

Habitat coupling mediates trophic cascades in an aquatic community

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Abstract. Trophic cascades and other indirect effects can significantly mediate community interactions. Movement of energy between systems has been shown to be important for trophic cascades in food webs, where coupling between habitats can be important for food web stability and species evenness. To investigate the effects of habitat coupling on the stability and dynamics of chlorophyll *a* (used as a proxy for phytoplankton biomass), mediated by the abundance and composition of zooplankton and macroinvertebrates, we manipulated habitat use by the predator perch. We show a greater indirect effect of predation on phytoplankton abundance when no habitat coupling occurs, indicating a stronger predation effect and a decrease in zooplankton grazing pressure leading to an increase in phytoplankton biomass. Although we found a significant effect on chlorophyll *a* between the treatments, this effect was not evident in the abundance of prey resources of perch (zooplankton and macroinvertebrates). Other indirect effects, not measured in this study, such as compositional changes in prey groups, could potentially explain the lack of effect in prey resources. While there is a strong theoretical argument for the stabilizing effects of habitat coupling, empirical evidence is scarce. Our study offers tentative support for these theoretical predictions in a natural system.

Key words: chlorophyll *a*; food web; habitat coupling; indirect effects; macroinvertebrates; *Perca fluviatilis*; trophic cascade; zooplankton.

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INTRODUCTION

Ecological models have shown that mobile consumers (for example predatory fish) should have a stabilizing effect on lake food webs by foraging over a larger spatial scale than their prey, thus linking resources in space and potentially also different habitats (for example littoral/benthic and pelagic habitats in lakes; McCann et al. 2005, Rooney et al. 2006, McCann 2012). When prey in one of two coupled habitats is overexploited, prey populations in the second habitat

will allow for recovery of the first habitat (Rooney et al. 2006). Hence, a species that is less vulnerable to predation can buffer another prey species from predation and thus allow the more vulnerable species to recover (Leibold 1989, Strong 1992, Pace et al. 1998, Persson 1999). However, stability then depends on whether the community contains species that are capable of responding differently to resource fluctuations (McCann 2000, Loreau 2010). The removal or addition of any species leading to changes in community composition and structure could

therefore be changing interactions and potentially increase the risk of destabilizing dynamics in the ecosystem (McCann 2000, Loreau 2010).

When switching between prey populations, predators should theoretically stabilize ecosystems by dampening oscillations and fluctuations at lower trophic levels. The ability of mobile predators to stabilize prey dynamics assumes that these predators have unequal preference for their prey types and that the predators can rapidly respond to fluctuations in prey populations (McCann et al. 2005, Rooney et al. 2006, McCann 2012). Depending on interaction strength, we would expect to see higher population fluctuations and potentially stronger trophic interactions if the predators are restricted to a specific habitat. A trophic cascade occurs when a predator in a food web suppresses its prey, thereby releasing the next trophic level down from predation (Carpenter et al. 1985, Pace et al. 1999, Polis et al. 2000, Borer et al. 2005). Among top predators, fish in particular are known to interact with all trophic levels in a food web either directly or indirectly through trophic cascades, nutrient transport (excretion), and/or resuspension (Sinistro 2010). If the predator is able to move freely between the habitats, we would predict a lower magnitude of population fluctuations (McCann et al. 2005, Rooney et al. 2006, McCann 2012). However, habitat coupling by a predator can also reinforce community-wide trophic cascades by obtaining energy from several habitats and increasing predation pressure on the lower trophic levels (Polis and Strong 1996, Vadeboncoeur et al. 2005). This transfer of nutrients between habitats shows that one habitat is not only regulated by its own resources and productivity but can also be influenced by the resources and productivity of another habitat (Persson 1999).

Here, we aim to test the theoretical prediction by McCann et al. (2005) that spatial structure combined with rapid behavioral movement of predators can influence food web dynamics. We conducted a pond experiment with one-year-old Eurasian perch (*Perca fluviatilis*), a fish which is omnivorous at this age and able to feed on both macroinvertebrates and zooplankton (Persson et al. 2000, 2003). In the experiment, we employed three different habitat coupling scenarios by (1) allowing the perch to move freely

between two habitats, (2) dividing and restricting the perch individuals to either of two habitats but, by manually moving them between the habitats, allowing partial habitat coupling, and (3) dividing and completely restricting the perch to either of two habitats, allowing no habitat coupling. We hypothesized that in the treatment where perch were allowed to couple the habitats, perch-prey interaction would be weaker, potentially leading to dampened population fluctuations of phytoplankton, mediated by a lower predation effect on zooplankton and macroinvertebrates. In the treatment where perch were unable to access both habitats, we hypothesized that they would impose the strongest top-down effect leading to fluctuations in phytoplankton biomass. Finally, we hypothesized that in the partially coupled treatment, where the predators had alternating access to both habitats, we would see an intermediate response of phytoplankton dynamics to perch predation.

METHODS

Study design

We conducted an experiment over 8 weeks from late July to September 2013 at the Institute of Freshwater Research, Drottningholm, Sweden, using five ponds. Each pond was approximately 23×6 m, had a mean water depth of 0.65 m, contained natural sediments, and was fed individually with water from a nearby lake. Before the start of the experiment, the ponds were emptied of water and vegetation was removed. Each pond was divided into the same number of experimental enclosures ($\sim 4.5 \times 6$ m) using nets with a mesh size of 4 mm. Each enclosure contained a pelagic and a benthic habitat of equal area, and each pond contained all treatments. The nets were secured to the bottom with chains and tubes filled with sand and rocks, and the upper edges of the nets were securely raised above the water surface with ropes. A pelagic environment was created in half of the enclosure by covering the substrate with a plastic sheet. In the other half of the enclosure, the fish had full access to the benthic resources (see Appendix S1 for a graphical display of one pond).

In July 2013, approximately 1200 one-year-old perch were caught in Lake Mälaren, adjacent to the research station, using a throw net. The fish

were kept in large holding tanks (7 m³) for approximately two weeks to acclimatize before the start of the experiment. The experiment started on 30 July 2013 when 60 perch of similar weight (mean 4.8 g ± 1.5 standard deviation) were released into each enclosure: 30 on the benthic side and 30 on the pelagic side. The following treatments were applied: (1) open (no net between habitats)—perch could move freely between pelagic and benthic habitats; (2) switched (net between habitats)—perch had access to alternating pelagic and benthic habitats every 2 weeks when they were manually moved between the two habitats (all of the individuals in the pelagic habitat were moved to the benthic habitat, while all of the individuals in the benthic habitat were moved to the pelagic habitat); (3) closed (net between habitats)—half of the population only had access to the pelagic habitat, while the other half only had access to the benthic habitat during the whole experimental period; and (4) control—no fish treatment. The switching of perch was carried out by seine netting the enclosures; each enclosure was seine-netted three times to ensure that all individuals were removed and then manually transferred between the benthic and pelagic habitats. To minimize potential disturbance differences between treatments due to netting, we performed the same seine netting procedure in all the other enclosures, but without transferring the fish to the other habitat.

Zooplankton, macroinvertebrates, and chlorophyll *a* (as a proxy for phytoplankton biomass) were sampled at the start of the experiment, then every two weeks, and at the end of the experiment. To determine phytoplankton biomass, we filtered 500 mL of water (GFF filter, 25 mm) taken from the middle from each enclosure and froze the filters for further processing in the laboratory. Chlorophyll *a* was extracted from the filters using standard methods with ethanol extraction and measured spectrophotometrically at 665 and 750 nm. Zooplankton were sampled using a 100- μ m mesh net with a diameter of 25 cm. The net was pulled horizontally through approximately 2 m of water in each enclosure, and samples were immediately preserved with lugol solution. In the laboratory, samples were allowed to settle in a cylindrical settling chamber, and then, all individuals in the sample were

identified and counted using an inverted microscope. We exhaustively counted the numbers of individuals in all samples unless there were very high numbers in the sample. In the cases with high numbers, we divided the sample into 10 and counted subsamples until we reached a sum of hundred individuals or more and the length of the first 15 randomly selected zooplankton specimens of each group was measured. Only crustaceans were identified and counted, and no nauplii were counted. Individuals were identified and divided into five categories: (1) Daphniidae, (2) Chydoridae, (3) Copepoda, (4) *Bosmina*, and (5) *Polyphemus*.

Macroinvertebrates were sampled with a Willner core sampler (core diameter 65 mm). Four samples were taken from each enclosure in the benthic habitat where the sediment surface was exposed to assess spatial variability. Samples were sieved using a mesh size of 0.5 mm, preserved in 70% ethanol, and stained with Bengal rose. In the laboratory, the macroinvertebrates were counted, identified, and divided into seven categories: (1) Chironomidae, (2) pelagic Diptera (*Chaoborus* spp., Chironomidae pupae), (3) Mollusca (Gastropoda and Bivalvia), (4) benthic Diptera (Ceratopogonidae and Oligochaeta), (5) Ephemeroptera (*Caenis* spp., *Cloeon* spp., *Ephemerella* spp.), (6) Ostracoda, and (7) Other (Coleoptera, Trichoptera, Odonata, Heteroptera, *Sialis* spp., *Asellus asellus*, *Gammarus* sp., Hydracarina, Hirudinea).

Statistical analyses

Mixed linear models were used to compare differences in chlorophyll *a* concentration, zooplankton, and macroinvertebrate abundances between the treatments over time. We also analyzed the abundance of the different groups of zooplankton and macroinvertebrates separately. Time (week) was a continuous variable and habitat was nested in treatment, and treatment was nested in pond. When a significant treatment \times time (week) interaction was found in the mixed linear model, sampling days were separately examined with a one-way ANOVA and post hoc tests (Tukey's honestly significant difference procedure). If necessary, log or square-root-transformations were conducted to conform the data to normal distribution. One replicate of each treatment was removed due to high fish

mortality rates, leaving four replicates per treatment. With the remaining replicates, we first tested the effect of fish density on the response variables. However, fish density was found to be non-significant and was therefore subsequently removed from the models. Habitat was also initially included in the models but was removed when found not to be significant. All the analyses were conducted using R (R Development Core Team 2016), with the lme4 (Bates et al. 2015) package and with the lmerTest package (Kuznetsova et al. 2017) using Type III ANOVA with Satterthwaite's approximation to obtain P -values. We used an ANOVA to test for differences in the coefficient of variation (CV) of chlorophyll a among treatments. We only included weeks 2–8 when calculating CV due to high variation in the chlorophyll a starting values.

Primer 7.0.9 (Clarke and Gorley 2015) with the PERMANOVA add-on package for multivariate analyses was used for all the multivariate data. PERMANOVA allows the user to work with any distance measure appropriate to the data and uses permutations to make it distribution free, as well as allowing for complex unbalanced designs. Zooplankton abundances (number/L) and macroinvertebrate abundances (number/m²) were square-root-transformed, and ordination was based on Bray–Curtis similarity. PERMANOVA was used to test the composition of species between treatments nested within ponds and crossed with time (week). Time, treatment, and habitat were fixed factors, and pond was random. Unrestricted permutations (9999 permutations) with type III sums of squares were used to test the significance of the model.

RESULTS

Chlorophyll a

The chlorophyll a concentration in the water differed significantly between treatments (mixed linear model: $F_{3, 201} = 3.89$, $P < 0.01$) where the closed treatment had a higher level of chlorophyll a concentration compared to the control (post hoc test, $P < 0.01$) and the switched treatment showed a slight but non-significant (post hoc test, $P = 0.056$) higher chlorophyll a concentration compared to the control. There was no significant difference between control and open treatment (post hoc test, $P > 0.05$). We also found

a time effect with an overall decrease in chlorophyll a concentration over the experimental period (mixed linear model: $F_{1, 198} = 22.99$, $P < 0.001$). There was no significant interaction effect of treatment \times time (mixed linear model: $F_{3, 198} = 0.69$, $P = 0.56$; Fig. 1). Coefficient of variation of chlorophyll a showed a weak but non-significant difference across treatments (ANOVA: $F_{3,13} = 2.58$, $P = 0.098$) with a tendency of highest variation in the closed treatment and lowest in the control (Fig. 2).

Zooplankton abundance

Total zooplankton abundance increased slightly over time and varied across treatments (Table 1, Fig. 3a), where the control had significantly higher abundances of zooplankton compared to the closed and the switched treatments (post hoc test, $P < 0.05$). There was no significant interaction effect of treatment \times time (Table 1, Fig. 3).

Daphniidae and *Polyphemus* abundances were similar across treatments at the start of the experiment but decreased significantly over time in the fish treatments (Table 1, Fig. 3b, f; see Appendix S2 results for details), with a clear drop in the percentage of Daphniidae and *Polyphemus* to total zooplankton over time

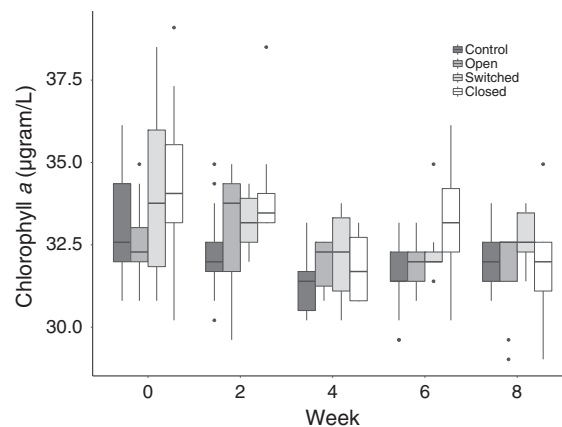


Fig. 1. Box-and-whisker plots of chlorophyll a as a proxy for phytoplankton biomass ($\mu\text{g/L}$) from the start (week 0) to the end of the experiment (week 8) in control, open, switched, and closed treatments. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to $\pm 1.5 \times$ interquartile range. Dots indicate outliers, that is, points located further than 1.5 times the interquartile range.

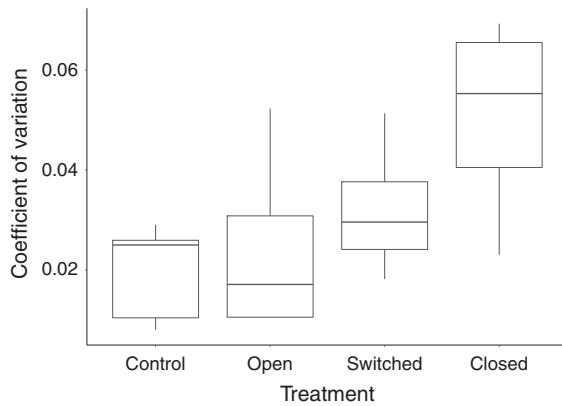


Fig. 2. Box-and-whisker plots of coefficient of variation of chlorophyll *a*, calculated over treatment from week 2 to week 8. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to $\pm 1.5 \times$ interquartile range.

Table 1. Summary of the results from the mixed linear model of total zooplankton, Daphniidae, Chydoridae, Copepoda, *Bosmina*, and *Polyphemus* abundances across time (week) and treatment.

Response	Effect	df	F	P
Total zooplankton	Treatment	3	6.58	<0.001
	Time	1	11.67	<0.001
	Treatment \times Time	3	1.42	0.24
Daphniidae	Treatment	3	8.19	<0.001
	Time	1	7.41	<0.01
	Treatment \times Time	3	4.99	<0.01
Chydoridae	Treatment	3	0.42	0.74
	Time	1	17.57	<0.001
	Habitat	1	4.07	0.045
	Treatment \times Time	3	1.62	0.19
Copepoda	Treatment \times Habitat	3	0.44	0.72
	Treatment	3	0.47	0.71
	Time	1	2.82	0.09
<i>Bosmina</i>	Treatment \times Time	3	0.43	0.73
	Treatment	3	1.90	0.13
	Time	1	113.04	<0.001
<i>Polyphemus</i>	Treatment \times Time	3	0.80	0.49
	Treatment	3	8.28	<0.001
	Time	1	26.22	<0.001
	Treatment \times Time	3	14.96	<0.001

Note: Values that are statistically significant are indicated in bold.

(Appendix S2: Fig. S1). Chydoridae and *Bosmina* abundances increased significantly over time, but there was no significant difference between treatments (Table 1, Fig. 3c, e), although the

percentage of Chydoridae and *Bosmina* abundances to total zooplankton over time indicated a larger abundance of Chydoridae and *Bosmina* in the fish treatments (Appendix S2: Fig. S1). There was also a significant habitat effect on Chydoridae abundance, with a marginally higher abundance in the benthic habitat (Table 1; Appendix S2: Fig. S2), although the post hoc test showed no contrast differences in Chydoridae abundance between the two habitats. The abundance of Copepoda did not significantly differ across treatments or time and showed a high variation both within and between treatments (Table 1, Fig. 3d) and was found in very low percentages relative to the other zooplankton groups (Appendix S2: Fig. S1).

Zooplankton size

The size of Daphniidae and *Bosmina* decreased significantly over the experimental period (Table 2, Fig. 4a, d). The size was not significantly different between the treatments at the start of the experiment or between the control at the start and end of the experiment. But there was a significant difference between the control and the fish treatments at the end (week 8) of the experiment (post hoc test, $P < 0.05$). There was also a significant difference in size of *Bosmina* between the switched treatment at week 0 to the switched and closed treatments in week 8 (post hoc test, $P < 0.05$). The mean length of Chydoridae and *Polyphemus* increased slightly over time but there was no other treatment or interaction effect (Table 2, Fig. 4b, e), although the difference in Chydoridae size seems to be driven by the greater increase of size in the control (Fig. 4b). The variation in size of *Polyphemus* was high, especially at the end of the experiment, possibly obscuring any potential treatment effect. There was no time, treatment, or interaction effect in mean length of Copepoda (Table 2, Fig. 4c).

Zooplankton community structure

Throughout the experiment, there was a significant difference in zooplankton community composition between treatments and between weeks (PERMANOVA treatment \times time: pseudo- $F = 1.87$, $P < 0.001$, time: pseudo- $F = 8.94$, $P < 0.001$, treatment: pseudo- $F = 12.27$, $P < 0.001$; Appendix S2: Fig. S3). The difference was already apparent from week 2 where the main difference was

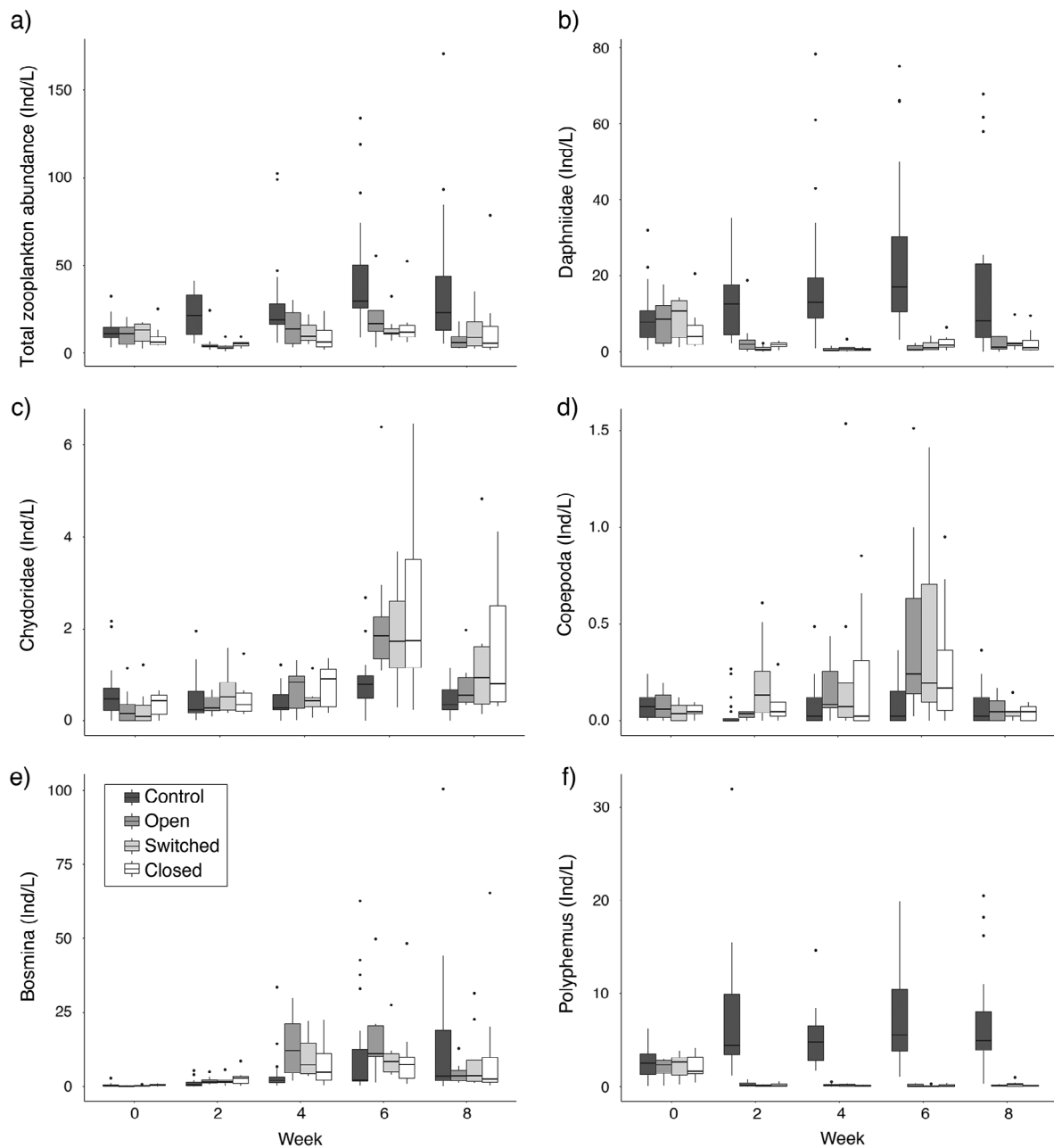


Fig. 3. Box-and-whisker plots of abundance (individuals/L) of zooplankton in the experiment from the start (week 0) to the end of the experiment (week 8) for all treatments and for all zooplankton groups together (a) and the five zooplankton groups separately: (b) Daphniidae, (c) Chydoridae, (d) Copepoda, (e) *Bosmina*, and (f) *Polyphemus*. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to $\pm 1.5 \times$ interquartile range. Dots indicate outliers, that is, points located further than 1.5 times the interquartile range.

between the control and the other treatments. Over time there was a change in community composition from week 2 to week 8, with weeks 6 and 8 being marginally non-significant from

each other (Appendix S2: Table S1). There was no significant difference in the zooplankton community composition between habitats (PERMANOVA: pseudo- $F = 0.87$, $P = 0.74$), but there was

Table 2. Summary of the results from the mixed linear model of the change in mean length of the five zooplankton groups, Daphniidae, Chydoridae, Copepoda, *Bosmina*, and *Polyphemus*, across time (start and end of the experiment) and treatment.

Response	Effect	df	F	P
Daphniidae	Treatment	3	0.81	0.492
	Time	1	122.68	<0.001
	Treatment × Time	3	15.22	<0.001
Chydoridae	Treatment	3	0.97	0.417
	Time	1	4.71	0.034
	Treatment × Time	3	1.30	0.282
Copepoda	Treatment	3	0.24	0.871
	Time	1	0.66	0.421
	Treatment × Time	3	1.75	0.169
<i>Bosmina</i>	Treatment	3	1.37	0.258
	Time	1	10.00	<0.01
	Treatment × Time	3	8.28	<0.001
<i>Polyphemus</i>	Treatment	3	0.43	0.730
	Time	1	11.07	<0.01
	Treatment × Time	3	1.41	0.249

Note: Values that are statistically significant are indicated in bold.

a significant pond effect (PERMANOVA: pseudo- $F = 12.92$, $P < 0.001$), and an interaction week × pond effect (PERMANOVA: pseudo- $F = 3.53$, $P < 0.001$).

Macroinvertebrate abundances

Week 0 was removed from the macroinvertebrate data because Ostracoda were not counted at this time point. In the mixed linear model, there was a weak time effect with an overall increase in the total macroinvertebrate abundance over time, but there was no treatment or interaction effect (Table 3, Fig. 5a). Chironomidae and Ostracoda showed no significant difference over time (Fig. 5b, g), whereas pelagic Diptera significantly decreased over time (Fig. 5c), of note is that *Chaoborus* was only found once in this group and as such this group mostly consisted of Chironomidae pupae. Mollusca, Benthic Diptera, Ephemeroptera, and Other groups (Fig. 5d, e, f, h) tended to increase over time. Notably pelagic Diptera, Mollusca, and Other taxa (Fig. 5c, d, h) only contributed to a very small percentage of the total number of macroinvertebrates (Appendix S2: Fig. S4). Overall there was no significant treatment or interaction effects on the different macroinvertebrate groups (Table 3).

Macroinvertebrate community structure

There was a significant change in macroinvertebrate community composition over time (PERMANOVA: pseudo- $F = 2.84$, $P < 0.01$) where the difference seemed to occur between week 2 and week 8 (Appendix S2: Fig. S5, Table S2). There was a significant treatment effect (PERMANOVA: pseudo- $F = 2.06$, $P < 0.001$), pond effect (PERMANOVA: pseudo- $F = 17.52$, $P < 0.001$), and a pond × time effect (PERMANOVA: pseudo- $F = 5.02$, $P < 0.0001$), and a non-significant treatment × time interaction effect (PERMANOVA: pseudo- $F = 1.12$, $P = 0.18$).

DISCUSSION

We demonstrate a greater indirect effect of predation on the phytoplankton levels when no habitat coupling by the predator (the perch) occurs. The chlorophyll *a* concentration was significantly lower in the control with the highest zooplankton abundance and significantly higher in the closed treatment where the habitats were decoupled. Also, the open and control treatments showed similar levels of chlorophyll *a*. Furthermore, we predicted that the open treatment would lead to dampened population fluctuations, while in the closed treatment we would see higher fluctuations of phytoplankton biomass. Our results, although not statistically conclusive, also indicated this pattern where the fluctuations of phytoplankton biomass in the open treatment were more similar to the control but tended to differ from the closed treatment. These results at least to some extent support predictions from models and other studies (McCann et al. 2005, Rooney et al. 2006, McCann 2012) and provide some empirical evidence that habitat coupling, or as in this experiment the lack thereof, governs trophic interactions in systems with different scenarios of habitat coupling.

While we saw a difference between treatments in the concentration of chlorophyll *a*, it was less clear whether this difference was driven by a reduction in predation effects mediated by changes in zooplankton and macroinvertebrate abundances. We found a significant overall fish effect on zooplankton abundance and size, with a dominance of larger cladocerans (such as Daphniidae) in the control, to a dominance of smaller cladocerans (such as *Bosmina* and

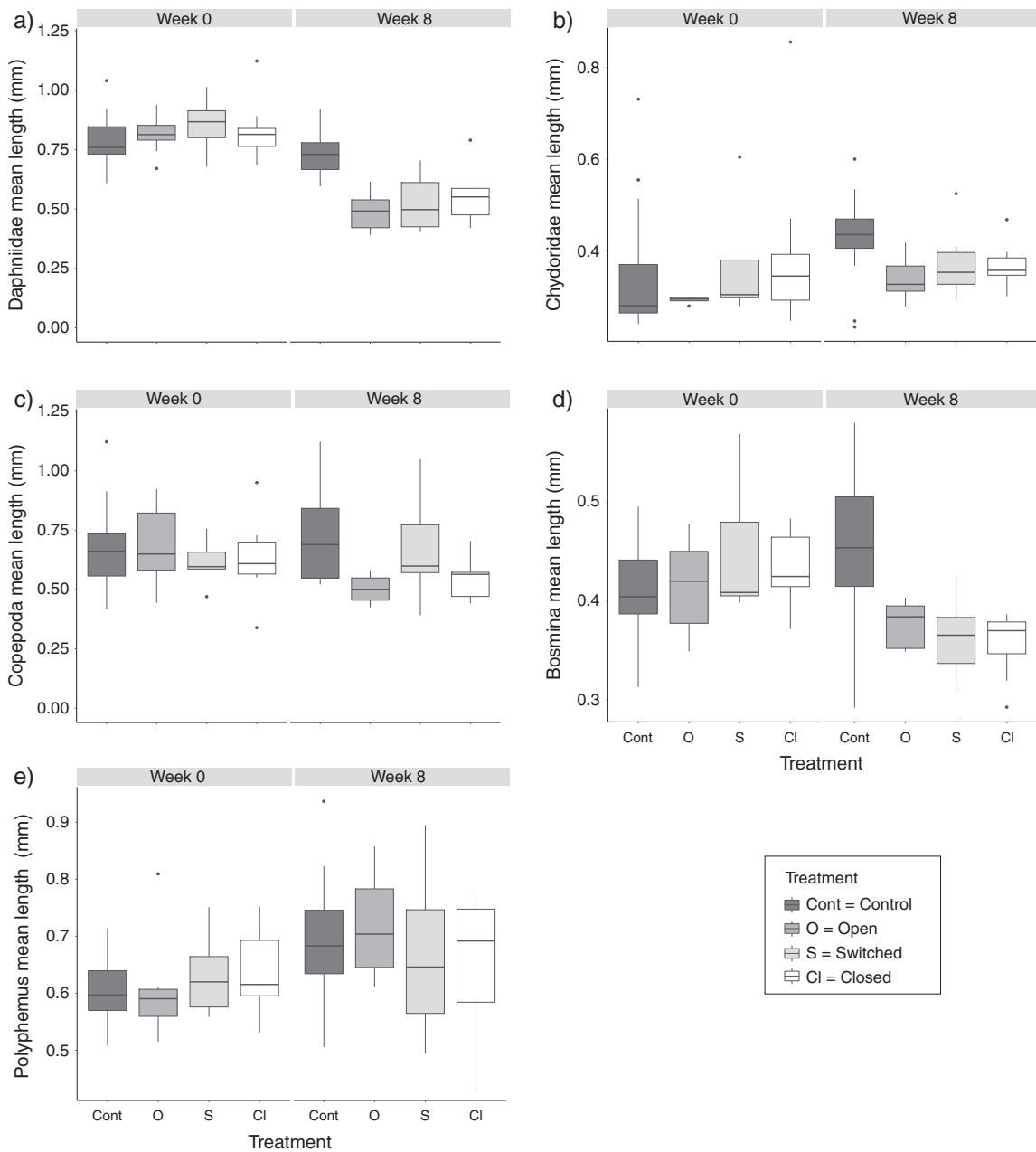


Fig. 4. Box-and-whisker plots of mean length of the five zooplankton groups for each treatment: Cont, control; O, open; S, switched; and CI, closed; at the start of the experiment (week 0) and at the end of the experiment (week 8) for (a) Daphniidae, (b) Chydoridae, (c) Copepoda, (d) *Bosmina*, and (e) *Polyphemus*. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to $\pm 1.5 \times$ interquartile range. Dots indicate outliers, that is, points located further than 1.5 times the interquartile range.

Chydoridae) in the fish treatments. Size selection of prey by predators enables smaller cladoceran species to increase in abundance leading to lower grazing rates which has repeatedly been shown

in other studies (Brooks and Dodson 1965, Hall et al. 1976, Shurin 2001, Hansson et al. 2007, Nicolle et al. 2011). There was also a significant reduction in the actual size of Daphniidae and

Table 3. Summary of the results from the mixed linear model of total macroinvertebrates, Chironomidae, pelagic Diptera, Mollusca, benthic Diptera, Ephemeroptera, Ostracoda, and Others abundances across time (week) and treatment.

Response	Effect	df	F	P
Total abundance	Treatment	3	0.42	0.74
	Time	1	3.87	0.054
	Treatment × Time	3	0.59	0.63
Chironomidae	Treatment	3	1.35	0.27
	Time	1	1.04	0.31
	Treatment × Time	3	0.88	0.46
Pelagic Diptera	Treatment	3	0.63	0.60
	Time	1	5.50	0.02
	Treatment × Time	3	0.24	0.87
Mollusca	Treatment	3	0.08	0.97
	Time	1	5.00	0.03
	Treatment × Time	3	0.57	0.64
Benthic Diptera	Treatment	3	0.32	0.81
	Time	1	29.62	<0.001
	Treatment × Time	3	0.22	0.88
Ephemeroptera	Treatment	3	0.57	0.64
	Time	1	94.10	<0.001
	Treatment × Time	3	2.51	0.07
Ostracoda	Treatment	3	0.23	0.87
	Time	1	0.98	0.33
	Treatment × Time	3	0.14	0.94
Other	Treatment	3	1.88	0.14
	Time	1	10.20	<0.001
	Treatment × Time	3	2.47	0.07

Note: Values that are statistically significant are indicated in bold.

Bosmina due to predation of fish which has also been reported in other studies (Brooks and Dodson 1965, Hall et al. 1976, Lynch 1979, Post and McQueen 1987, Shurin 2001, Nicolle et al. 2011).

High fish predation pressure on zooplankton can eventually lead to population crashes independent of zooplankton resource abundance (Nicolle et al. 2011). Potentially, the predation pressure on predator sensitive species like Daphnia was so high that they were not able to control the phytoplankton levels. Indirect effects of fish predation mediated by shifts in zooplankton size and composition could possibly contribute to changes in phytoplankton grazing capacity (Jeppesen et al. 1996). Zooplankton grazing is considered an important controlling factor for phytoplankton biomass (Lynch and Shapiro 1981, Lampert et al. 1986, Carpenter et al. 1987, Shurin 2001). In particular, larger cladocerans are

important grazers on the phytoplankton community as they can graze over a greater size range (Brooks and Dodson 1965, Hall et al. 1976, McQueen et al. 1986). It is therefore possible that predation shifted the zooplankton community to less predation-sensitive taxa, which might have influenced our chlorophyll *a* results. However, there were no differences between the fish switching treatments in zooplankton abundance or in size distribution. This means that the indirect positive effect on chlorophyll *a* in the closed treatment is unlikely driven by differences in total zooplankton abundance across treatments. Nevertheless, species-specific changes in abundance of zooplankton to predation by perch could possibly have contributed to the treatment differences in chlorophyll *a* levels across treatments. A possibility is that chlorophyll *a* levels were influenced by one part of the zooplankton community that we did not measure, such as rotifers and naupli, which are likely to increase with competitive release from larger cladocerans (Kirk 1991). Still, the mechanisms behind the significant increase in chlorophyll *a* between the control and closed treatment are unclear.

While we saw a strong predation effect on the zooplankton community, there was no, or very little, effect of predation on the macroinvertebrate community, although we found evidence of macroinvertebrate predation by fish in the experiment (see Marklund et al. 2018 for study based on the same experiment). Macroinvertebrates increased slightly over time, mainly driven by Ephemeroptera and benthic Diptera. If anything, we would have expected a decrease in abundance in some groups such as Ephemeroptera, Ostracoda, and Chironomidae in the fish treatments since these groups are sensitive to predation, and perch are known to heavily feed on these groups (Diehl 1992). Macroinvertebrates that emerge in the autumn (Diehl 1992), or display antipredator behavior (Sih 1982, McIntosh and Townsend 1996, Uiblein et al. 1996, Warfe and Barmuta 2006) could potentially explain the lack of predation effect and might also explain why several other studies have found little effect of fish on benthic communities (Thorp and Bergy 1981, Allan 1982, Flecker and Allan 1984).

Numerous weak interactions, and a more generalist dominated food web have more stabilizing effects on communities (McCann et al. 1998).

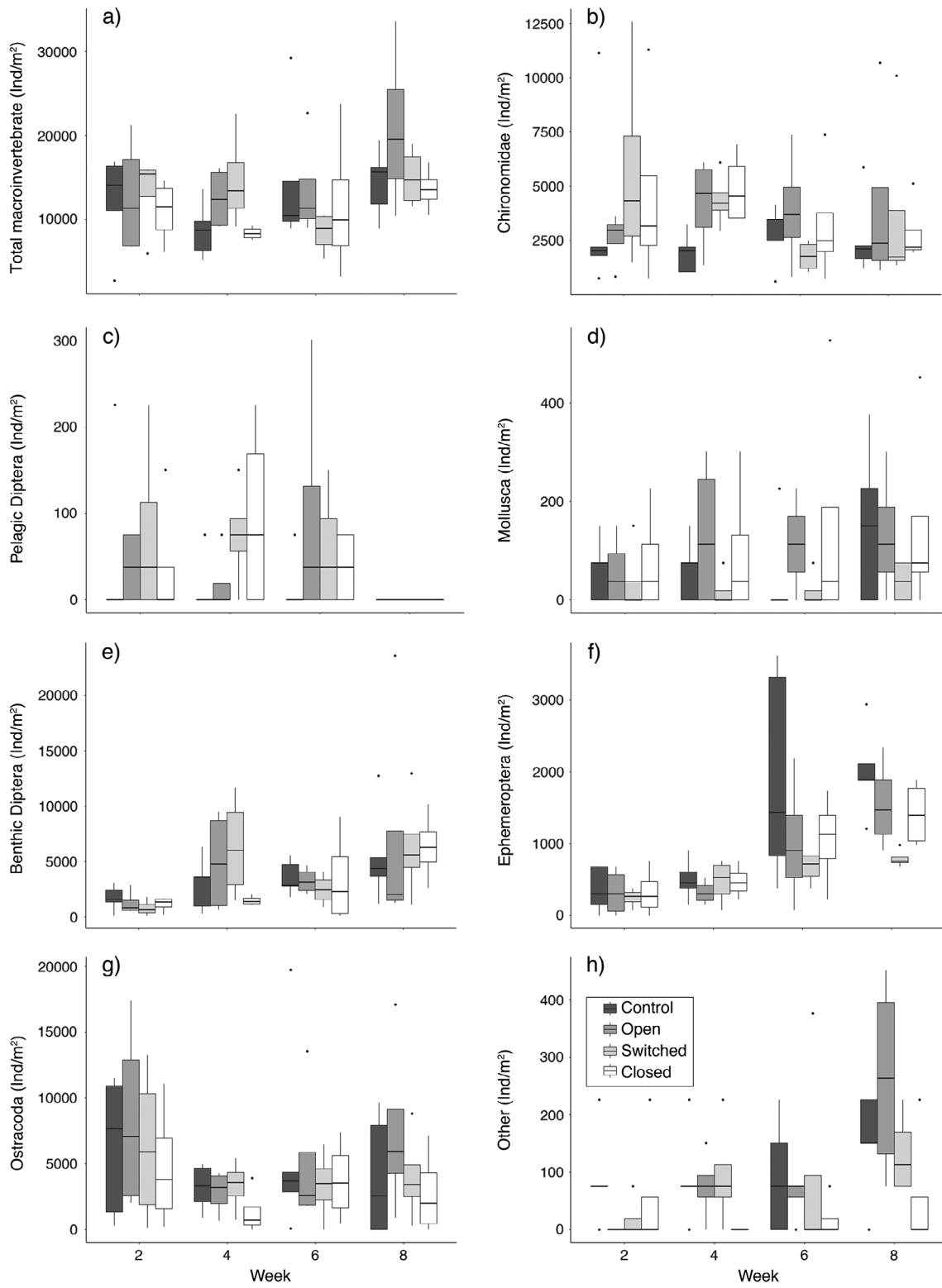


Fig. 5. Box-and-whisker plots of abundance (individuals/m²) of macroinvertebrates in the experiment from

(Fig. 5. *Continued*)

week 2 to the end of the experiment (week 8) for all treatments and for all macroinvertebrate groups together (a) and the seven macroinvertebrate groups separately: (b) Chironomidae, (c) pelagic Diptera, (d) Mollusca, (e) benthic Diptera, (f) Ephemeroptera, (g) Ostracoda, and (h) Other. Week 0 is not included due to missing data for Ostracoda. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to ± 1.5 times interquartile range. Dots indicate outliers, that is, points located further than 1.5 times the interquartile range.

Although perch are generalists at the population level, they can be specialists at the individual level. Previous studies have shown that individual diet and morphological specializations in perch can influence their habitat coupling ability, where the individual specialization might prevent perch from efficiently coupling habitats (Marklund et al. 2018, Quevedo et al. 2009, also Matich et al. 2011 for a non-perch example), thereby creating fewer but stronger interactions. In another study, based on the same experiment we showed that individual diet specialization of perch varied across treatments (Marklund et al. 2018). It is possible that beyond the effects of habitat switching, individual specialization could also have contributed to changes in interaction strength and variability in resources either directly through stronger predator–prey connections or indirectly through decreasing habitat coupling (Quevedo et al. 2009, Marklund et al. 2018).

Habitat complexity may also increase community stability and persistence by reducing the potential for population outbreaks (i.e., overpopulation; Floater 2001). Removal of energy channels (food links) or environmental variations that reduce the heterogeneity in a system, as well as removal of mobile predators, are thought to destabilize systems (Rooney et al. 2006). A major prediction of the hypothesis of McCann et al. (2005) is that small fragmented habitats, such as lakes or island food webs, should be more prone to destabilizing top-down cascades. However, a mobile consumer could increase the stability of the overall food web by allowing the predator to utilize and couple desynchronized resources but also couple fragmented landscapes (McCann et al. 2005, Rooney et al. 2006, McCann and Rooney 2009). Our experiment was conducted in ponds, and hence, the habitat might in reality be considered spatially compressed (sensu McCann et al. 2005). But, in spite of this we identified significant influence on prey resources in the

decoupled, fragmented treatment (closed treatment), giving tentative support to the destabilizing potential of a specialist consumer in a fragmented habitat (McCann et al. 2005).

We believe that the consequences of individual diet specializations depend on the ability of the predator to continue to respond adaptably to changing conditions over short time scales (see also McMeans et al. 2016). While many models and theoretical concepts have suggested that mobile predators stabilize cross-habitat movement of energy (Polis and Strong 1996, Post et al. 2000a, b, McCann et al. 2005, Rooney et al. 2006), there is little empirical evidence for this occurring in natural systems. For future studies, we believe it is important to consider the organisms' individual specialization since this can play an important role in changing the interactions in spatial separated food webs.

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