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HAL Id: mnhn-02920029
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Submitted on 24 Aug 2020

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Trait-dependency of trophic interactions in zooplankton food webs

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Declarations

Acknowledgements – AB and GL warmly thank Françoise Lescher-Moutoué for her contribution in conceiving the experimental design and for her contribution to the experiment.

Funding – FV was funded by a grant from Sorbonne Université (CARESE-SU J15R323). GL and FV were supported by the International Program For Scientific Cooperation (project PICS06763) of the French National Center of Scientific Research. AB was funded by a NSERC Discovery grant (RGPIN-2017-05451). EE was supported by a research grant from Rennes Métropole (AIS program – project number 18C0356).

Author contributions – All authors designed the study, AB and GL performed the experiment and produced the data, FV and EE analysed the data, all authors wrote the paper.

Conflicts of interest – The authors declare no conflict of interest.

Permit(s) – Fish manipulations were performed under the control of authorities and in compliance with applicable laws.
Introduction

Trophic interactions determine population dynamics, evolutionary trajectories and the stocks and fluxes of energy in ecosystems (Polis and Winemiller 1996). Therefore, uncovering general rules that shape trophic interactions represents a central objective of ecological research. To reach this goal, researchers classically either use *a priori*-built models whose predictions are compared to observed food webs, or infer general rules *a posteriori* through mechanistic or statistical models fitted to observed networks (Rohr et al. 2017). Both approaches require high-quality, detailed food-web data built from direct observations. Such data are scarce and costly to acquire. A third, cost-effective but indirect approach to inferring trophic interactions is to experimentally measure community response to manipulating presence-absence of particular predators in the food web (Hulot et al. 2014).

Experimental manipulations of predator-prey systems have a long history in ecological research and, in particular, have proven powerful to reveal whether and how trophic interactions are predictable from single-trait phenotypes (Bolker et al. 2003, Werner and Peacor 2003, Schmitz 2008). Such studies have, for instance, confirmed the major role played by body size in structuring trophic interactions (Emmerson and Raffaelli 2004), a role that was already envisioned by Elton (1927) and robustly explored since then (Cohen et al. 1993, Woodward et al. 2005, Brose et al. 2006). Recently, such manipulative experiments have demonstrated that predator hunting mode interacts with prey antipredator behaviour in controlling predator-prey interactions and, from there, in determining both the strength of trophic cascades (Schmitz et al. 2004, Schmitz 2008) as well as the architecture of whole food webs (Lazzaro et al. 2009).
Besides body size, hunting mode and antipredator behaviour, other phenotypic traits may be involved in controlling the occurrence and strength of trophic links (e.g. palatability, chemical defences or mimicry). However, these other traits are often difficult to identify or measure, and are poorly reported in the literature. To tackle this complexity issue, phylogeny may be used as a “holistic trait” encapsulating the complex phenotypes that determine trophic niches. Accordingly, several studies suggest that phylogeny (using taxonomy as a proxy) has a higher power than body size in predicting trophic links in observed terrestrial and aquatic food webs (Cattin et al. 2004, Naisbit et al. 2012). Recently, some authors have further suggested that even a coarse phylogenetic resolution might still retain enough information to efficiently predict trophic links (Gauzens et al. 2013).

To our knowledge, however, no study has quantified the respective contributions of body size, antipredator behaviour, and phylogeny at different resolutions in driving the presence and strength of trophic interactions in complex food webs. To contribute bridging this knowledge gap, we measured the numerical response of a zooplankton community to the experimental manipulation of their fish predators in lake enclosures. We expected fish predation to have both direct effects through fish-zooplankton trophic interactions, and indirect effects through reorganizations of zooplankton-zooplankton and zooplankton-phytoplankton trophic interactions. To investigate the role of zooplankton traits in driving both these direct and indirect effects, we grouped zooplankters based on their body size, antipredator behaviour or on both their body size and antipredator behaviour, and we made qualitative predictions on whether and how each zooplankton group should numerically respond to fish. Specifically, we predicted fish to deplete large-bodied zooplankton, and to favour increased abundances of small-bodied zooplankton due to relaxed predation and competition from large-bodied zooplankton. We further predicted that, at a constant total fish biomass, smaller-bodied fish should have a higher cumulated attack rate on large-bodied zooplankton. Based on antipredator behaviour, we
predicted (i) “fleeing” zooplankton strategists to efficiently escape predation from cruising-foraging fish but not from visual-feeding fish, (ii) “hiding” zooplankton strategists to efficiently escape predation from both type of fish, and (iii) “no escape” zooplankton strategists to be equally depleted by both type of fish. Adding the effects of body size on top of the effects of antipredator behaviour changed (i) the predicted response of small-bodied, “no escape” zooplankton strategists to fish from negative to positive, and (ii) the predicted response of “hide” zooplankton strategists from nil to positive because they feed on small-bodied, “no escape” zooplankton. We formulate more detailed and referenced predictions in the Methods section.

We compared these qualitative predictions with observed effect sizes and, additionally, we adopted a model selection procedure that quantified the relative power of size- and behaviour-based zooplankton groups to predict zooplankton response to fish manipulation. We further grouped zooplankters based on phylogeny at a low, medium or high resolution, and included these phylogeny-based groups into the model selection procedure. In doing so, we combined phylogeny-based grouping with ontogeny-based grouping among Copepods (i.e., nauplii vs. copepodites and adults), as is usual when describing zooplankton communities. We show that body size-based zooplankton grouping outperformed behaviour-based zooplankton grouping in predicting zooplankton numerical response to fish, but performed less well than a grouping structure combining both zooplankton body size and behaviour. A phylogeny-based zooplankton grouping structure provided the overall best and most parsimonious fit to the data, and was therefore most powerful at predicting zooplankton numerical response to fish predators, but only at a high to medium phylogenetic resolution and when ontogeny was also accounted for.
Materials and Methods

Experimental setup

Nine enclosures made of translucent polyethylene were installed on a floating pontoon on Lake Crétéil, a 42-ha shallow lake of 4 m mean depth (max depth 6m). Whereas they did not include lake sediments, our enclosures were 1.5 m x 1.5 m x 4.5 m deep (9.5 m³) and, hence, realistically reproduced lake vertical heterogeneity. Enclosures were filled with lake water pumped from a 1.5-meter depth from June 29th to July 3rd 1995. After filling, enclosures were enriched with living zooplankton sampled from the pelagic area of the lake. In order to avoid nutrient limitation of phytoplankton, inorganic nutrients were added twice a week with a liquid mixture of potassium phosphate (KH₂PO₄) and ammonium nitrate (NH₄NO₃) with a N:P ratio of 20:1 by weight, for a load of phosphorus of 3.16 μg L⁻¹ d⁻¹. At the start of the experiment (July 13th), the zooplankton biomass was > 200 μg dry weight L⁻¹. Additional details on the experimental setup can be found in Bertolo et al. (1999b) and in Bertolo et al. (2000).

On July 13th, three different triplicate treatments were applied randomly to the enclosures: (i) “Control”: fishless; (ii) “Perch”: 18 planktivorous perch (aged 0+), measuring 5.97 cm ± 0.55 cm (fork length) and weighting 2.45 ± 0.76 g (fresh weight); (iii) “Roach”: six roach aged of at least a year (1+), measuring on average 8.13 ± 0.37 cm and weighting on average 7.50 ± 0.50 g. The different numbers of roach and perch per enclosure were used to standardize fish biomass at 20 g.m⁻², which can be considered as a moderate stocking rate (Williams and Moss 2003). Hence, in our design fish identity is confounded with fish density, body size and hunting mode (see below), and we could thus not identify which fish traits would actually determine different zooplankton response when comparing perch to...
roach. For this reason, our study is based on exploring zooplankton rather than fish traits and how these influence zooplankton response to fish.

**Sampling**

In order to alleviate constraints inherent to mesocosms (higher fish biomass than in natural systems, limited movements of zooplankters, and severe prey depletion), we limited the duration of the experiments to 20 days. Water was sampled at every 30-cm depth in each enclosure using a 2-L Friedinger bottle on three dates (July 18\textsuperscript{th} and 25\textsuperscript{th}, August 1\textsuperscript{st} 1995). All samples from the same enclosure were pooled (24 L in total). Zooplankton of the pooled sample was filtered through a 50 µm sieve and fixed in 4% formalin. One to two litres of 50 µm-sieved water (depending on filter clogging) were filtered on a GF/C glass fiber filter (nominal cut-off: 1.2 µm) for estimation of chlorophyll \textit{a} content. Algal cells were strongly dominated by small algae (< 25 µm) mainly belonging to Chlorophyceae, Cryptophyceae and diatoms (Bertolo et al. 1999b, 2000), and a negligible fraction was retained on the 50 µm sieve. Chlorophyll \textit{a} was measured spectrophotometrically (µg L\textsuperscript{-1}) after grinding the samples in 90% acetone and centrifugation (AFNOR 1990).

Before being analysed under a stereomicroscope, each zooplankton sample was subsampled and diluted so as to standardize abundances. Zooplankton counts from diluted subsamples were then transformed to zooplankton concentration (mean count L\textsuperscript{-1}) in each enclosure. Zooplankton individuals were identified at the species level when only one species was present and at the genus level when two congeneric species co-occurred. Copepods were present in two development stages, specifically as nauplii \textit{vs.} copepodites and adults (Reid and Williamson 2010). Copepod nauplii were segregated into nauplii of Calanoids and nauplii of Cyclopoids. Cladocera, and copepodites of Copepods were measured for body length (in mm, 40 individuals per zooplankton category and per sample).
Zooplankton taxa

We identified five herbivorous cladoceran genera: *Ceriodaphnia* [*C. pulchella* Sars 1862 and *C. quadrangula* (O.F. Müller 1785)], *Bosmina* [*B. longirostris* (O.F. Müller 1785)], *Diaphanosoma* [*D. brachyurum* (Liévin 1848)] and *Daphnia* (*D. longispina* complex), listed according to their relative abundance. The omnivorous copepods were represented by the Calanoid species *Eudiaptomus gracilis* (Sars 1863) and the Cyclopoid species *Acanthocyclops robustus* (Sars 1863), *Thermocyclops crassus* (Fischer 1853), and *Th. oithonoides* (Sars 1863). The herbivorous rotifers were dominated by *Polyarthra* sp. and *Hexarthra mira* (Hudson 1871), while the predatory genus *Asplanchna* (*A. girodi* De Guerne, 1888, *A. priodonta* Gosse, 1850) represented the carnivorous rotifers. Other zooplankton taxa, such as undetermined Chydorids, the calanoid Copepod *Eurytemora velox* (Lilljeborg 1853), and the rotifers *Keratella quadrata* (O.F. Müller 1786), *K. cochlearis* (Gosse 1851), and *Lecane* spp., were only found very occasionally and were not taken into account in the subsequent analyses.

Assigning zooplankton taxa to trophic groups from prior knowledge

We assumed that the assembly of zooplankton trophic groups (and associated trophic interactions with fish and other zooplankters) was controlled by zooplankton (i) body size only, (ii) antipredator behaviour only, (iii) body size and behaviour combined, and (iv) phylogeny (using taxonomy as a proxy) at different resolutions and combined with ontogeny for Copepod taxa. Below, we present the criteria used to assign zooplankton taxa into trophic groups and predict their associated numerical response to perch and roach (summarized in Table 1).

Body size-based zooplankton trophic groups
During summer, zooplankton in Lake Créteil include few large-bodied organisms and thus have a relatively narrow body-size range. They may be separated among small-bodied organisms (50-200 µm), which include mainly herbivores (Rotifers and nauplii of Copepods), and medium to large-bodied organisms (200-2000 µm, among which 8.7 % were > 1000 µm), which include both herbivorous or omnivorous/carnivorous microcrustaceans and carnivorous Rotifera (Bertolo et al. 1999a). In order to take into account other realistic ways of classifying zooplankton, we split it into three size classes: 50-200 µm (Rotifers and nauplii of Copepods), 200-600 µm (Bosmina, Ceriodaphnia and Thermocyclops) and 600-2000 µm organisms (Asplanchna, Daphnia, Diaphanosoma, Eudiaptomus, Acanthocyclops). When fitting models to zooplankton count data (see below), however, this three size-class grouping structure did not perform better than the two size-class grouping structure (LR test: Chi-square = 2.5382, Df = 3, p = 0.4684), and was penalized in terms of Akaike’s information criterion (AIC, 2674.1 vs. 2670.6). We therefore retained the two-size-classes grouping structure for further analyses.

Fish preferentially consume large-bodied zooplankters, while small-bodied zooplankters are both dominated competitors and prey for larger zooplankton (Brooks and Dodson 1965). Hence, we predicted that small-bodied zooplankton abundance should increase in the presence of fish (Table 1, Body size). Moreover, based on perch and roach differences in body size, we predicted perch to impose a stronger predation pressure than roach and thus, in turn, to have a larger positive effect on small-bodied zooplankton (Table 1, Body size). This prediction emerges from general body-mass scaling rules, where average attack rate for freshwater vertebrate ectotherms equals $8.2 \cdot 10^{-6} m^{0.31}$ (where $m$ is individual body mass, Rall et al. 2012). Using this relationship, cumulated attack rate on zooplankton from 18 perch weighing 2.45 g is predicted to be twice as large than that from six roach weighing 7.50 g. Finally, we predicted this higher cumulated attack rate from perch to result in a
stronger trophic cascade (i.e. increase in phytoplankton abundance) than in the presence of roach (Table 1, Body size).

Behaviour-based zooplankton trophic groups

Possible behavioural responses of zooplankters facing predation from fish or from other invertebrates may be either (i) “fleeing” reaction, (ii) hiding in a spatial refuge or (iii) no escape. Whereas these behaviour-based zooplankton trophic groups are not mutually exclusive, we assigned each zooplankton organism to only one group based on prior literature knowledge about their predominant behaviour.

Specifically, nauplii of both Calanoid and Cyclopoid copepods have limited escape capabilities, while copepodite stages of are often equally categorized as “flee” strategists due to their jump-swimming behaviour. However, Calanoids occupy the upper water layers at both the nauplius and copepodite stages (Angeli et al. 1995, Lacroix and Lescher-Moutoué 1995, Lieschke and Closs 1999, Bertolo et al. 1999a, Titelman and Fiksen 2004, Doulka and Kehayias 2011), and thus can not avoid encounters with fish. Hence, we categorized Calanoids as “no escape” strategists at the nauplius stage and as “flee” strategists at the copepodite stage. In contrast, Cyclopoids prefer the deep layers of the water column in Lake Créteil (Lacroix and Lescher-Moutoué 1995) and may even be regularly found in near-bottom habitats at both the nauplius and copepodite stages (Papińska and Prejs 1979, Papińska 1981). Hence, Cyclopoids may efficiently hide from fish predators by preferentially occupying deep water layers. We considered hiding as a more efficient antipredator strategy than fleeing, and we categorized Cyclopoids as “hide” strategists at both the nauplius and copepodite stages.

We also categorized as “flee” strategists Diaphanosoma spp., a jump-swimmer rapidly alternating sinking with powerful strokes of antennae (Williamson 1983, Chang and Hanazato 2003), but also
Bosmina spp., which use a “dead-man response” (in addition to having a hard carapace) to deter predation from copepods (Kerfoot 1978, Williamson 1983, Sakamoto and Hanazato 2008). Although jumping and a dead-man response are sharply different behaviours, we grouped them in a common “flee” category because their common purpose is to reduce mortality from unavoidable predator encounters. This choice was further justified a posteriori by fitting statistical models to zooplankton count data. A model considering Bosmina separately as a “passive escape” strategist did not fit the data better than a model grouping Bosmina together with Diaphanosoma and copepodites of Calanoids (LR test: Chi-square = 3.8594, Df = 3, p = 0.2771), and was penalized in terms of AIC (2688.7 vs. 2686.6).

Finally, Daphnids have a reduced ability to escape by jumping. Additionally, in Lake Créteil both Ceriodaphnia spp. and Daphnia spp. preferentially use the upper layers of the water column (Lacroix and Lescher-Moutoué 1995), and thus are highly susceptible to predation by planktivorous fish. We thus categorized Daphnids as “no escape” strategists, together with Rotifers.

Perch and roach also have contrasted hunting modes. Planktivorous perch are typical visual feeders (Lacroix et al. 1996) able to feed on zooplankton only when light intensity is relatively high (Nurminen et al. 2010, Kestemont et al. 2015). They are stimulated by conspicuous prey, and prey movement can trigger an attack (Peterka and Matěna 2009). Perch are stop-and-burst predators that can repeatedly strike, particularly so when feeding on evasive copepods (Peterka and Matěna 2011). Hence, we predicted perch to efficiently deplete both “no escape” and “fleeing” zooplankton strategists, but to be less efficient on “hide” strategists (Table 1, Behaviour).

In contrast with perch, roach are cruising foragers that use continuous and rapid swimming, punctuated by slowdowns (Peterka and Matěna 2011, Helenius et al. 2015). They are able to switch between
particulate feeding and gulping, depending on zooplankton body size, abundance and light conditions (Van Den Berg et al. 1993, Helenius et al. 2015). Roach foraging efficiency is almost independent of the light intensity (Diehl 1988, Nurminen et al. 2010), indicating that they only optionally rely on visual cues to locate their prey. Moreover, even when light intensity is relatively high, roach are poorly capable to prey on “fleeing” zooplankton strategists like copepods (Lacroix et al. 1996, Peterka and Matěna 2009, 2011). Hence, we expected roach in our experiment to deplete “no escape” zooplankters, but not “fleeing” or “hide” strategists (Table 1, Behaviour).

Mixture of size- and behaviour-based zooplankton trophic groups

Body size should be important to predict zooplankton-fish trophic links only for zooplankters that are unable to behaviourally avoid encounters with fish. Hence, we separated “no escape” zooplankton strategists into “large-bodied” and “small-bodied” zooplankton trophic groups. “Fleeing” strategists were similar in body sizes and were thus not partitioned into different body size-based zooplankton trophic groups. Finally, “hide” strategists, by efficiently avoiding predation from both perch and roach, were free from any size-dependency in their response to fish and were also not partitioned into different body size-based zooplankton trophic groups. Because they are omnivorous, however, we predicted “hide” strategists to increase in parallel with the increasing abundance of “small, no escape” strategists on which they feed. The predictions resulting from this zooplankton grouping structure are summarized in Table 1 (Body size and behaviour).

Phylogeny-based zooplankton trophic groups

We identified 12 genera or species and two development stages for copepods (see above), yielding a total of 14 trophic groups. Reaching this taxonomic resolution in zooplankton counts, however, is a time-consuming task which is relieved if taxa may be lumped. It is therefore important to quantify the
effect of taxonomic lumping on information loss in predicting food-web structure (Gauzens et al. 2013). Accordingly, we varied zooplankton lumping in our dataset from low to high to reach a (i) low-level lumping (12 trophic groups: Ceriodaphnia, Bosmina, Diaphanosoma, Daphnia, Eudiaptomus, Acanthocyclops, Thermocyclops, nauplii of Calanoids, nauplii of Cyclopoids, Polyarthra, Hexarthra, Asplanchna), (ii) medium-level lumping (10 trophic groups: Daphnidae, Bosminidae, Sididae, Diaptomidae, Cyclopidae, nauplii of copepods, Hexarthridae, Synchaetidae, Asplanchnidae) and (iii) high-level lumping (4 trophic groups: Cladocera, copepodite of copepods, nauplii of copepods, and Rotifera).

**Data analysis**

**Zooplankton counts**

Our analysis of zooplankton count data aimed at (i) quantifying the numerical response of the different zooplankton trophic groups to the fish treatments, (ii) identifying which zooplankton grouping structure provided the best and most parsimonious fit to the data, and (iii) quantifying, for each zooplankton grouping structure, the importance of considering perch and roach as having different effects on zooplankton numbers. We based our analysis on comparing the fit to zooplankton count data of the resulting 12 different generalized linear mixed models (Table 2), which corresponded to the six zooplankton grouping structures described above times two different fish effects: fish absent vs. fish present or fish absent vs. perch present vs. roach present. We provide below more details on the analyses.

Zooplankton counts included a high proportion (25 %) of zeros, and positive counts were highly overdispersed. We thus modelled this data using a zero-inflated negative binomial model (Ntzoufras 2009):
\[ C_i \sim NB(\phi_i, r_i) \]
\[ \phi_i = \frac{r_i}{r_i + \lambda_i(1 - \theta_i)} \]
\[ \theta_i \sim B(\psi_i) \]
\[ \ln(\lambda_i) = \alpha + \beta Z_{[i]} + \gamma F_{[i]} + \delta_{Z_{[i]}, F_{[i]}} + \epsilon_{E_{[i]}, D_{[i]}} + \zeta_{T_{[i]}} \]
\[ \epsilon_{E_{[i]}, D_{[i]}} \sim N(0, \sigma_\epsilon^2) \]
\[ \zeta_{T_{[i]}} \sim N(0, \sigma_\zeta^2) \]

where subscript \( i \) indexes sampling events corresponding to a taxon (low-level phylogenetic lumping, 12 groups) in a given enclosure on a given sampling day (\( n = 324 \) sampling events), \( \sim \) means “follows distribution”, and \( NB \) is the negative binomial distribution with success probability \( \phi \) and number of failures \( r \). The \( \theta \) latent variable for absence of organisms was modelled as a Bernoulli process (B distribution) with probability \( \psi \).

Line 4 in Eq. (1) shows that we modelled positive (non-zero) counts \( \lambda_i \) with a GLM including a natural logarithm (ln) link and a linear predictor in which \( \alpha \) was an intercept, and \( \beta \) described deviations from the intercept associated with zooplankton trophic group \( Z \), which corresponded to the six different grouping structures based on (i) body size (two \( Z \) groups), (ii) antipredator behaviour (four \( Z \) groups), (iii) body size and behaviour combined (five \( Z \) groups), (iv) low-level phylogenetic lumping (12 \( Z \) groups), (v) medium-level phylogenetic lumping (10 \( Z \) groups) and (vi) high-level phylogenetic lumping (four \( Z \) groups).

\( \gamma \) described deviations from the intercept associated with fish treatment \( F \), which took either two levels (fish absent vs. present) or 3 levels (fish absent vs. perch present vs. roach present). \( \delta \) described deviations from the intercept due to the interaction between \( Z \) and \( F \). The model also
included the normally-distributed random effect of enclosures $E$ on a given sampling date $D$ ($\epsilon$ effect, $n = 9 \times 3 = 27$ levels), and of the low-level phylogenetic lumping $T$ ($\zeta$ effect, $n = 12$ levels), because these effects generated non-independence among observations but were not the primary focus of statistical inference (for further motivations to use random effects, see Kéry and Schaub 2012). Note that $T$ was confounded with $Z$ for the low-level (12-group) phylogenetic lumping model, and $\zeta$ was thus omitted from this particular model.

We assessed the relative fit of the 12 different candidate models (six different $Z$ times two different $F$) to the count data using statistical model selection. Specifically, we ranked models based on their parsimony, as measured by AIC computed as $AIC = -2 \ln(L) + 2k$ and Bayesian information criterion (BIC, also known as Schwarz's Bayesian criterion) computed as $BIC = -2 \ln(L) + \ln(n_{obs})k$, where $L$ is the likelihood of the estimated model, $k$ is the total number of parameters that are estimated in the model and $n_{obs}$ is the number of observations to which the model was fitted ($n = 324$). The pseudo $R^2$ of each model was computed from the linear regression of observations on fitted model values. The statistical significance of fixed effect terms in the most parsimonious model (Table 3) was tested using likelihood ratio tests comparing the likelihood of the full model with that of a model omitting the focal term.

**Zooplankton body sizes**

In addition to zooplankton counts, our dataset included body size measurements for crustaceans (see above). We predicted fish predation to select for decreased body sizes in zooplankton, with the amplitude of body downsizing being proportional to the intensity of predation (Brooks and Dodson...
To test this prediction, we modelled the effect of fish on natural log-transformed, individual zooplankton body sizes $S_i$ using a linear mixed model:

$$S_i \sim N(\mu, \sigma^2)$$

$$\mu_i = \alpha + \beta Z_{[i]} + \delta F_{[i]} + \epsilon E_{[i]}, D_{[i]}$$  \hspace{1cm} (Eq. 2),

$$\epsilon E_{[i]}, D_{[i]} \sim N(0, \sigma^2_\epsilon)$$

where subscript $i$ indexes zooplankton individuals ($n = 3291$ individuals), $N$ is the normal (Gaussian) distribution, and $\mu$ and $\sigma^2$ are the mean and variance of $S_i$, respectively. Other parameters are as described in Eq. 1 and the grouping structure for $Z$ was that yielding the lowest AIC in fitting model 1 to the count data. This structure was provided by the low-level taxonomic lumping (see Results) which explains why, compared to Eq. 1, the $\zeta T_{[i]}$ term is lacking in Eq. 2. We modelled fish treatment $F$ using three levels (fish absent vs. perch present vs. roach present), which yielded a lower AIC (689 vs. 709) than using two levels (fish absent vs. present).

**Phytoplankton concentration**

We modelled chlorophyll $a$ concentration $P$ ($\mu g \ L^{-1}$), a proxy for phytoplankton concentration, using a linear mixed model:

$$P_i \sim N(\mu, \sigma^2)$$

$$\mu_i = \alpha + \beta F_{[i]} + \delta D_{[i]}$$  \hspace{1cm} (Eq. 3),

$$\delta D_{[i]} \sim N(0, \sigma^2_\delta)$$

where subscript $i$ indexes a lake enclosure ($n = 9$ enclosures) on a given sampling date ($n = 2$ sampling dates). Here also, a three-level fish treatment $F$ yielded a lower model AIC (61 vs. 74) than a two-levels $F$. Other subscripts are as described in Eq. 1.
All statistics were performed in R version 3.6.0 (R Core Team 2019). We fitted model 1 using the `glmmTMB()` function from the `glmmTMB` package (Brooks et al. 2017). Predictions with confidence intervals for model 1 were obtained using the `predict.glmmTMB()` function with a family = `nbinom2` argument. We fitted models 2 and 3 using the `lmer()` function from the `lme4` package (Bates et al. 2015) and obtained predictions with confidence intervals for these models using the `sim()` function from the `arm` package (Gelman and Hill 2007). Significance tests of each term in the best-fitting version of model 1 (Table 3) were performed using the default `anova()` function.

### Results

**Zooplankton abundances and zooplankton trophic groups**

Overall, we found a relatively good agreement between our qualitative predictions and observed response of zooplankton abundance to perch and roach (Table 1), indicating that prior literature knowledge is a reliable source of information to roughly predict trophic interactions. In particular, perch and roach had remarkably different effects on zooplankton counts. For all of the six different zooplankton grouping structures, considering perch and roach as having different effects on zooplankton counts strongly improved model fit (Table 2).

Our qualitative predictions of the effects of perch and roach on body-size based and behaviour-based zooplankton trophic groups were also relatively well supported by observations, except for the “Hide” trophic group, which largely increased in response to roach when we predicted no response (Table 1, Behaviour-based – an increase which was mainly driven by *Acanthocyclops*, Fig. 1). This mismatch between predictions and observations suggests that body size was a more parsimonious predictor of zooplankton numerical response to fish than behaviour. Accordingly, the body size-based zooplankton
grouping structure ($n = \text{two zooplankton trophic groups}$) ranked better than the behaviour-based one ($n = \text{three zooplankton trophic groups}$) in terms of both pseudo $R^2$ and parsimony (Table 2).

Interestingly, the combined body size- and behaviour-based zooplankton grouping structure, in which “no escape” zooplankters were categorized as either large- or small-bodied ($n = \text{four zooplankton trophic groups}$), was more parsimonious in terms of both AIC and BIC than the size-dependent model (Table 2), indicating that body size becomes a more important predictor of trophic interactions when behaviour can not deter predators. However, here also our predictions were poorly validated for “hide” zooplankton strategists, which abundances were mainly unchanged by perch when we predicted a strong increase, and were strongly increased by roach when we predicted a moderate increase (Table 1, Body size- and Behaviour-based).

Body size- or/and behaviour-based zooplankton grouping structures were largely outperformed by phylogeny-based structures in terms of both pseudo $R^2$ and parsimony (Table 2). This was true for both the low (12 zooplankton trophic groups) and medium taxonomic-lumping models (10 zooplankton trophic groups), but not for the high taxonomic-lumping model (four zooplankton trophic groups), which was outperformed by the combined size- and behaviour-based zooplankton grouping structure (Table 2). Note that the lower parsimony of the low taxonomic lumping model (Table 2) was not due to the loss of a random-effect term ($\zeta$ in Eq. 1), which penalized AIC and BIC through increasing the number of model parameters (a random intercept counts as one parameter when the fixed effect counted as 12 parameters).

A significant fish treatment-by-zooplankton group interaction (Table 3) indicated that the high performance of phylogeny in predicting zooplankton response to fish was explained by taxon-specific
patterns that could not accurately fit into body size- and behaviour-based trophic groups. Accordingly, among large-bodied zooplankters some decreased in response to fish (e.g., Ceriodaphnia, Daphnia), while others increased (e.g., Acanthocyclops) or were unaffected (e.g., Diaphanosoma, Fig. 1). Similarly, among “hide” strategists the strongly positive effect of fish on Acanthocyclops did not match with the absence of any effect on Thermocyclops (Fig. 1), indicating that similarly-behaving prey genera did not respond similarly to their joint predators.

Finally, we found that accounting for copepod ontogenetic stages was crucial to the performance of phylogeny at a high resolution, but not at a medium or low resolution (Table S1), indicating ontogeny-by-phylogeny interactions in copepod response to fish. Accordingly, Calanoids (i.e. Eudiaptomus) were similarly affected by fish at the nauplius and copepodite stages, while among Cyclopoids of either stages only copepodites of Acanthocyclops responded to fish (Fig. 1).

Crustacean zooplankton body size

There was a highly significant interaction between phylogeny and fish treatments on crustacean zooplankton body sizes (Fig. 2, LR-test, Chisq = 189.9, df = 12, p < 0.001), which tended to mirror the phylogeny-fish interaction on zooplankton abundances described above. Specifically, pairwise t-tests (not shown) revealed that perch significantly decreased body sizes in all the seven crustacean genera but Daphnia (which were too few in fish treatments to draw statistical inference), while roach significantly reduced body sizes in Bosmina, Ceriodaphnia, Diaphanosoma and Acanthocyclops only (Fig. 2).

Phytoplankton
Fish induced a trophic cascade in which chlorophyll $a$ concentration almost doubled in presence of roach and almost tripled in presence of perch (Table 1, Fig. 3). This result fits with the *a priori* predictions that both body size and hunting mode were making perch more efficient zooplankton predators than roach under the conditions of our experiment (Table 1).

**Discussion**

To our knowledge, the relative contributions of body size, antipredator behaviour, and phylogeny in determining trophic interactions has not been previously assessed in a particular system. By using freshwater zooplankton communities as model, we showed that body size alone is a better predictor of trophic interactions than behaviour alone, but that prey body size and behaviour combined outperformed both. We further found that zooplankton phylogeny was a far better predictor of zooplankton trophic interactions than body size and behaviour combined when phylogeny was informed at a high (genus-level) to medium (family-level) resolution, but not at a low resolution (high-level taxonomic groups). These results have several general implications for food-web research.

Recent studies have highlighted that the interplay between predator hunting mode and prey antipredator behaviour is an important driver of trophic interactions (Schmitz 2008, Belgrad and Griffen 2016). Our results suggest, however, that zooplankton behaviour is less important than zooplankton body size in driving trophic interactions in food webs of shallow lakes. Our results are in line with the well-known importance of body size in driving trophic interactions in aquatic systems (Elton 1927, Cohen et al. 2003, Emmerson and Raffaelli 2004, Woodward et al. 2005, Brose et al. 2006). Further studies would be needed to test whether our results hold true also in terrestrial systems, where body size is expected...
to be less important than in aquatic communities to determining trophic interactions (Shurin et al. 2006).

Our results testify for the importance of phenotypic traits in driving the strength of trophic interactions and ecosystem function at the plankton level. At the fish level also, traits were involved in driving the differential effects of perch and roach. Despite identical biomasses, perch more severely depleted zooplankters than roach, and induced a trophic cascade that was more than twice as large as the trophic cascade induced by roach (Table 1 effect sizes, Fig. 3). Our experimental design, however, varied fish identity in parallel with fish density and body size (owing to a constant fish biomass), but also in parallel with fish hunting mode. Hence, we could not rank the contributions of body size (and related fish density) and hunting modes in controlling the differential predatory effects of perch and roach on zooplankters. The strength of ecological interactions is classically considered as driven by the biomass of interacting species (Oksanen et al. 1981, Carpenter et al. 1985, Brett and Goldman 1996, Jeppesen et al. 2003), a rule dubbed “law of mass action”. Our result demonstrate that this paradigm is not sufficient to predict the strength of ecological interactions, in line with previous studies that demonstrated the importance of fish body size in determining the strength of their induced trophic cascades (Persson et al. 2003, Shackell et al. 2010, Renneville et al. 2016).

Despite the important role of body size and behaviour in determining zooplankton trophic groups, our results bring support to the previous contention that phylogeny is an even more powerful predictor of food-web structure (Cattin et al. 2004, Naisbit et al. 2012). Phylogenetic relatedness is a surrogate for a host of unknown or poorly documented traits that potentially influence trophic interactions, but that are not captured by body size or behavioural strategies such as, for instance, food preferences, diel activity cycles, body shape, mechanical defences (e.g. spines, helmets, carapaces), colouration or camouflages.
(Boukal 2014). However, in our study phylogeny at a high resolution was the best predictor of the trophic structure only when combined with copepod ontogeny (i.e., nauplius vs. copepodite stages, Table S1), which is another synthetic proxy encapsulating information on body-size, behaviour or feeding preferences (Werner and Gilliam 1984). Ontogeny further accounts for the fact that juveniles are often more abundant than adults. Hence, phylogeny does not capture all the traits that determine trophic niches, which are probably best predicted by combining phylogeny with other, non-redundant and synthetic sources of information. We further found that the power of phylogeny in predicting trophic structure degraded at a low resolution, indicating that body size combined with behaviour (but not alone) should be preferred predictors of trophic niches when information on phylogenetic resolution is limited. However, information on hunting mode or antipredator behaviour may also be limited, or dependent on detailed phylogenetic information (e.g., species among the same genus may vary in behaviour), in which case the most readily implementable predictor of trophic niches remains body size.

Our study illustrates how food-web perturbation experiments may be used to infer trophic interactions. Our approach included two steps. First, we formed qualitative predictions from literature knowledge for the effects of fish manipulation on the abundance of planktonic organisms while assuming trophic interactions to be dependent on body size only, on antipredator behaviour only, or on body size and behaviour combined (Table 1). Second, we statistically modelled the effects of fish manipulation on plankton grouped into body size- and behavioural trophic groups (alone or mixed) and into phylogenetic trophic groups (combined with ontogeny). This modelling step allowed us to (i) compute effect sizes to which our qualitative predictions could be compared (Table 1), and (ii) to quantify the relative efficiencies of body size, behaviour and phylogeny in predicting plankton response to fish manipulation (Table 2).
Compared to classical approaches to study food-web structure, this experimental approach has the strong advantage not to require any *a priori* data on observed trophic networks. High-quality of such food-web data are costly to acquire and, often, only report presence or absence of pairwise trophic links with no information on the strength or potential transience of the links. In contrast, our approach allowed us to quantify the *realized* effects of controlled changes in the trophic structure. A drawback of our approach, however, is that realized affects do not separate direct from indirect effects of trophic interactions. Additionally, our approach still required prior knowledge to group organisms into separate body size and behavioural trophic groups. Body size data are readily available, but pertinent cutoffs for body size binning values are not necessarily easy to define. Here, we defined these cutoff values for zooplankton body sizes arbitrarily, based on the observed body-size distributions. Predator hunting mode and prey antipredator behaviour might also not be readily available from the literature, or simply for the taxonomic level at which organisms were determined. Therefore, just as approaches relying on *a priori* food-web data, our approach might be limited to organisms for which substantial prior knowledge is available.

To conclude, our results illustrate how experiments aiming at exploring community response to top-down perturbations may also be used to infer the rules that control food-web assembly. In taking this approach, we found that body size, behaviour, phylogeny and ontogeny were all pertinent predictors of trophic niches in zooplankton food webs of Lake Créteil, but that phylogeny combined with ontogeny was most powerful. This result highlights that, beyond the important roles of body size and behaviour, other traits are involved in structuring food webs. Uncovering these traits remains highly needed if we are to understand the ecological mechanisms that shape trophic networks and support biodiversity.
References


Peterka, J. and Matěna, J. 2009. Differences in feeding selectivity and efficiency between young-of-the-year European perch (Perca fluviatilis) and roach (Rutilus rutilus) — field observations and laboratory experiments on the importance of prey movement apparency vs. evasiveness. - Biologia (Bratisl.) 64: 786–794.


Table 1. Qualitative predictions and observed effect sizes for the numerical response to perch and roach of zooplankton taxa assigned to trophic groups, based either on body size only, on antipredator behaviour only, or on body size and behaviour combined. Qualitative predictions were formed based on prior literature knowledge. Predicted - (- -), + (+ +) or = represent a negative (very negative), positive (very positive) or non-existent numerical response by zooplankton to fish, respectively. Observed % effects sizes were computed as $100\left(\mu_F - \mu_C\right)/\mu_C$, where $\mu_F$ and $\mu_C$ are mean plankton counts in fish and control treatments, respectively, as estimated from statistical models described in Eq. 1 (zooplankton) and Eq. 3 (phytoplankton).

<table>
<thead>
<tr>
<th>Basis for trophic groups</th>
<th>Zooplankton groups</th>
<th>Zooplankton Phyla</th>
<th>Predicted Perch effect</th>
<th>Observed Perch effect (%)</th>
<th>Predicted Roach effect</th>
<th>Observed Roach effect (%)</th>
<th>Explanation of predicted fish effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large zooplankton</td>
<td>Asplanchna, Ceriodaphnia, Daphnia, Diaphanosoma, Bosmina, Acanthocylops, Thermocyclops, Eudiaptomus</td>
<td>- -</td>
<td>-81.3</td>
<td>-22.6</td>
<td>Higher cumulated attack rate in perch than roach.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body size</td>
<td>Small zooplankton</td>
<td>Hexarthra, Polyarthra, nauplii of Calanoids, nauplii of Cyclopoids</td>
<td>+ +</td>
<td>39.5</td>
<td>23.1</td>
<td>Depletion of large-bodied zooplankton favours competitively dominated smaller zooplankton.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Phytoplankton</td>
<td>+ +</td>
<td>190.0</td>
<td>82.2</td>
<td>Trophic cascade driven by decreased grazing from large-bodied zooplankton.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flee</td>
<td>Bosmina, Diaphanosoma, Eudiaptomus</td>
<td>- -</td>
<td>-91.2</td>
<td>6.7</td>
<td>Fleeing strategy by zooplankton inefficient against perch but efficient against roach.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hide</td>
<td>Acanthocylops, Thermocyclops, nauplii of Cyclopoids</td>
<td>-</td>
<td>8.3</td>
<td>72.2</td>
<td>&quot;Hide&quot; strategy by zooplankton of efficient against both perch and roach.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>No escape</td>
<td>Asplanchna, Ceriodaphnia, Daphnia, Hexarthra, Polyarthra, nauplii of Calanoids</td>
<td>- -</td>
<td>-58.8</td>
<td>-42.1</td>
<td>&quot;No escape&quot; zooplankton strategies are similarly depleted by perch and roach.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Phytoplankton</td>
<td>+ +</td>
<td>190.0</td>
<td>82.2</td>
<td>Stronger trophic cascade when both &quot;no escape&quot; and &quot;fleeing&quot; strategies are depleted.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flee</td>
<td>Bosmina, Diaphanosoma, Eudiaptomus</td>
<td>- -</td>
<td>-90.9</td>
<td>9.2</td>
<td>Response of &quot;fleeing&quot; zooplankton strategies is driven by behaviour only.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hide</td>
<td>Acanthocylops, Thermocyclops, nauplii of Cyclopoids</td>
<td>+ +</td>
<td>8.3</td>
<td>70.8</td>
<td>&quot;Hide&quot; zooplankton strategies are carnivorous and benefit from increasing abundances of small, no escape zooplankters on which they feed.</td>
<td></td>
</tr>
<tr>
<td>Body size and behaviour</td>
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<td>Asplanchna, Daphnia, Ceriodaphnia</td>
<td>- -</td>
<td>-92.1</td>
<td>-69.0</td>
<td>Response of &quot;no escape&quot; plankton strategies is driven by body size only.</td>
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</tr>
<tr>
<td></td>
<td>Small, no escape</td>
<td>Hexarthra, Polyarthra, nauplii of Calanoids</td>
<td>+ +</td>
<td>70.4</td>
<td>39.1</td>
<td>Response of &quot;no escape&quot; plankton strategies is driven by body size only.</td>
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</tr>
<tr>
<td></td>
<td>Phytoplankton</td>
<td>+ +</td>
<td>190.0</td>
<td>82.2</td>
<td>Trophic cascade driven by decreased grazing from large-bodied zooplankton and stronger when both &quot;no escape&quot; and &quot;fleeing&quot; zooplankters are depleted.</td>
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Table 2. Fit of the 12 candidate models to zooplankton count data. Columns “Candidate grouping structure” and “Separate perch-roach effects” correspond to zooplankton trophic groups $Z$ and fish groups $F$, respectively, as described in Eq. 1. Non-shaded lines correspond to models that included a separate effect for perch and roach (i.e., three-level $F$). Shaded lines correspond to models that did not include a separate effect for perch and roach (i.e., two-level $F$). Df gives the number of parameters in the model. Delta AIC compares each model to the lowest-AIC model.

<table>
<thead>
<tr>
<th>Candidate zooplankton grouping structure</th>
<th>Separate Perch-Roach effects</th>
<th>df</th>
<th>Deviance</th>
<th>Pseudo $R^2$</th>
<th>BIC</th>
<th>AIC</th>
<th>Delta AIC</th>
</tr>
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<tr>
<td>Phylogeny and ontogeny High resolution</td>
<td>Yes</td>
<td>39</td>
<td>2456.0</td>
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<td>2681</td>
<td>2534</td>
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<td></td>
<td>No</td>
<td>27</td>
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<td>0.50</td>
<td>2724</td>
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<tr>
<td>Phylogeny and ontogeny Medium resolution</td>
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<td>31</td>
<td>2507.1</td>
<td>0.66</td>
<td>2704</td>
<td>2575</td>
<td>41</td>
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<td></td>
<td>No</td>
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<td>2612.2</td>
<td>0.50</td>
<td>2751</td>
<td>2660</td>
<td>126</td>
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<td>Body size x Behaviour</td>
<td>Yes</td>
<td>16</td>
<td>2597.2</td>
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<td>2690</td>
<td>2629</td>
<td>95</td>
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<tr>
<td></td>
<td>No</td>
<td>12</td>
<td>2660.9</td>
<td>0.50</td>
<td>2730</td>
<td>2685</td>
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<tr>
<td>Phylogeny and ontogeny Low resolution</td>
<td>Yes</td>
<td>16</td>
<td>2638.1</td>
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<td>2731</td>
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<td>2675.3</td>
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<td>Body size</td>
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<tr>
<td>Behaviour</td>
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<td>153</td>
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<tr>
<td></td>
<td>No</td>
<td>10</td>
<td>2704.7</td>
<td>0.46</td>
<td>2762</td>
<td>2725</td>
<td>191</td>
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</table>
Table 3. Significance tests for focal terms in models 1 (zooplankton counts) and 2 (crustacean zooplankton body sizes). In fitting models 1 and 2, we used the fish $F$ and zooplankton $Z$ grouping structures that provided the best fit (i.e., $F = 3$ groups from fish absent vs. perch present vs. roach present, and $Z = 12$ groups from a low-level lumping, high resolution phylogeny combined with copepod ontogeny, see Table 2).

<table>
<thead>
<tr>
<th>Effect</th>
<th>Parameter</th>
<th>Model</th>
<th>Chisq</th>
<th>Df</th>
<th>P-value</th>
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<tr>
<td>Zooplankton group</td>
<td>$\beta$</td>
<td>1</td>
<td>676.0</td>
<td>33</td>
<td>$&lt;0.001$</td>
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<tr>
<td></td>
<td></td>
<td>2</td>
<td>2772.1</td>
<td>18</td>
<td>$&lt;0.001$</td>
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<tr>
<td>Fish treatment</td>
<td>$\gamma$</td>
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<td>205.9</td>
<td>24</td>
<td>$&lt;0.001$</td>
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<tr>
<td></td>
<td></td>
<td>2</td>
<td>230.4</td>
<td>14</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Fish treatment x</td>
<td>$\delta$</td>
<td>1</td>
<td>190.4</td>
<td>22</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Zooplankton group</td>
<td></td>
<td>2</td>
<td>189.9</td>
<td>12</td>
<td>$&lt;0.001$</td>
</tr>
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</table>
Fig. 1. Zooplankton numerical response to fish treatments. Filled, red symbols show mean predicted counts with 95% confidence intervals as predicted from model 1. For a sampling date-specific equivalent of this figure, see Fig. S1. Circles: fishless control treatment; triangles: perch treatment, squares: roach treatment. Open, gray symbols show the raw data. Zooplankton taxa were separated among A: Cladocerans (BOSM = Bosmina longirostris, CERIO = Ceriodaphnia pulchella and C. quadrangula, DAPH = Daphnia longispina complex, DIAPH = Diaphanosoma brachyurum), B: Copepodite stages (ACANT = Acanthocylops robustus, EUDIA: Eudiaptomus gracilis, THERM = Thermocyclops crassus and T. oithonoides), C: NAUCA = nauplii of Calanoids, ASPL = Asplanchna girodi and A. priodonta, D: NAUPLCY = nauplii of Cyclopoids, HEXA = Hexarthra mira, POLY = Polyarthra sp.
**Fig. 2.** Body-size response of crustacean zooplankton to fish treatments. Filled, red symbols show mean predicted counts with 95% confidence intervals as predicted from model 2. Circles: fishless control treatment; triangles: perch treatment, squares: roach treatment. Open, gray symbols show the raw data. Zooplankton taxa were separated among A: Cladocerans (BOSM = *Bosmina longirostris*, CERIO = *Ceriodaphnia pulchella* and *C. quadrangula*, DAPH = *Daphnia longispina* complex, DIAPH = *Diaphanosoma brachyurum*), B: Copepodite stages of copepods (ACANT = *Acanthocyclops robustus*, EUDIA: *Eudiaptomus gracilis*, THERM = *Thermocyclops crassus* and *T. oithonoides*).
Fig. 3. Phytoplankton response to fish treatments. Filled, red symbols show mean predicted counts with 95% confidence intervals as predicted from model 2. Circles: fishless control treatment; triangles: perch treatment, squares: roach treatment. Open, gray symbols show the raw data.
Table S1. Fit of ontogeny-free phylogeny-based models to zooplankton count data. Other models appear shaded, are as in Table 2 and are provided to ease comparison. Models were ranked according to their AIC score. All models included a 3-level fish treatment considering fish absent vs. perch present vs. roach present.

<table>
<thead>
<tr>
<th>Candidate food-web Model</th>
<th>df</th>
<th>Deviance</th>
<th>Pseudo $R^2$</th>
<th>BIC</th>
<th>AIC</th>
<th>Delta AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylogeny and ontogeny High resolution</td>
<td>39</td>
<td>2456</td>
<td>0.67</td>
<td>2681</td>
<td>2534</td>
<td>0</td>
</tr>
<tr>
<td>Phylogeny and ontogeny Medium resolution</td>
<td>34</td>
<td>2507</td>
<td>0.66</td>
<td>2704</td>
<td>2575</td>
<td>41</td>
</tr>
<tr>
<td>Phylogeny alone Medium resolution</td>
<td>28</td>
<td>2528</td>
<td>0.62</td>
<td>2690</td>
<td>2584</td>
<td>50</td>
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<tr>
<td>Body size x Behaviour</td>
<td>16</td>
<td>2597</td>
<td>0.59</td>
<td>2690</td>
<td>2629</td>
<td>95</td>
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<tr>
<td>Phylogeny alone High resolution</td>
<td>33</td>
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<td>0.41</td>
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<td>2638</td>
<td>0.57</td>
<td>2731</td>
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<td>136</td>
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<td>Body size</td>
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<td>2651</td>
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<td>2671</td>
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<td>Behaviour</td>
<td>13</td>
<td>2661</td>
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</tbody>
</table>
Fig. S1. Zooplankton numerical response to fish treatments at each sampling date. Circles: fishless control treatment; triangles: perch treatment, squares: roach treatment. Model predictions are not shown due to model over-parametrization resulting in inaccurate predictions. Zooplankton taxa were separated among A: Cladocerans (BOSM = *Bosmina longirostris*, CERIO = *Ceriodaphnia pulchella* and *C. quadrangula*, DAPH = *Daphnia longispina* complex, DIAPH = *Diaphanosoma brachyurum*), B: Copepodite stages (ACANT = *Acanthocyclops robustus*, EUDIA: *Eudiaptomus gracilis*, THERM = *Thermocyclops crassus* and *T. oithonoides*), C: NAUCA = nauplii of Calanoids, ASPL = *Asplanchna girodi* and *A. priodonta*, D: NAUPLCY = nauplii of Cyclopoids, HEXA = *Hexarthra mira*, POLY = *Polyarthra* sp.