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Differential responses of size-based functional groups to bottom–up and top–down perturbations in pelagic food webs: a meta-analysis

Florence D. Hulot, Gérard Lacroix and Michel Loreau

F. D. Hulot (florence.hulot@u-psud.fr), Laboratoire Ecologie, Systématique et Evolution, UMR 8079, Univ. Paris-Sud, Orsay, France. – G. Lacroix, UMR iEES Paris (CNRS, UPMC, INRA, IRD, AgroParisTech, UPEC), Inst. of ecology and environmental sciences - Paris, Univ. Pierre et Marie Curie, 7 quai St.-Bernard, FR-75005 Paris, France, and: UMS 3194 - CEREEP Ecotron IDF (CNRS, ENS), 78 rue du Château, FR-77140 Saint-Pierre-Lès-Nemours, France. – M. Loreau, Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS, FR-09200 Moulis, France.

We performed a meta-analysis of 31 lake mesocosm experiments to investigate differences in the responses of pelagic food chains and food webs to nutrient enrichment and fish presence. Trophic levels were divided into size-based functional groups (phytoplankton into highly edible and poorly edible algae, and zooplankton into small herbivores, large herbivores and omnivorous zooplankton) in the food webs. Our meta-analysis shows that 1) nutrient enrichment has a positive effect on phytoplankton and zooplankton, while fish presence has a positive effect on phytoplankton and a negative effect on zooplankton in the food chains; 2) nutrient enrichment has a positive effect on highly edible algae and small herbivores, but no effect on poorly edible algae, large herbivores and omnivorous zooplankton in the food webs. Planktivorous fish have a positive effect on highly edible algae and small herbivores, a negative effect on large herbivores and omnivorous zooplankton, and no effect on poorly edible algae. Our meta-analysis confirms that nutrient enrichment and planktivorous fish affect functional groups differentially within trophic levels, revealing important changes in the functioning of food webs. The analysis of fish effects shows the well-described trophic cascade in the food chain and reveals two trophic cascades in the food web: one transmitted by large herbivores that benefit highly edible phytoplankton, and one transmitted by omnivorous zooplankton that benefit small herbivores. Comparison between the responses of food webs and simple food chains also shows consistent biomass compensation between functional groups within trophic levels.

After decades of research, it is now widely recognised that both resources and consumers control ecosystem productivity (Hunter and Price 1992, Leibold et al. 1997, Polis 1999, Rothhaupt 2000). The effects of resources are obvious since they are essential to sustain higher trophic levels, and their abundance may determine the number of trophic levels (Oksanen et al. 1981, Kaunzinger and Morin 1998). The interaction between consumer and resource controls, or respectively top–down and bottom–up controls, has also led to controversial debates. The fundamental issue in these debates is the importance of consumers' cascading control on autotroph biomass relative to the resource control. This has led to numerous field experiments in freshwater, marine and terrestrial ecosystems and subsequent meta-analyses (Brett and Goldman 1996, 1997, Leibold et al. 1997, Micheli 1999, Schmitz et al. 2000, Gruner et al. 2008).

In freshwater ecosystems, Brett and Goldman (1996) showed that zooplanktivorous fish reduced zooplankton biomass and increased phytoplankton biomass. However, phytoplankton response to consumer control was highly skewed: it was very strong in slightly more than one-third of the 54 cases studied and weak in the other cases. In a second meta-analysis of 11 factorial experiments, Brett and Goldman (1997) showed that 1) phytoplankton biomass was under strong resource control and moderate fish control whereas zooplankton biomass was under strong consumer control and weak resource control; and 2) contrary to theoretical predictions, there were no significant interactions between resource and consumer controls of phytoplankton and zooplankton. More recently, Gruner et al. (2008) analysed the bottom–up and top–down controls on producer biomass across ecosystems. They reached the same conclusion as Brett and Goldman's (1997). It should be stressed that aquatic trophic cascades have been assessed at the community level, i.e. they affect whole trophic levels, whereas species-level cascades affect one or a few species at each trophic level (Polis 1999). Meta-analyses conducted on community-level cascades in aquatic ecosystems suggest that the discrepancies between theoretical predictions and experimental results hinge on the weak coupling between primary producers and their consumers. This weak coupling might be due to interference within zooplankton (Leibold 1989, Hunter and Price 1992, Strong 1992, Polis and Strong 1996, Leibold et al. 1997, McCann et al. 1998) or to differences in edibility within phytoplankton (Leibold 1989, Watson et al. 1992), which dampen the control of plants by herbivores (Power 1992, Shurin et al. 2002). Testing these hypotheses, however, implies considering a food web with multiple species per trophic level rather than a simple food chain.

In addition to resource availability and predation, the trophic structure of the community is also an important factor controlling species or groups of species that benefit from nutrient enrichment (Leibold and Wilbur 1992, Abrams 1993, Leibold et al. 1997, Hansson et al. 1998, Persson 1999, Hulot et al. 2000, Thébault and Loreau 2003, Hulot and Loreau 2006, Loreau 2010, Wollrab et al. 2012). Trophic structure, defined as the partitioning of biomass among groups of species (Leibold et al. 1997), involves not only trophic levels but also trophic groups within trophic levels. In freshwater ecosystems, trophic levels are often split into trophic or functional groups generated by a differential planktivory (the size-efficiency hypothesis: Brooks and Dodson 1965, Dodson 1974). The relative abundance of these trophic groups may change depending on both the abiotic environment and fish stock (Hrbácek et al. 1961, Brooks and Dodson 1965, Dodson 1974, Hall et al. 1976). Zooplanktivorous fish generally prey selectively upon large herbivores and invertebrate carnivores. Predation by invertebrate carnivores is also limited by the size and shape of their prey. The body size of herbivorous zooplankton determines their grazing selectivity pattern and the size range of grazed algae. Thus, several functional groups can be distinguished within zooplankton forming the basis of pelagic food-web model (Carpenter and Kitchell 1993, Hansson et al. 1998, Hulot et al. 2000): small herbivores, which feed mainly upon small and unprotected algae, and large herbivores, which feed on a wider size range of algae, including larger and protected algae; invertebrate carnivores feed mainly on small herbivores. Within phytoplankton, two groups of algae can also be distinguished according to their vulnerability to herbivores: highly edible algae that are small and unprotected, and poorly edible algae that are larger or more or less protected. Because zooplanktivorous fish prey mainly upon large herbivores and invertebrate carnivores, fish presence or absence can shift dominant associations within the plankton community.

In this study, we report the results of a meta-analysis conducted on 31 lake mesocosm experiments analysing the effects of nutrient enrichment and zooplanktivorous fish on phytoplankton and zooplankton. Our meta-analysis specifically addresses the different responses of different functional groups within trophic levels to perturbations both at the top and at the bottom of the food web. This approach allows us 1) to assess whether responses to perturbations are homogeneous within trophic levels; 2) to formulate hypotheses regarding the effects of phytoplankton edibility and a potential interference within zooplankton, and therefore to gain an insight into the importance of these mechanisms for food-web dynamics.

Methods

To conduct the analysis, we searched for studies performed in mesocosms based on the following criteria. They should report results from cross-classified treatments of nutrient low/high × fish presence/absence. The experiments should have a balanced factorial design. Some experiments included sediments in mesocosms, for instance by keeping their bottom open and sealing it in the lake sediments. We excluded these experiments from our analysis because our objective is to analyse experiments that focus on the pelagic organisms and their interactions. We discuss how this might have influenced our results in the Discussion. Selected experiments also should display results in which species or groups of species would be identified or, at least, identifiable. For instance Lynch and Shapiro (1981) reported separate responses by 'rotifers' and *Asplanchna priodonta* to nutrient enrichment and fish. Since *A. priodonta* is a carnivorous rotifer, we deduced that 'rotifers' are small herbivores. The literature search included an electronic search, an examination of the main ecological and limnological reviews and papers' bibliography. The literature search provided 21 published studies reporting the results of 31 independent experiments (Table 1).

In addition to the detailed treatments, each experiment provided a set of data: either phytoplankton response values, or zooplankton response values, or both phytoplankton and zooplankton response values. Phytoplankton and zooplankton response values were taken directly from tables or figures (Supplementary material Appendix 1 Table A1–A3). The data were from the final sampling. If some data were missing, we took the data from the last common sampling date. Each species or group of species was assigned to a group according to its biology and/or size. Highly edible phytoplankton includes small algae (length $\leq$ 20–50 μm according to the study), and poorly edible phytoplankton includes algae protected by their size (length $>$ 20–50 μm), thick walls or gelatinous sheaths (Supplementary material Appendix 1 Table A2). Note that the discrepancy between the limits set by the authors might affect the analysis, in particular the interaction between experiments and the effects that are explored. Small herbivores are roughly 50 to 200 μm long and feed mainly on highly edible phytoplankton whereas large herbivores are roughly 400 μm to 2 mm long and feed on highly edible algae and may also feed on poorly edible algae (Supplementary material Appendix 1 Table A3). The third group of zooplankton includes invertebrate carnivores. Note that Calanoids, which have been frequently considered as herbivorous organisms, can also consume zooplankton (Brandl 2005). Then, in this meta-analysis, calanoids were considered as omnivorous zooplankton.

Fish foraging behaviour may drive food-web topology and ultimately ecosystem functioning (Lazzaro et al. 2009). For instance, visual feeders that feed upon large zooplanktonic prey increase the ratio of poorly edible algae, and induce more trophic cul-de-sac, i.e. organisms without consumers, within phytoplankton than filter feeders (Lazzaro et al. 2009). Therefore, we assigned fish species to one foraging behaviour, either filter or visual feeder (Table 1), and we tested for this effect.

Table 1. Papers included in the meta-analysis.

Article	Experiment	Mesocosm volume (m^3)	Duration (weeks)	No. of replicates	Nutrient addition	Fish species and biomass level
Acuna et al. 2008	–	0.8	2.5	2	initial concentration of 1027 lg l^{-1} TN and 40.78 lg l^{-1} TP in the enrichment treatments	*Cheirodon interruptus*: 7.0 g m^{-3}
Beresford and Jones 2010	within-lake experiment	1.76	8	3	4 mg l^{-1} nitrate and 200 μg l^{-1} phosphate every two weeks	*Cyprinus carpio* (25.0 g wet weight m^{-3})
Dickman et al. 2008, Mette et al. 2011	high-light treament	5	8	3 (2–4)	50 μg N l^{-1} and 5 μg of P l^{-1} three times per week	*Dorosoma cepedianum*: 0.543 mg fish l^{-1} (250 fish per mesocosm)
Drenner et al. 1989	OU and TCU	7.0 and 5.5	4	3	200 μg P l^{-1} the first day	*Gambusia affinis*: 1.4 g wet weight m^{-3}
Drenner et al. 1990	main experiment	5.5	3	3	210.1 μg N l^{-1} D^{-1} and 10 μg P l^{-1} D^{-1}	*Lepomis macrochirus*: 7.1 g wet weight m^{-3}
Faafeng et al. 1990	spring and summer	7	4 and 3 respectively	3	3.2 mg NO_3-N l^{-1} and 0.6 mg PO_4-P l^{-1}	*Rutilus rutilus*: 3.0 g wet weight m^{-3}
Fernandez-Alaez et al. 2004	1998 and 1999	0.79	5	3 and 2	1998: 10.0 mg N l^{-1} and 1000 μg P l^{-1} 1999: 3.0 mg N l^{-1} and 300 μg P l^{-1}	1998 and 1999 - *Chondrostoma arcasii*: 20 g wet weight m^{-2}
Hansson et al. 2004	–	0.79	5	2	3.0 mg N l^{-1} and 300 μg P l^{-1}	*Rutilus rutilus*: 16 to 20 g wet weight m^{-3}
Hietala et al. 2004	1998 and 1999	0.79	7	3 and 2	1998: 10.0 mg N l^{-1} and 1000 μg P l^{-1} 1999: 3.0 mg N l^{-1} and 300 μg P l^{-1}	*Rutilus rutilus*: 20 g wet weight m^{-2} in 1998 and 1999
Lacroix and Lescher-Moutoué 1991	–	9.5	8	3	low treatment: 6.4 μg N l^{-1} D^{-1} and 0.32 μg P l^{-1} D^{-1} high treatment: 63.6 μg N l^{-1} D^{-1} and 3.16 μg P l^{-1} D^{-1}	*Rutilus rutilus* and *Abramis brama*: 0.26 and 0.5 g wet weight m^{-3}
Lynch and Shapiro 1981	experiment 2	1.4	6	2	330 μg N l^{-1} and 33 μg P l^{-1} weekly	*Lepomis macrochirus*: 2 small fish (60–75 mm)
Markosová and Jezek 1993	–	110	16	2	4 g P m^{-3} one month after the beginning of the experiment	*Cyprinus carpio* (600 small fish, 10 cm length)
Mazumder et al. 1990	–	150	15	2	84.54 μg N l^{-1} and 6.49 μg P l^{-1} biweekly	yellow perch (75–80 kg ha^{-1})
McQueen et al. 1992	–	600	15	2	P and N weekly (see Table 1 for chronology)	yellow perch (3.09 ± 0.57 kg ha^{-1})
Menezes et al. 2010	–	9.8	5	5	1000 μg l^{-1} N-NO_3 and 100 μg l^{-1} P-PO_4	*Oreochromis niloticus*: one fish m^{-3}
Proulx et al. 1996	deep and shallow	600 and 150	10	2	47.97 mg N m^{-2} D^{-1} 3.69 mg P m^{-2} D^{-1}	*Phoxinus eos* × *P. heogaeus*: 5 g wet weight m^{-2}
Qin and Culver 1995	pond	0.57	4.5	2	Final 0.6 mg N l^{-1} and 0.03 mg P l^{-1}; weekly	larval *Stezostedion vitreum vitreum*: 80 mg m^{-3}
Riemann 1985	–	5.3	3	3	227 μg PO_4-P l^{-1}	*Rutilus rutilus*: 50 g wet weight m^{-2}
Romo et al. 2004	1998 and 1999	0.79	6 and 7	3 and 2	1998: 10.0 mg N l^{-1} and 1000 μg P l^{-1} 1999: 3.0 mg N l^{-1} and 300 μg P l^{-1}	1998 and 1999 – *Gambusiaholbrooki*: 20 g wet weight m^{-2}
Stephen et al. 2004	1998 and 1999	0.79	5 and 6	3 and 2	1998: 10.0 mg N l^{-1} and 1000 μg P l^{-1} 1999: 3.0 mg N l^{-1} and 300 μg P l^{-1}	1998 and 1999 – *Gasterosteus aculeatus*: 20 g wet weight m^{-2}
Van de Bund et al. 2004	1998 and 1999	0.79	5 and 6	3 and 2	1998: 10.0 mg N l^{-1} and 1000 μg P l^{-1} 1999: 3.0 mg N l^{-1} and 300 μg P l^{-1}	1998 and 1999 – *Scardinius erythrophthalmus*: 20 g wet weight m^{-2}
Vanni 1987a, b	1980 and 1981	1 and 4.7	6	3	300 μg N l^{-1} and 10 μg P l^{-1} weekly	*Lepomis macrochirus* 1980: 1 fish/enclosure 1981: 2 fish/enclosure

To test nutrient enrichment and fish effects we conducted block analyses of variance without replication (ANOVA). For each functional group and each experiment, the treatment responses corresponded to the sum of the component responses. The data from each experiment were considered as a block of observation without replication and were transformed as in Brett and Goldman (1997), that is, response = log(treatment mean/geometric mean), where the geometric mean is taken over the four treatments. In the calculation of the *F*-statistic, the overall interaction term for fish × nutrients × experiment replaced the residual sum of squares. In order to test for the effect of fish behaviour, we also ran analyses with the behaviour as a nested factor of the fish presence. However, we did not observe any significant effect of fish behaviour (data not shown). Thus, we focus only on the effect of fish presence in this paper. The p-levels considered for significance and marginal significance are respectively 0.05 and 0.10.

Results

Phytoplankton response to nutrient enrichment and fish presence

Both nutrient enrichment and fish presence had a positive significant effect on phytoplankton ($p \leq 0.0001$; Fig. 1a). These effects depended on experiments (experiment interaction with nutrient enrichment ($p \leq 0.001$), but not fish presence ($p = 0.10$)). There was no interaction between nutrient enrichment and fish presence on phytoplankton ($p = 0.45$).

Effects on highly and poorly edible phytoplankton were different than on phytoplankton overall. Nutrient enrichment had a positive effect on highly edible phytoplankton ($p \leq 0.005$; Fig. 1c); this effect did not depend on experiment ($p = 0.26$). Fish presence had also a positive effect on highly edible algae ($p = 0.015$) that did not depend on the experiment ($p = 0.21$). The responses of poorly edible phytoplankton differed from the responses of highly edible phytoplankton: there was no effect of nutrient enrichment and fish presence ($p = 0.63$ and $p = 0.33$ respectively; Fig. 1d) but these responses depended at different levels on the experiment ($p = 0.07$ and $p = 0.009$ respectively; Fig. 1d). There was no significant interaction between nutrient enrichment and fish presence for both groups of phytoplankton.

Zooplankton response to nutrient enrichment and fish presence

Nutrient enrichment had a positive effect on zooplankton ($p = 0.01$; Fig. 1b) and this result did not depend on the experiment ($p = 0.23$). Fish presence had a negative effect on zooplankton ($p = 0.02$) and this effect depended marginally on the experiment ($p \leq 0.07$).

Zooplankton was split into three trophic groups: small and large herbivores and omnivorous zooplankton. Nutrient enrichment had a positive effect on small herbivores ($p = 0.002$; Fig. 1e), a marginal negative effect on large herbivores ($p = 0.07$; Fig. 1f) and no effect on omnivorous zooplankton ($p = 0.56$; Fig. 1g). These effects depended marginally on the experiment (small herbivores: $p = 0.08$; large herbivores: $p = 0.05$) but there was no significant interaction for omnivorous zooplankton ($p = 0.95$). Fish presence had a positive effect on small herbivores ($p \leq 0.001$; Fig. 1e), a negative effect on large herbivores ($p \leq 0.001$; Fig. 1f) and on omnivorous zooplankton ($p = 0.03$; Fig. 1g). Again, these effects depended on the experiment, marginally for small herbivores ($p = 0.07$) and significantly for large herbivores ($p = 0.04$). The effects of fish presence interacted significantly with nutrient enrichment ($p = 0.02$).

Discussion

The aim of the present meta-analysis was to assess the responses of food chains and size-based functional groups to two perturbations, i.e. nutrient addition and presence of planktivorous fish, in freshwater mesocosms. The results reveal a positive effect of nutrient enrichment on phytoplankton and zooplankton and a fish-induced trophic cascade. They also show that functional groups belonging to the same trophic level do not respond in the same way to perturbations and may sometimes have opposite responses (see Fig. 2 for a summary of the results). Contrary to theoretical models (Leibold 1997, Hulot et al. 2000, Hulot and Loreau 2006, Wollrab et al. 2012), we observe no effect of nutrient enrichment on poorly edible phytoplankton while we would expect that they benefit from nutrient addition at the expense of highly edible but poorly defended phytoplankton. Although various hypotheses could explain this result, one possible explanation is that this result reflects different experimental designs. We discuss this hypothesis in the ‘Nutrient enrichment effects’ section. The responses of the various functional groups to nutrient addition and fish presence also show some discrepancies with theoretical predictions (Hulot et al. 2000, Wollrab et al. 2012). We discuss various hypotheses that may explain these results in the following sections. We then conclude on robust responses and the concrete mechanisms that underlie these responses.

Nutrient enrichment effects

Nutrient enrichment had a clear positive effect on phytoplankton and zooplankton as whole trophic levels. But these responses were heterogeneous among trophic groups: highly and poorly edible phytoplankton had different responses (positive and non significant, respectively) and among zooplankton, only small herbivores responded with an increase in biomass (Fig. 2). The response of phytoplankton to nutrient enrichment reflects the response of highly edible phytoplankton whereas we would expect a positive effect on poorly edible phytoplankton. The differential response of the two phytoplankton groups does not support the hypothesis of a species compositional turnover with increased productivity from highly competitive but poorly defended species to less competitive but better defended species (Leibold 1996). Several hypotheses could explain this result. First, poorly edible phytoplankton

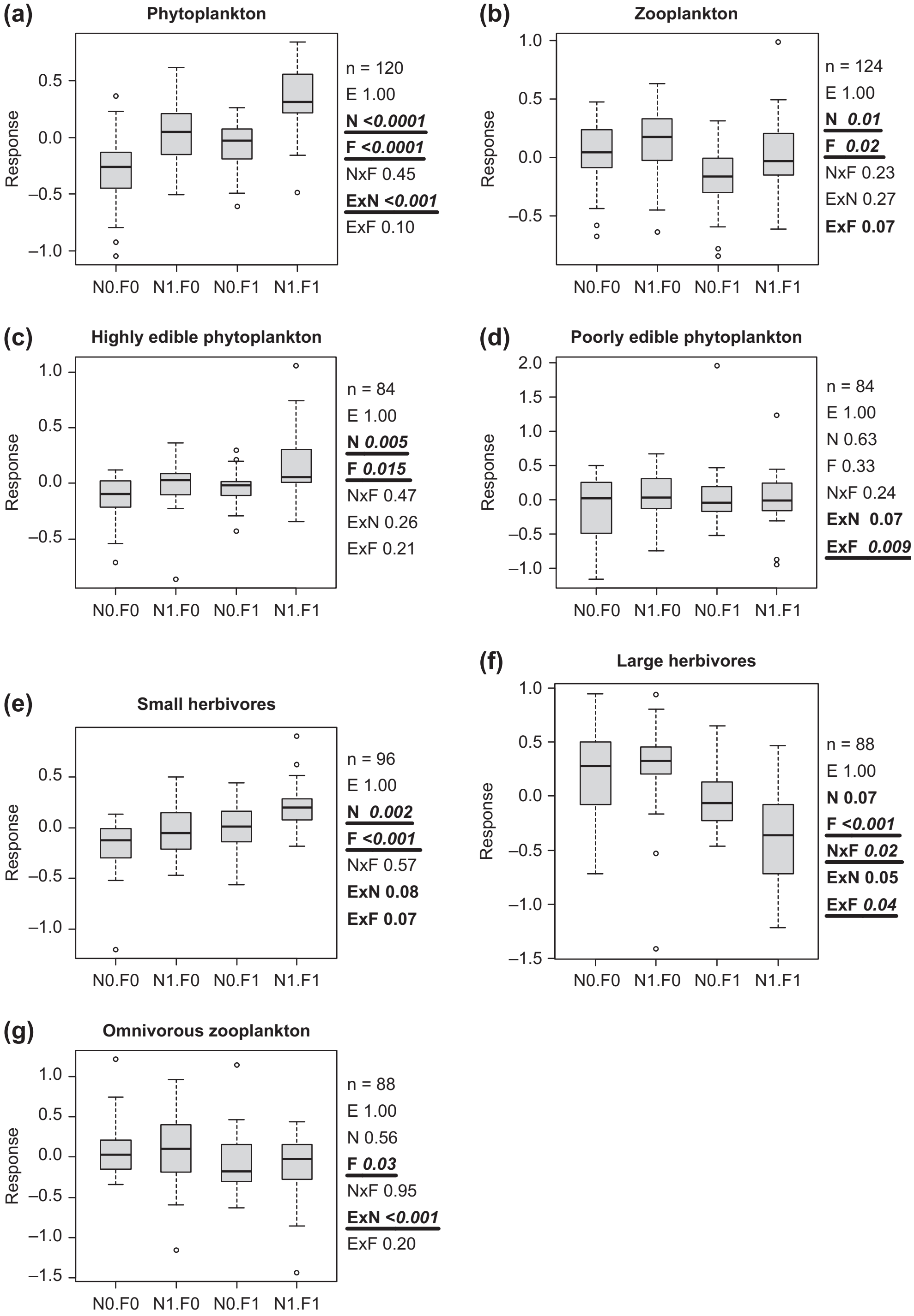

Figure 1. Response of plankton groups to nutrient addition and fish presence. The horizontal line, the top and the bottom of the box represent the median, the 25th and the 75th percentiles respectively. The vertical dashed lines represent either the minimum or maximum value or, in presence of outliers (open circles), the interquartile range of the data times 1.5. Number of data sets (n) and probability values from ANOVA of experiment (E), nutrient addition (N), fish presence (F) effects and their interaction effects (N × F: nutrient addition × fish presence; E × N and E × F: experiment in interaction with nutrient addition and fish presence respectively) are indicated to the right of each graph.

might be partly controlled by omnivorous zooplankton. In this case, we would expect a positive effect of nutrient enrichment on omnivorous zooplankton as their other prey, i.e. small herbivores, also responded positively to this perturbation. But omnivorous zooplankton did not respond to nutrient enrichment even though there were variations among experiments. Second, poorly edible phytoplankton might be partly controlled by fish. However, the fish used in most of the experiments and included in the meta-analysis are visual feeders and do not prey on poorly edible algae

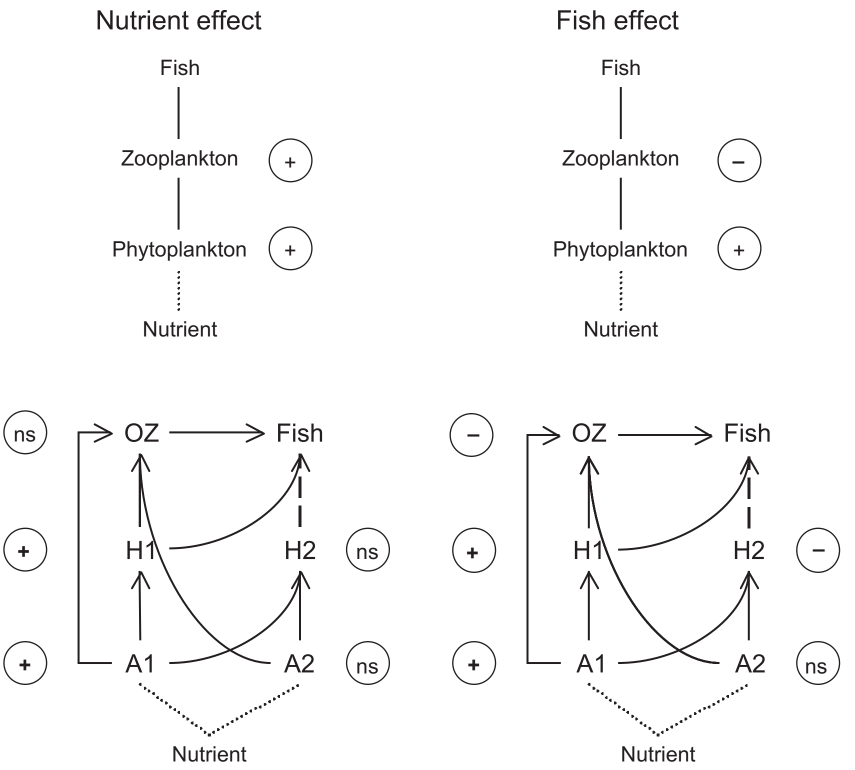

Figure 2. Main effects of nutrient enrichment and fish presence on plankton groups (A1: highly edible phytoplankton; A2: poorly edible phytoplankton; H1: small herbivores; H2: large herbivores; OZ: omnivorous zooplankton). The sign next to each functional group represents the main effect (+: positive effect; −: negative effect; ns: non significant). Plain lines: predation interactions. Dotted lines show the potential exploitative competition of the two algae groups for a limiting nutrient.

(Menezes et al. 2010). Moreover, we did not find any significant effect of fish behaviour on the response of poorly edible algae. Therefore, we cannot explain the response of this group of algae by control by a predator.

An alternative hypothesis relies on experimental design. Usually, the phytoplankton developing in mesocosms comes from pond or lake water, with one initial introduction. The initial diversity may sharply decrease at the beginning of the experiment, as observed by Mette et al (2011), as a consequence of species selection in the experimental mesocosms. This initial step may select small phytoplankton species with a high growth rate. A tradeoff between growth rate and cell size, which offers higher grazing resistance, seems ubiquitous (Litchman and Klausmeier 2008) and species that grow slowly and are present in very low density at the beginning of the experiment may either not be introduced in mesocosms, or be excluded or lost by sedimentation if introduced. In particular, sedimentation might be high in some enclosures (Bloesch et al. 1988), and this phenomenon might affect more severely large than small phytoplankton. Moreover, the study of succession in phytoplankton communities shows that large inedible phytoplankton species become abundant by the end of the summer (Sommer et al. 2012). Methodological sections in the analysed papers suggest that plankton species were introduced in most cases at the beginning of experiments only. Regular introductions of species during the experiment might be necessary for ensuring their development in mesocosms when favourable conditions are met. In addition, sediments contain a bank of dormant cells that may seed water during the growing season (Rengefors et al. 2004) or following sediment bioturbation by macro-invertebrates or fish (Adamek and Marsalek 2013). For instance, *Microcystis aeruginosa*, a large colonial cyanobacteria, may build up dense blooms from dormant cells that emerge from the sediments during the spring and summer (Verspagen et al. 2005). Because we excluded from the meta-analysis experiments with mesocosms that included sediments, we also excluded from the data basis experiments with a endogeneic source of species. In conclusion, theoretical models predict a positive response of poorly edible phytoplankton to nutrient enrichment (Leibold 1997, Hulot and Loreau 2006). The marginally negative response revealed by our meta-analysis might be explained by the typical experimental design of nutrient manipulation in mesocosms, which does not offer an optimal environment for the development of large phytoplankton. The absence of response to nutrient enrichment of poorly edible phytoplankton is in accordance with the results of Sarnelle (1992), who assessed the effects of nutrient enrichment by a survey of enclosure (5) and whole-lake (1) experiments (Table 4) and of different total phosphorus concentrations. Even in eutrophic lakes, his survey shows that *Daphnia* grazing prevents the development of resistant algae (Sarnelle 1992).

The positive response of zooplankton to nutrient enrichment hinges mainly on small herbivores. Herbivorous rotifers are known to prey selectively upon small phytoplankton species. Because nutrient enrichment seemed to benefit highly edible phytoplankton, small herbivores might have echoed the response of their prey without fuelling omnivorous zooplankton.

Fish effects and trophic cascades

Our meta-analysis shows a clear trophic cascade at the community level with a negative effect on zooplankton and a positive effect on phytoplankton. These results are consistent with previous studies, including meta-analyses (Brett and Goldman 1996, Shurin et al. 2002, Gruner et al. 2008). However the responses are not homogenous within trophic levels. The negative response of large herbivores and omnivorous zooplankton is probably largely due to direct mortality since zooplanktivorous fish prey mainly upon large zooplankton (Hrbácek et al. 1961, Brooks and Dodson 1965, Dodson 1974, Hall et al. 1976). The positive effect of fish on highly edible phytoplankton is presumably a consequence of zooplanktivory, revealing a trophic cascade at the level of functional groups involving fish, large herbivores and small algae. Again we expected a positive effect on poorly edible phytoplankton, which would be released from grazing by large herbivores and, to a lesser extent, by omnivorous zooplankton. The absence of such a response might be explained by the same factors as those suggested previously. The highly significant interaction between fish addition and experiment might reveal biological effects of fish. For instance, Menezes et al (2010) used Nile *Tilapia*, which feeds directly on large phytoplankton. Two studies (McQueen et al. 1992, Proulx et al. 1996) discuss the indirect positive effects of fish on small phytoplankton at the expense of large phytoplankton through nutrient regeneration.

Fish had a significant positive effect on small herbivores. This effect might involve several indirect mechanisms. Since the two size groups of herbivores were in competition for the exploitation of highly edible algae, the selective removal of large herbivores and the positive effect of fish on highly edible phytoplankton might benefit small herbivores. Moreover, large herbivores might have a direct negative effect on small herbivores through mechanical interference. For instance, *Daphnia* can damage or ingest small rotifers while filtering water and be an additional source of mortality (Gilbert 1988). Fish may also induce changes in the life-history parameters of large herbivores; for instance, they can reduce their body size (Vanni 1987a, Pourriot 1995, Borcic et al. 1998, Bertolo et al. 2000). Because the size range of filtered particles is related to the body size of herbivorous zooplankton (Burns 1968) and fish prey on large herbivores (Brooks and Dodson 1965, Dodson 1974), the direct negative effect of large herbivores on small ones is decreased in the presence of fish. Thus the negative effect of fish on large herbivores might benefit small herbivores. The positive response of small herbivores to fish presence might also be the result of a trophic cascade mediated by omnivorous zooplankton, which responded negatively to fish predation.

Interactions between nutrient enrichment and fish presence

Our analysis did not reveal any significant interaction between nutrient enrichment and fish presence, except for large herbivores ($p = 0.02$). In their meta-analysis, Brett andGoldman (1997) did not find such interactions in either phytoplankton or zooplankton. Our results for the phytoplankton are also consistent with those of Borer et al. (2005) and Gruner et al. (2008), who did not find interactive effects between nutrient and herbivore controls in aquatic and terrestrial habitats. The interaction effect observed for large herbivores (the biomass of which tended to increase with nutrients in absence of fish and to decrease with nutrients in presence of fish) is more intriguing. Such a pattern might result from complex ecological interactions and modifications of life-history parameters of the species included in the group. For example, Borcic et al. (1998) observed a strong decrease in body size within *Daphnia galeata* populations along an experimental gradient of fish abundance (mean size of adults ranging from 1650 μm in the absence of fish to 1050 μm when fish were abundant). This size reduction appeared to be independent of nutrient load. One consequence of this reduction in body size is a greater susceptibility of large herbivores to invertebrate predators. Indeed, according to the experimental results of Caramugo and Boavida (2000), the predation rate exerted by adult females of the cyclopoid copepod *Acanthocyclops robustus* would be tenfold to twentyfold higher on 1050-μm *Daphnia* than on 1650-μm *Daphnia*. In the presence of fish, increased nutrient abundance would not necessarily benefit large herbivores due to predation by both omnivorous zooplankton and zooplanktivorous fish. In the absence of fish, a positive response is expected due to reduced predation pressure by invertebrate omnivores. Statistically, such a pattern might lead to a fish × nutrient interaction effect.

Compensatory mechanisms within trophic levels

The community regulation hypothesis suggests that trophic cascades may be limited by compensation between species or functional groups within trophic levels (Gonzalez and Loreau 2009) due to their diversity (Holt and Polis 1997, Pace et al. 1999). In their analysis of trophic cascades in different ecosystems, Borer et al. (2005) examined trophic cascade intensity as a function of species diversity. Their results showed no significant relationship between species diversity at three trophic levels and trophic cascade intensity. But they concluded that species diversity might have been limited in the experiments they surveyed.

In our analysis, compensation was assessed through changes in trophic group biomass. At the level of phytoplankton, our results do not show strong evidence for compensation: the responses of phytoplankton to nutrient enrichment or fish presence mirror the responses of highly edible phytoplankton while poorly edible phytoplankton shows non significant responses. But our meta-analysis shows that zooplankton groups are differentially affected by zooplanktivorous fish, and that the positive response of small herbivores to fish is buffered by the negative response of large herbivores and omnivorous zooplankton. These three groups of zooplankton are usually mixed in analyses. It is often assumed that trophic cascades do not propagate to lower trophic levels because of compensatory mechanisms (Leibold 1989, Hunter and Price 1992, Strong 1992, Polis and Strong 1996, Leibold et al. 1997, McCann et al. 1998).

Our results show that the responses of large herbivores and omnivorous zooplankton mask the positive response of small herbivores such as rotifers to fish presence, which nevertheless reveals a significant change in ecosystem functioning. For instance, the dynamics of bacterioplankton and small heterotrophic eukaryotes (i.e. protists) is controlled by small herbivores (Lepère et al. 2007, Riemann 1985). Regarding the effects of nutrient enrichment on zooplankton, our results showed a positive response of small herbivores with no significant response of the other two groups. These heterogeneous responses might be an explanation for the weak responses of the entire zooplankton trophic level to nutrient enrichment.

Conclusions

The positive effects of nutrient enrichment on phytoplankton and zooplankton in the food chain and on highly edible phytoplankton and small herbivores in the food web turn out as robust responses. Nutrient enrichment fuels competitive phytoplankton species that support small herbivores and food-chain responses echo the responses of these functional groups (Fig. 2). The analysis of fish effects shows the well-described trophic cascade in the food chain and reveals two trophic cascades in the food web: one transmitted by large herbivores that benefit highly edible phytoplankton and one transmitted by omnivorous zooplankton that benefit small herbivores (Fig. 2). The negative effect of fish on large herbivores might also benefit small herbivores through a release of highly edible phytoplankton exploitation. The absence of response of less edible phytoplankton and the role of omnivorous zooplankton deserve more research. More generally, our meta-analysis shows that the response of some trophic groups to nutrient enrichment and fish presence may be hidden when species are aggregated in trophic levels. Differential responses to perturbations within trophic levels result from the interplay between direct and indirect interactions and reveal important aspects of food-web functioning in response to perturbations. The discrepancy between theoretical predictions and the results of our analysis suggests that the spatio-temporal dynamics of plankton, i.e. exchanges between the water column and the sediments through sedimentation, resuspension and seeding, may be of great importance for pelagic food-web dynamics.

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Supplementary material (available online as Appendix oik.01116 at <www.oikosjournal.org/readers/appendix>). Appendix 1.