De Roos, A.M. & Persson, L. (2013) *Population and community ecology of ontogenetic development*.
 622 Princeton University Press.
- 623 De Roos, A.M., Schellekens, T., Van Kooten, T. & Persson, L. (2008) Stage-specific predator species
 624 help each other to persist while competing for a single prey. *Proceedings of the National*
 625 *Academy of Sciences of the United States of America*, **105**, 13930-13935.
- 626 De Roos, A.M., Schellekens, T., van Kooten, T., van de Wolfshaar, K.E., Claessen, D. & Persson, L.
 627 (2007) Food-dependent growth leads to overcompensation in stage-specific biomass when

- 628 mortality increases: The influence of maturation versus reproduction regulation. *American*
629 *Naturalist*, **170**, E59-E76.
- 630 Dodson, S.I. (1970) Complementary feeding niches sustained by size-selective predation. *Limnology*
631 *and Oceanography*, **15**, 131-&.
- 632 Dodson, S.I. (1974) Zooplankton competition and predation - experimental test of size-efficiency
633 hypothesis. *Ecology*, **55**, 605-613.
- 634 Dumitru, C., Sprules, W.G. & Yan, N.D. (2001) Impact of *Bythotrephes longimanus* on zooplankton
635 assemblages of harp lake, canada: An assessment based on predator consumption and prey
636 production. *Freshwater Biology*, **46**, 241-251.
- 637 Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., Dettmers, J.M. & Belonger, B. (2006) Foraging
638 selectivity by larval yellow perch (*Perca flavescens*): Implications for understanding
639 recruitment in small and large lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**,
640 28-42.
- 641 Gal, G., Rudstam, L.G., Mills, E.L., Lantry, J.R., Johannsson, O.E. & Greene, C.H. (2006) Mysid and fish
642 zooplanktivory in lake ontario: Quantification of direct and indirect effects. *Canadian Journal*
643 *of Fisheries and Aquatic Sciences*, **63**, 2734-2747.
- 644 Gliwicz, Z.M. & Pijanowska, J. (1989) The role of predation in zooplankton succession. *Plankton*
645 *ecology: Succession in plankton communities* (ed. U. Sommer), pp. 253-296. Springer Berlin
646 Heidelberg.
- 647 Gurevitch, J., Morrison, J.A. & Hedges, L.V. (2000) The interaction between competition and
648 predation: A meta-analysis of field experiments. *American Naturalist*, **155**, 435-453.
- 649 Hansson, L.A., Bergman, E. & Cronberg, G. (1998) Size structure and succession in phytoplankton
650 communities: The impact of interactions between herbivory and predation. *Oikos*, **81**, 337-
651 345.
- 652 Hildrew, A.G., Raffaelli, D.G. & Edmonds-Brown, R. (2007) *Body size: The structure and function of*
653 *aquatic ecosystems* CUP, New York.
- 654 Hjelm, J. & Persson, L. (2001) Size-dependent attack rate and handling capacity: Inter-cohort
655 competition in a zooplanktivorous fish. *Oikos*, **95**, 520-532.
- 656 Hoffman, J.C., Smith, M.E. & Lehman, J.T. (2001) Perch or plankton: Top-down control of daphnia by
657 yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake? *Freshwater*
658 *Biology*, **46**, 759-775.
- 659 Huss, M. & Nilsson, K.A. (2011) Experimental evidence for emergent facilitation: Promoting the
660 existence of an invertebrate predator by killing its prey. *Journal of Animal Ecology*, **80**, 615-
661 621.
- 662 Huss, M., Persson, L. & Bystrom, P. (2007) The origin and development of individual size variation in
663 early pelagic stages of fish. *Oecologia*, **153**, 57-67.
- 664 Jensen, K.T. (1992) Dynamics and growth of the cockle, *Cerastoderma edule*, on an intertidal mud-flat
665 in the danish wadden sea - effects of submersion time and density. *Netherlands Journal of*
666 *Sea Research*, **28**, 335-345.
- 667 Jensen, K.T. (1993) Density-dependent growth in cockles (*Cerastoderma edule*) - evidence from
668 interannual comparisons. *Journal of the Marine Biological Association of the United Kingdom*,
669 **73**, 333-342.
- 670 Kerfoot, W.C. & Sih, A. (1987) *Predation. Direct and indirect impacts on aquatic communities*. New
671 England, USA.
- 672 Kristensen, I. (1957) Differences in density and growth in a cockle population in the dutch wadden
673 sea. *Archives Néerlandaises de Zoologie*, **12**, 351-453.
- 674 Lane, P.A. (1979) Vertebrate and invertebrate predation intensity on freshwater zooplankton
675 communities. *Nature*, **280**, 391-393.
- 676 Leibold, M. & Tessier, A.J. (1991) Contrasting patterns of body size for daphnia species that segregate
677 by habitat. *Oecologia*, **86**, 342-348.

- 678 McCoy, M.W., Bolker, B.M., Warkentin, K.M. & Vonesh, J.R. (2011) Predicting predation through prey
679 ontogeny using size-dependent functional response models. *American Naturalist*, **177**, 752-
680 766.
- 681 Milbrink, G. & Bengtsson, J. (1991) The impact of size-selective predation on competition between 2
682 daphnia species - a laboratory study. *Journal of Animal Ecology*, **60**, 1009-1028.
- 683 Murdoch, W.W. & Scott, M.A. (1984) Stability and extinction of laboratory populations of
684 zooplankton preyed on by the backswimmer notonecta. *Ecology*, **65**, 1231-1248.
- 685 Nicholson, A.J. (1957) The self-adjustment of populations to change. *Cold Spring Harbor Symposia on*
686 *Quantitative Biology*, **22**, 153-173.
- 687 Nunn, A.D., Tewson, L.H. & Cowx, I.G. (2012) The foraging ecology of larval and juvenile fishes.
688 *Reviews in Fish Biology and Fisheries*, **22**, 377-408.
- 689 Olson, M.H., Green, D.M. & Rudstam, L.G. (2001) Changes in yellow perch (*Perca flavescens*) growth
690 associated with the establishment of a walleye (*Stizostedion vitreum*) population in
691 canadarago lake, new york (USA). *Ecology of Freshwater Fish*, **10**, 11-20.
- 692 Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65-&.
- 693 Persson, L. (1987) The effects of resource availability and distribution on size class interactions in
694 perch, *Perca fluviatilis*. *Oikos*, **48**, 148-160.
- 695 Persson, L., Andersson, J., Wahlström, E. & Eklov, P. (1996) Size-specific interactions in lake systems:
696 Predator gape limitation and prey growth rate and mortality. *Ecology*, **77**, 900-911.
- 697 Persson, L., Bystrom, P., Wahlström, E., Nijlunsing, A. & Rosema, S. (2000) Resource limitation during
698 early ontogeny: Constraints induced by growth capacity in larval and juvenile fish. *Oecologia*,
699 **122**, 459-469.
- 700 Persson, L., Bystrom, P., Wahlström, E. & Westman, E. (2004) Trophic dynamics in a whole lake
701 experiment: Size-structured interactions and recruitment variation. *Oikos*, **106**, 263-274.
- 702 Persson, L. & de Roos, A.M. (2013) Symmetry breaking in ecological systems through different energy
703 efficiencies of juveniles and adults. *Ecology*, **94**, 1487-1498.
- 704 Persson, L. & Greenberg, L.A. (1990) Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a
705 resource gradient. *Ecology*, **71**, 1699-1713.
- 706 Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. & Christensen, B. (1998) Ontogenetic
707 scaling of foraging rates and the dynamics of a size-structured consumer-resource model.
708 *Theoretical Population Biology*, **54**, 270-293.
- 709 Peters, R.H. (1983) *The ecological implications of body size*. CUP, New York.
- 710 Schroder, A., Persson, L. & de Roos, A.M. (2009) Culling experiments demonstrate size-class specific
711 biomass increases with mortality. *Proceedings of the National Academy of Sciences of the*
712 *United States of America*, **106**, 2671-2676.
- 713 Sommer, U., Sommer, F., Santer, B., Jamieson, C., Boersma, M., Becker, C. & Hansen, T. (2001)
714 Complementary impact of copepods and cladocerans on phytoplankton. *Ecology Letters*, **4**,
715 545-550.
- 716 Sprules, W.G. (1972) Effects of size-selective predation and food competition on high-altitude
717 zooplankton communities. *Ecology*, **53**, 375-&.
- 718 Sutherland, W.J. (1982) Do oystercatchers select the most profitable cockles. *Animal Behaviour*, **30**,
719 857-861.
- 720 ten Brink, H., Mazumdar, A.K.A., Huddart, J., Persson, L. & Cameron, T.C. Data from: Do intraspecific
721 or interspecific interactions determine responses to predators feeding on a shared size-
722 structured prey community? Dryad Digital Repository, doi:10.5061/dryad.qg372
- 723 Touchon, J.C., Jimenez, R.R., Abinette, S.H., Vonesh, J.R. & Warkentin, K.M. (2013) Behavioral
724 plasticity mitigates risk across environments and predators during anuran metamorphosis.
725 *Oecologia*, **173**, 801-811.

- 726 Vanderploeg, H.A., Liebig, J.R. & Omair, M. (1993) *Bythotrephes* predation on great-lakes
 727 zooplankton measured by an insitu method - implications for zooplankton community
 728 structure. *Archiv Fur Hydrobiologie*, **127**, 1-8.
- 729 Vanni, M.J. (1986) Competition in zooplankton communities - suppression of small species by
 730 *Daphnia pulex*. *Limnology and Oceanography*, **31**, 1039-1056.
- 731 Vonesh, J.R. (2005) Sequential predator effects across three life stages of the african tree frog,
 732 *Hyperolius spinigularis*. *Oecologia*, **143**, 280-290.
- 733 Vonesh, J.R. & Osenberg, C.W. (2003) Multi-predator effects across life-history stages: Non-additivity
 734 of egg- and larval-stage predation in an african treefrog. *Ecology Letters*, **6**, 503-508.
- 735 Wahlström, E., Persson, L., Diehl, S. & Bystrom, P. (2000) Size-dependent foraging efficiency,
 736 cannibalism and zooplankton community structure. *Oecologia*, **123**, 138-148.
- 737 Wahlström, E. & Westman, E. (1999) Planktivory by the predacious cladoceran *Bythotrephes*
 738 *longimanus*: Effects on zooplankton size structure and abundance. *Canadian Journal of*
 739 *Fisheries and Aquatic Sciences*, **56**, 1865.
- 740 Wang, N. & Appenzeller, A. (1998) Abundance, depth distribution, diet composition and growth of
 741 perch (*Perca fluviatilis*) and burbot (*Lota lota*) larvae and juveniles in the pelagic zone of lake
 742 constance. *Ecology of Freshwater Fish*, **7**, 176-183.
- 743 Yan, N.D. & Pawson, T.W. (1997) Changes in the crustacean zooplankton community of harp lake,
 744 canada, following invasion by *Bythotrephes cederstroemi*. *Freshwater Biology*, **37**, 409-425.
- 745 Yurista, P.M. & Schulz, K.L. (1995) Bioenergetic analysis of prey consumption by *Bythotrephes*
 746 *cederstroemi* in lake michigan. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 141-
 747 150.
- 748 Yurista, P.M., Vanderploeg, H.A., Liebig, J.R. & Cavaletto, J.F. (2010) Lake michigan *Bythotrephes* prey
 749 consumption estimates for 1994-2003 using a temperature and size corrected bioenergetic
 750 model. *Journal of Great Lakes Research*, **36**, 74-82.
- 751 Zaret, T.M. (1980) *Predation and freshwater communities*. Yale University Press, New Haven, USA.
- 752 Zimmerman, M.S. (2006) Predator communities associated with brook stickleback (*Culaea*
 753 *inconstans*) prey: Patterns in body size. *Canadian Journal of Fisheries and Aquatic Sciences*,
 754 **63**, 297-309.
- 755 Zwarts, L. & Blomert, A.M. (1992) Why knot *Calidris canutus* take medium-sized *Macoma balthica*
 756 when 6 prey species are available. *Marine Ecology Progress Series*, **83**, 113-128.

757

758 **Supporting Information**

759 The following Supporting Information is available for this article online:

760 Table S1: Breakdown of model selection and Akaike weights for *Bythotrephes* abundance

761 Table S2: Breakdown of model selection and Akaike weights for *Holopedium* analysis

762 Figure S1: Full time series of prey size frequency histogram per predator treatment

763 Figure S2: Full time series of small and large prey biomass per predator treatment

764 Figure S3: Full time series of total zooplankton biomass per predator treatment

765

766

767 **Figure legends**

768 **Figure 1.** Mean number of *Bythotrephes* per m³ volume per predator treatment from weeks 3-
769 7. Error bars are bias corrected and adjusted bootstrapped 95% confidence intervals of the
770 mean (n=1000), and those that do not overlap the mean of a comparable treatment can be
771 considered statistically different at $\alpha = 0.05$.

772 **Figure 2.** Plots of the **a)** size frequency of individual zooplankton per treatment and **b)** mean
773 biomass (micrograms/litre) of small (≤ 0.75 mm) or large (> 0.75 mm) body sized prey for
774 weeks 3-5. Full plot of distributions in weeks 1-7 can be found in supplementary online
775 material. Error bars on biomass plots are bias corrected and adjusted bootstrapped 95%
776 confidence intervals of the mean (n=1000), and those that do not overlap the mean of a
777 comparable treatment can be considered statistically different at $\alpha = 0.05$.

778

779 **Figure 3.** Mean biomass (micrograms/litre) of **a)** adult or **b)** juvenile *Holopedium* per
780 predator treatment from weeks 1-7. Error bars are bias corrected and adjusted bootstrapped
781 95% confidence intervals of the mean (n=1000), and those that do not overlap the mean of a
782 comparable treatment can be considered statistically different at $\alpha = 0.05$.

783 **Figure 4.** Barchart of the mean absolute biomass per predator treatment each week and the
784 community composition of that biomass. Copepods are divided into two main taxonomic
785 groups; calanoids and cyclopoids.

786 **Figure 5.** Plots of community species composition per mesocosm halfway through the
787 experiment (week 4) colour coded by predator treatment, along two redundancy analysis axes.
788 In plot **a)** the axes are constrained to the variance in species composition explained by
789 treatment and in plot **b)** to the variance in species and body size composition explained by
790 treatment. The arrows points to the plot space occupied by a given explanatory variable (e.g.
791 increased calanoid copepod biomass).

792

793

794 **Table 1.** Summary of the average of maximum capture/attack rates either calculated from raw
795 capture data (*) or estimated attack rates from fitting functional response model to raw
796 capture data. Mean across all predator sizes is shown. Standard Errors are shown unless
797 otherwise stated (CI= 95% confidence interval). Perch attack rates estimated using Hollings
798 Type II^a or Rogers random predation equation^b (average over all sizes, see methods). Perch
799 attack rates on *Bosmina*^c and copepods (*Cyclops* sp.^d) taken from (Wahlström *et al.* 2000)
800 and (Persson 1987) respectively. Attack rates of perch larvae and small juveniles/YOY on
801 *Bythotrephes* or copepods are unknown. Prey selectivity experiments show that small juvenile
802 perch have strong positive selection for copepods over cladocerans in the 12-25mm size class
803 (Fulford *et al.* 2006; Huss, Persson & Bystrom 2007).

804

805

806

807

808

809

810

811

812

813

814

815

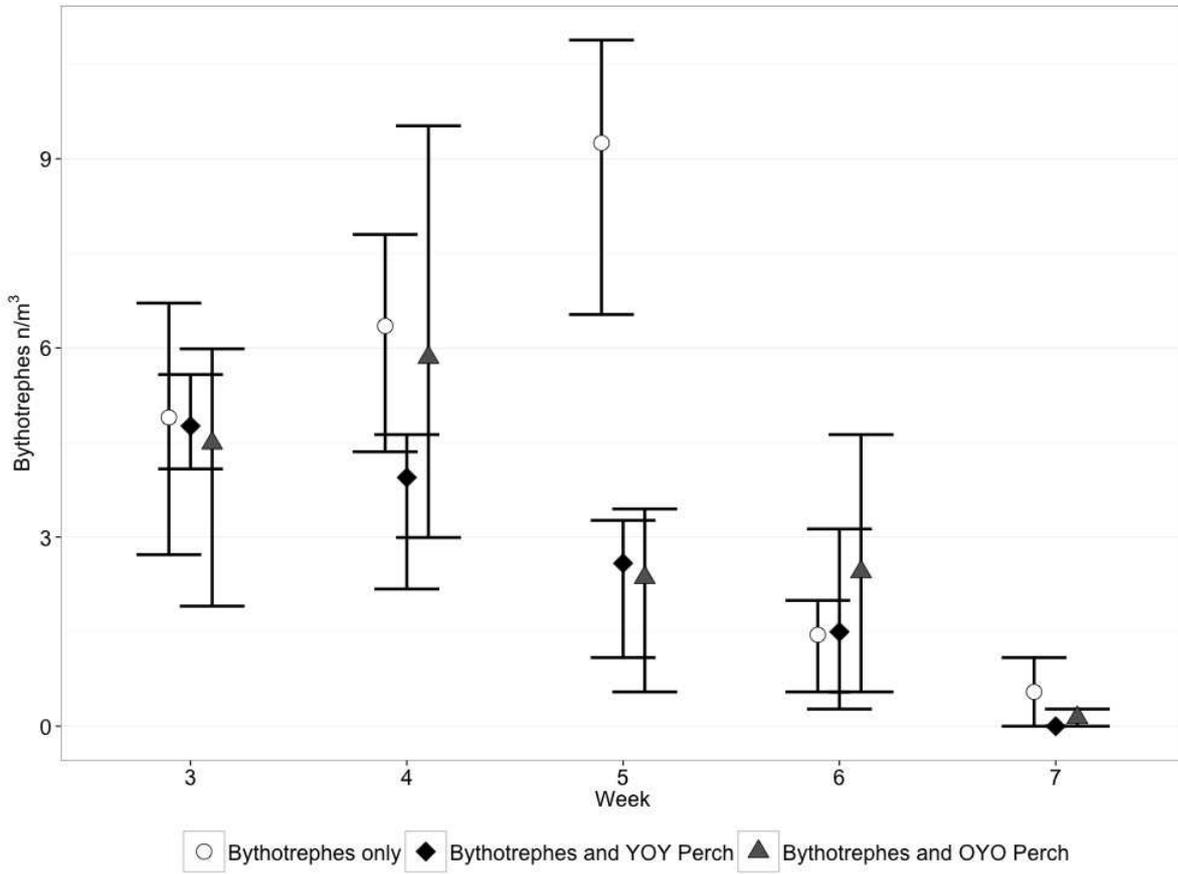
816

817

818

819

820



821 **Figure 1**

822

823

824

825

826

827

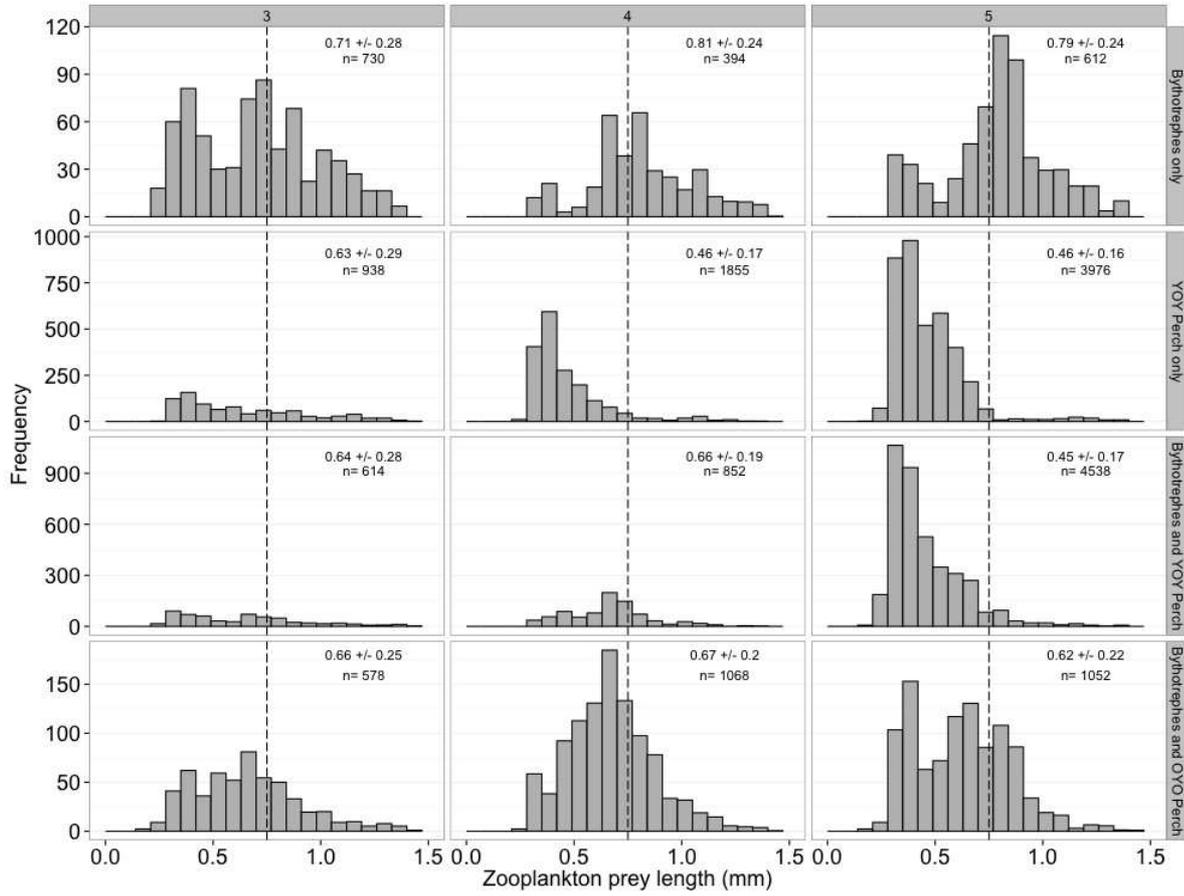
828

829

830

831

832



833

834 **Figure 2a**

835

836

837

838

839

840

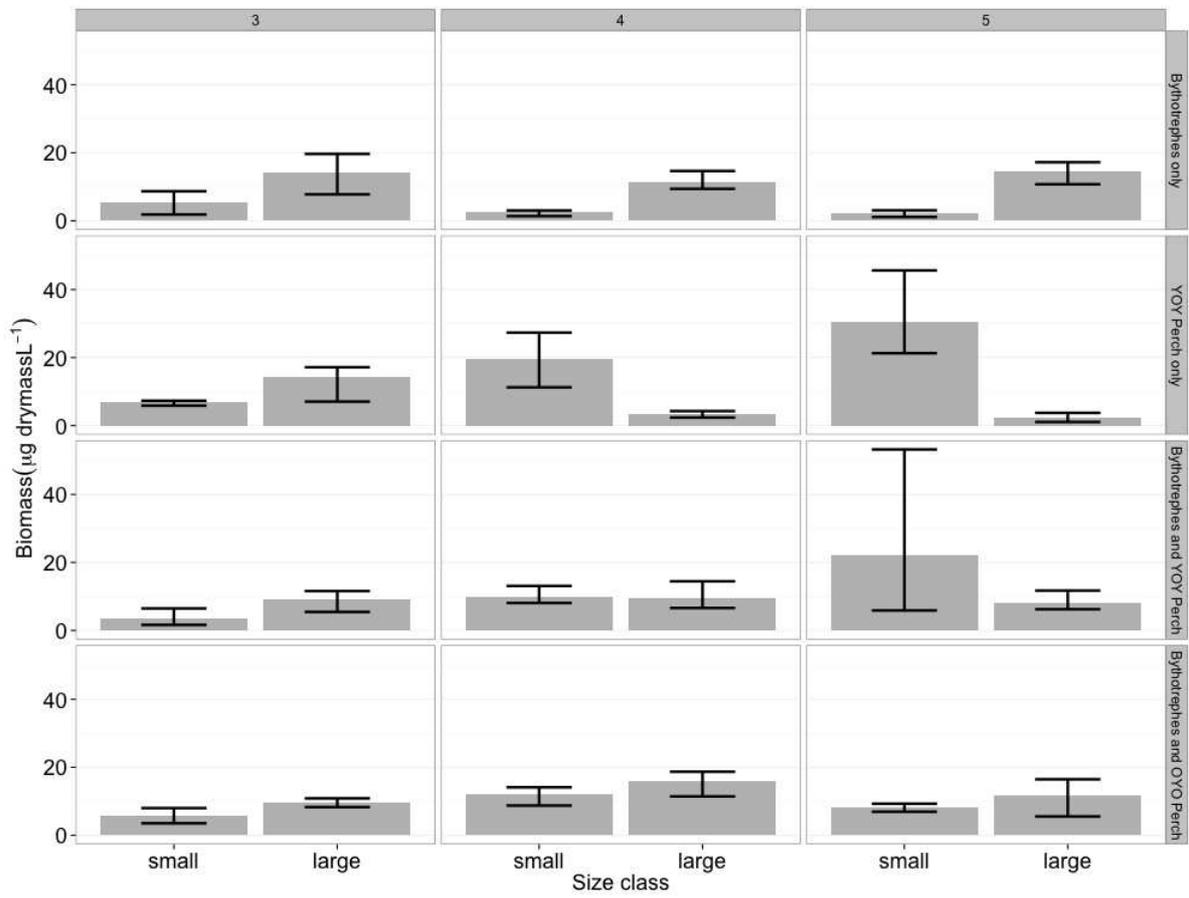
841

842

843

844

845



846

847 **Figure 2b**

848

849

850

851

852

853

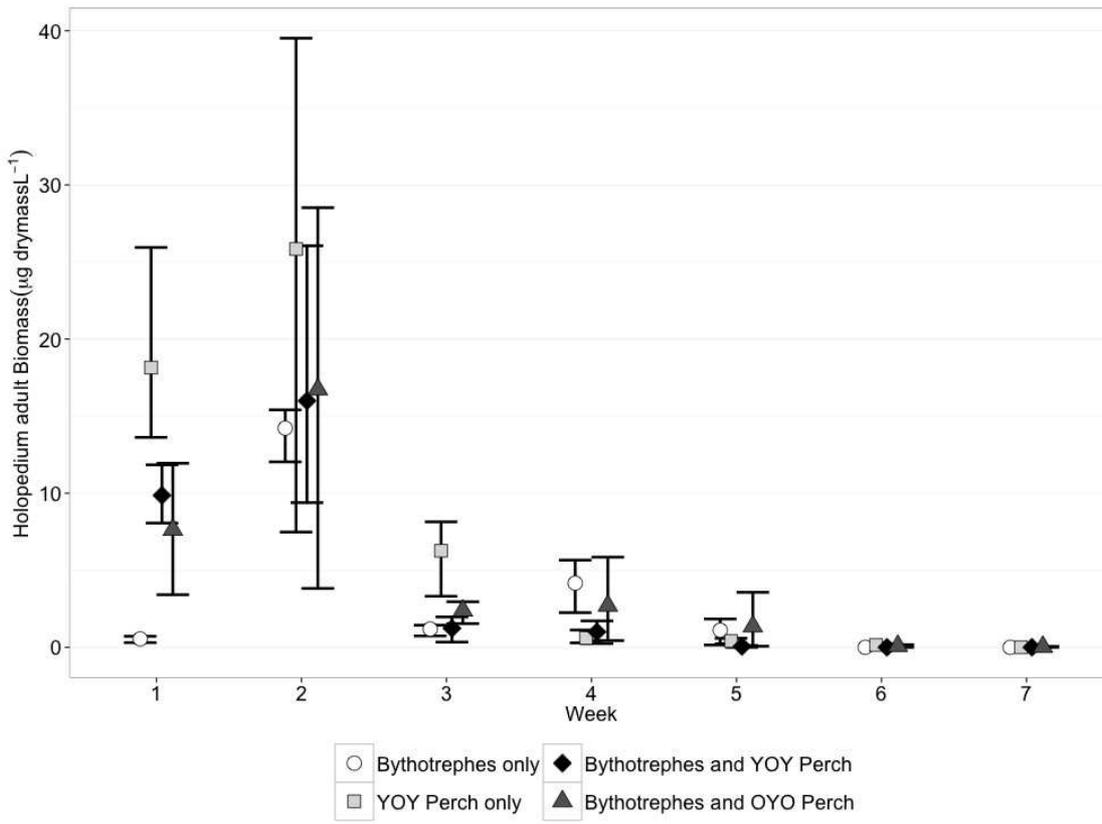
854

855

856

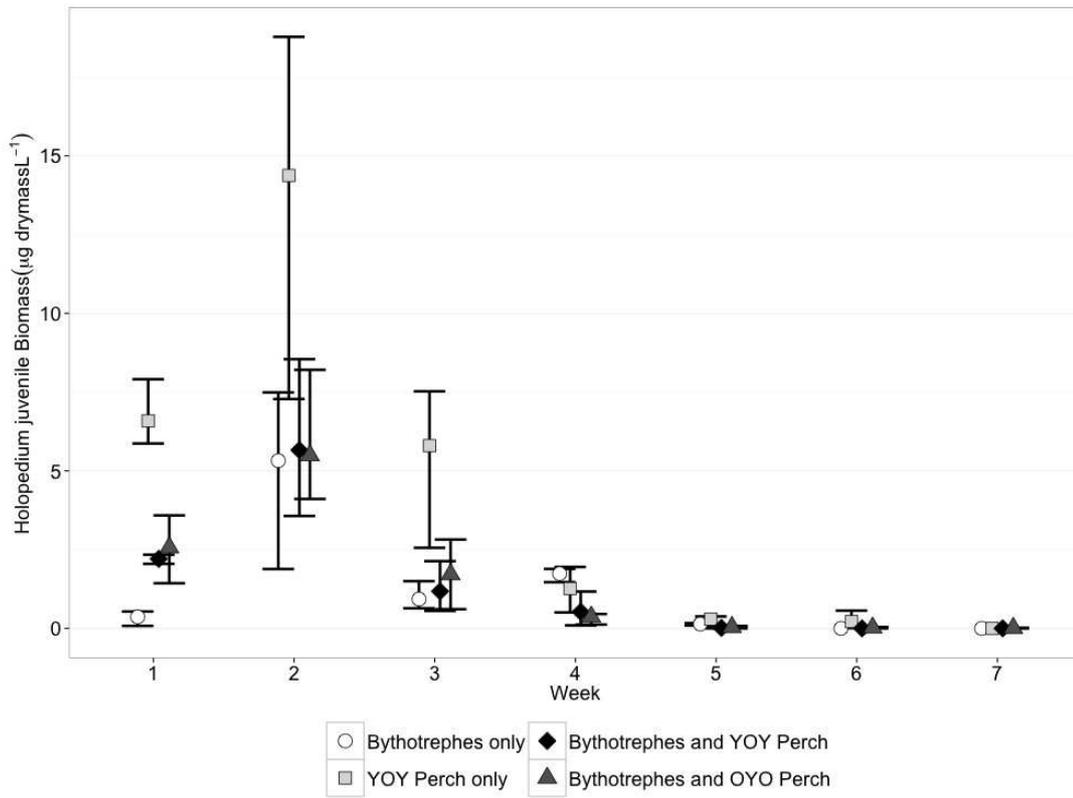
857

858



859

860 **Figure 3a**

861 **Figure 3b**

862

863

864

865

866

867

868

869

870

871

872

873

874

875

876

877

878

879

880

881

882

883

884

885

886

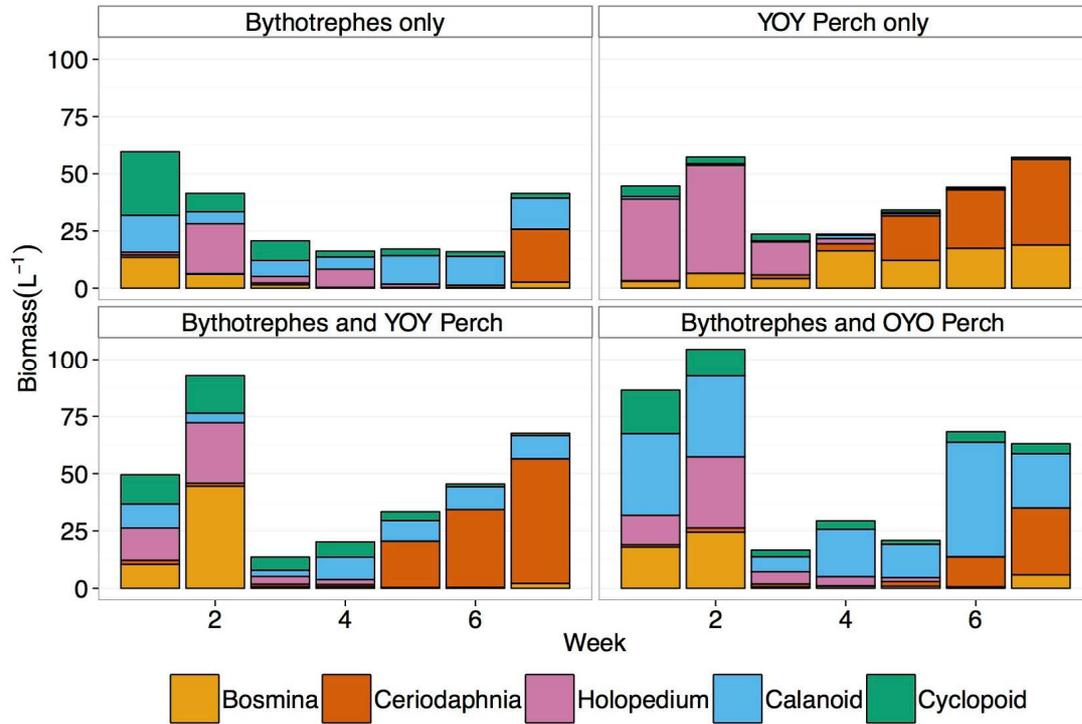
887

888

889

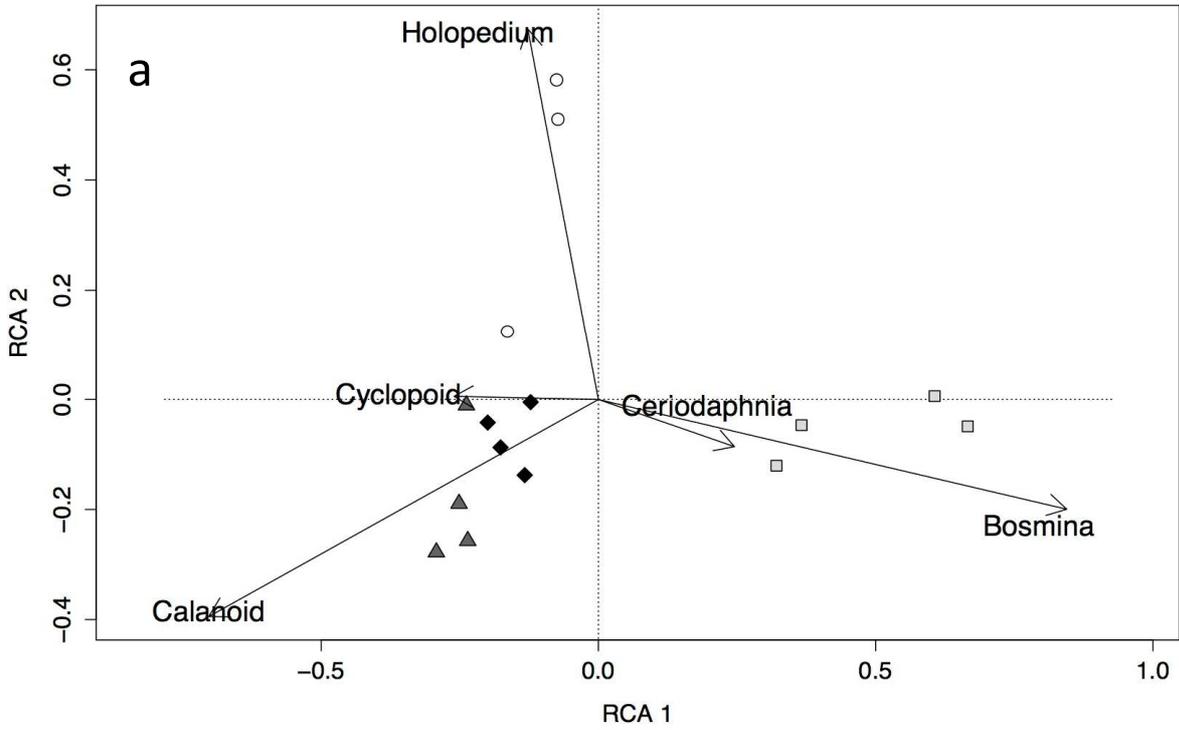
890
891
892
893
894
895

Figure 4

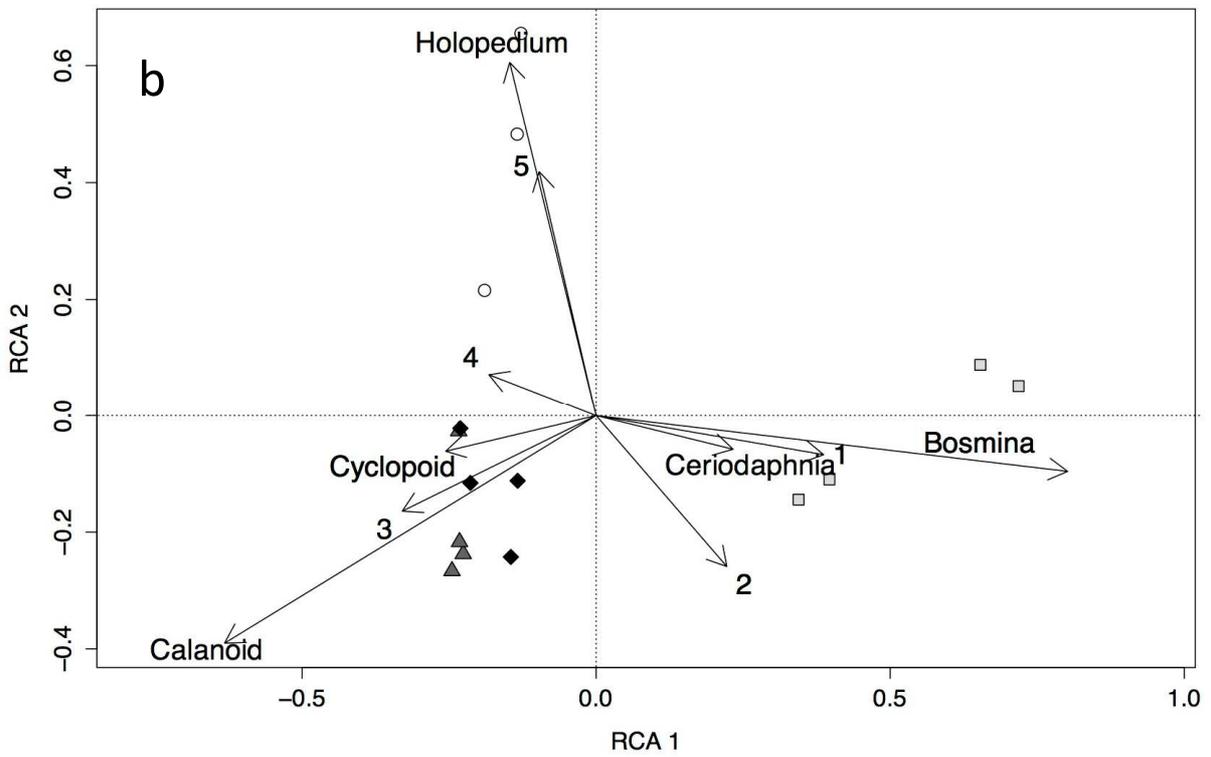


896
897
898
899
900
901
902
903
904
905
906
907
908
909

910 **Figure 5**



911



912

913

914

915 **Table 1**

916

Predator	Average Capture/ Attack Rate on Prey			
	<i>Holopedium</i> ^a	<i>Bythotrephes</i> ^b	Small Cladoceran ^c (e.g. 0.5mm <i>Bosmina</i>)	Copepods
<i>Bythotrephes</i> [*]	0.005 L/s ± 0.001	-	0.008 L/s ± 0.001	0.004 L/s ± 0.001
YOY Perch (12-30mm)	zero	0.215 L/s ± 0.04 (only 24mm+)	0.05 L/s ^c	-
OYO (45-100mm)	0.06 L/s ± 0.006	0.41 L/s ± 0.05	0.15 L/s ^c	0.04 L/s ± 0.02(CI) ^d

917

918

919

920

921

922

923

924

925

926

927

928

929

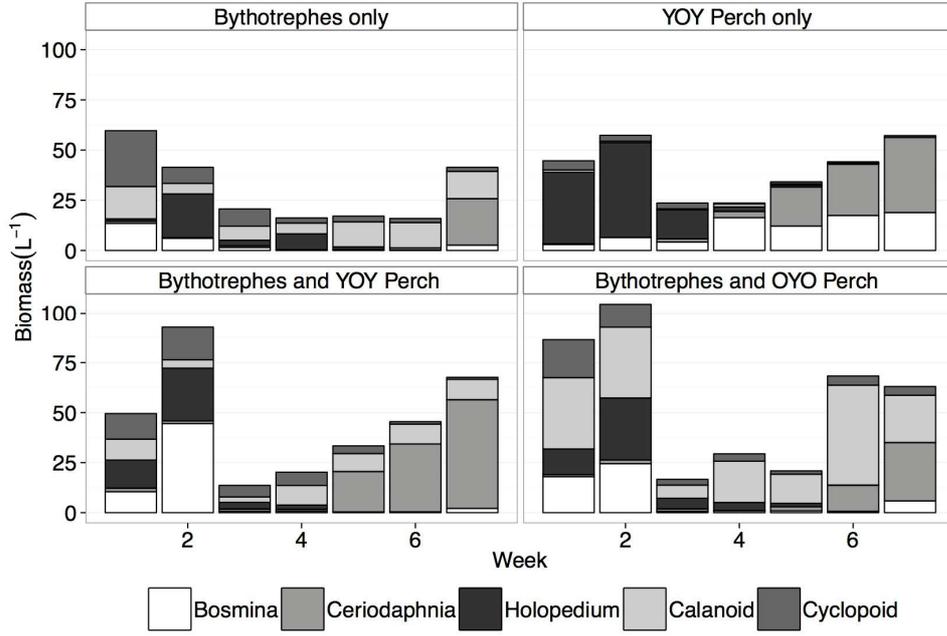
930

931

932

933

934 Figure 4 (greyscale)



935