

Response of macroinvertebrates to warming, nutrient addition and predation in large-scale mesocosm tanks

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Abstract There is increasing concern about the effect of climate change on aquatic systems. We examined changes in macroinvertebrate communities caused by increased temperature (3°C above ambient during summer only and continuous 3°C above ambient all year round), influences of fish (*Gasterosteus aculeatus* L.) and addition of nutrients (nitrogen and phosphorus) in 48 large-scale (3000 l) tanks over a 2 year period. While numbers of Isopoda, *Chaoborus*, Corixidae, Ephemeroptera, Notonectidae and Odonata were reduced by the presence of fish, nutrient addition caused isopods, corixids, mayflies and odonates to increase in abundance. Impacts of temperature increase were surprisingly low, with only gastropods increasing in heated tanks, suggesting that, overall abundances of most macroinvertebrate taxa will not be severely affected by the predicted temperature rise. To determine if taxa were sampled representatively during the experiment, net sweep samples taken towards the end of the experiment were com-

pared with final macroinvertebrate abundances when the complete contents of each tank were harvested. We found that net sweeping is an appropriate semi-quantitative method for most taxa in mesocosm tanks. However, mites, coleopteran adults and larvae, dipterans and *Chaoborus* were not adequately sampled. This might explain why we could not detect any treatment effects of temperature, fish or nutrients on mites, coleopterans and dipterans and calls for different sampling techniques for these taxa, especially in ponds with vegetation stands.

Keywords Global climate change · Temperature · Sampling technique · Sweep net · *Gasterosteus aculeatus*

Introduction

Global temperature is rising, and is predicted to rise a further 3 to 5°C in the next half century in the UK and most parts of Europe (Houghton et al., 2001; Schiermeier, 2004; IPCC 2007). However, knowledge on the effects of warming on ecosystems or species diversity is still limited. In general, detection of natural community changes induced by warming require spatial or temporal correlations, such as long term records (e.g. Sagarin et al., 1999) or sampling over a latitudinal temperature gradient (e.g. Noges et al., 2003).

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Shallow lakes in a changing world

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Most studies concentrate on population changes over a climate gradient (e.g. Walker et al., 1991) because costs prevent the investigation of more complex systems. Artificial outdoor large-scale mesocosm tanks, however, provide an opportunity to study community responses in the medium-term. Open-air mesocosms provide an intermediate scale between laboratory and natural environmental conditions. Further, the identical design and similar initial species composition allow direct comparisons between treatments or manipulations thereby allowing quantification of causal relationships.

As macroinvertebrate species are often used as water quality indicators (e.g. Rosenberg & Resh, 1992), adequate sampling techniques are essential. There are various ways of sampling macroinvertebrates from lakes or streams, such as grab samplers, surber samplers, artificial substrates, box samplers and air lift samplers. Methods used mainly depend on the substratum of interest. However, the most common and widespread method is net sweeping. To determine which sampling technique is most appropriate for representative sampling, comparisons between different methods have been made by various authors. However, this is a difficult approach as volumes sampled are often hard to quantify and untypical species could be sampled with artificial substrates (Stark, 1993; Merritt et al., 1996; Humphries et al., 1998; Muzaffar & Colbo, 2002; Connor et al., 2004).

Comparing sampling techniques with one another, however, is a restricted approach as no absolute values of species abundances present in natural environments can be obtained. Large mesocosms allow for absolute comparisons by an exhaustive final sampling, where all macroinvertebrates present in the tanks can be removed and numbers compared with the last experimental sampling. This quantitative approach allows conclusions about which macroinvertebrates were sampled adequately with net sweeps and which were not.

First, we hypothesised that macroinvertebrate abundance and diversity would be reduced in the presence of fish through predation, and increased by warming and nutrient addition owing to faster development, higher survival and more nutritious

food supply. Changes in the zooplankton, phytoplankton and macrophyte communities within the experiment are documented in McKee et al. (2002a, 2002b) and Moss et al. (2003). Secondly, the opportunity to assess sampling methods by comparing results of a standardised sampling to the actual abundances in the mesocosms derived from a final collection when mesocosms were emptied was taken.

Methods

Experimental set up

Forty-eight mesocosm tanks, each 1 m deep and 2 m in diameter, were installed in Ness Gardens, near Liverpool, UK, each containing around 3,000 l of groundwater (for details see McKee et al., 2003). They simulated shallow lakes and were sunk into the ground for insulation. For a detailed outline of the site, see McKee et al. (2000). A 5-cm sediment layer (7:1 sand:loam), an inoculum of plankton and macroinvertebrates from a local canal and 3 macrophyte species were introduced into the tanks. Equal weights of *Lagarosiphon major* Ridl. Moss, *Elodea nuttallii* Planch. H. St. John, and *Potamogeton natans* L. were planted some months before the experimental start to allow the plants to establish in the tanks (for details see McKee et al., 2002b). To ensure similar starting conditions, plankton and macroinvertebrates were cross-mixed between tanks several times in advance of the experimental period. Cross-mixing was conducted by collecting and pooling sweep net samples from all tanks and thorough mixing of the pooled sample before re-distribution to the tanks. The experiment ran over a 2-year period, from September 1998 to September 2000.

Treatments

A computer-controlled heating system allowed heating of 32 tanks to 3°C above ambient temperature via hot water pumped through a heating element in the bottom of the tanks (for details see McKee et al., 2000). Sixteen tanks were heated year round, while warming of

another sixteen was restricted to warmer months only (April 1 to September 30). The remaining 16 tanks were not heated and served as controls. In addition to temperature treatments, the effects of nutrients and predation by fish were investigated in a randomised block design with 4 replicates per treatment. Two additional tanks served as storage for de-ionised water, used to replace water lost from experimental tanks through evaporation.

To investigate predatory impact, 21 adult three-spined Sticklebacks (*Gasterosteus aculeatus* L.) were added to each of half of the tanks at the start. During the 2-year experiment they were allowed freely to breed, the final mean biomass per mesocosm tank being $27.0 \pm 18.2 \text{ g m}^{-3}$. Nutrient treatments (24 tanks) received constant nutrient addition, following a 3-weekly cycle during winter and a 2-weekly cycle during the 6 summer months. Nitrogen was added to the relevant tanks as sodium nitrate, phosphorus as sodium phosphate, to give added concentrations of $500 \mu\text{g l}^{-1}$ nitrogen and $50 \mu\text{g l}^{-1}$ phosphorus in winter and $170 \mu\text{g l}^{-1}$ nitrogen and $17 \mu\text{g l}^{-1}$ phosphorus in summer, respectively. These values were established from nutrient loadings on local eutrophic shallow lakes.

Macroinvertebrate methods

The initial macroinvertebrate community introduced to the tanks was obtained from local ponds. The stock community was well mixed before a standard aliquot was added to each tank and cross-mixed for several weeks thereafter. Macroinvertebrates were sampled every 8 to 10 weeks with three standardised net sweeps (250 μm mesh size) per mesocosm tank. After counting and identifying of all sampled individuals on site, they were returned to the relevant mesocosm. All sweeps were carried out by the same person for the 2 year sampling period. At termination, all macroinvertebrates were removed, counted and identified during a final exhaustive harvest of all tanks.

Before applying a 3-way univariate analysis of variance (ANOVA) with time as the repeated measure and polynomial contrasts (Gurevitch & Chester, 1986), all data were Hellinger-transformed. Warming, fish and nutrients were used

as the three factors including all interactions. Where a significant effect of warming was found, slopes of regression lines of treatment means were compared via ANCOVA in order to determine which of the two warming treatments caused the effect.

For assessment of the accuracy of the net sweeps, data from the last sampling of macroinvertebrates of the experiment (14th of September 2000) were compared with counts made at the final harvest four days later (18th of September 2000). Owing to skewed data, fourth root transformation was applied to both datasets. Regression analyses were used to establish a relationship between numbers of the final sweep and the final exhaustive analyses.

Results

Initially introduced species included Ephemeroptera, Odonata, Hydracarina, Corixidae, Diptera and Coleoptera, *Chaoborus* and Isopoda. Gastropoda were introduced along with macrophytes. Identification of taxa to species level was carried out at the end, but not at the start of the experiment. Overall, abundance and composition of the macroinvertebrate community changed between tanks and over time. Ephemeroptera and Gastropods, however, were the dominant families in most tanks over the entire 2-year period. During that time, only one invader family was found (notonectids), however usually in low numbers. Comparison of the means of all tanks on the first (15th of October 1998) and last sampling (14th of September 2000) showed a similar pattern, with the highest relative increases in abundance of odonates, corixids and *Chaoborus* (Table 1).

Most macroinvertebrate taxa were significantly reduced by the presence of fish, with only gastropods, coleopterans, mites and dipterans showing no significant response, and corixids increasing when fish were present in the tanks (Fig. 1A, Table 2). Gastropod numbers significantly increased with both warming treatments ($P < 0.05$), being lowest in unheated tanks and highest in tanks heated all year round (Fig. 1C and Table 2). Coleopterans, mites and dipterans

Table 1 Mean macroinvertebrate composition at first (15th of October 1998) and last sampling (14th of September 2000). Percentages of taxa abundances are shown

Group	First sampling	Last sampling
Isopoda	1.1	0.3
<i>Chaoborus</i>	0.9	3.2
Corixidae	0.2	4.7
Gastropoda	17.6	23.4
Ephemeroptera	76.4	62.7
Notonectidae	0	0.2
Odonata	0.3	6.6
Coleoptera juveniles	0.4	0
Coleoptera adults	0.1	0.2
Diptera	1.2	2.5
Hydracarina	1.9	0.9

however responded neither to the impact of fish, nor to nutrient addition nor warming. Isopod, corixid, mayfly and odonate abundances increased in tanks receiving nutrient addition (Fig. 1B and Table 2). Note that Fig. 1 shows overall effects during the experiment, as abundances were pooled for all sampling occasions. Statistical results however are shown from analyses of variance with time as the repeated measure.

Abundances of macroinvertebrates sampled by sweep netting and counts from the final harvest four days later, showed taxon-dependent results. Final abundances of Isopod Crustacea (*Asellus aquaticus* L.), Ephemeroptera (*Cloeon dipterum* L.), Gastropoda (*Bithynia tentaculata* L., *Lymnaea peregra* Müll., *Lymnaea stagnalis* L., *Physa fontinalis* L., *Planorbis* sp., *Potamo-pyrgus jenkinsi* Smith), Odonata (*Aeshna juncea* L., Coenagrionidae, *Libellula depressa* L., *Sympetrum striolatum* Charpentier) and Corixidae had a highly significant R^2 with net sweep counts. An example is given in Fig. 2 for gastropods. Notonectid abundances showed

Fig. 1 Means of macroinvertebrate abundances for the entire 2-year experimental period for the different treatments applied. Graph A: fish absent (black bars) and present (white bars); Graph B: no nutrient addition (black bars) and nutrient addition (white bars); Graph C: no heating (black bars), summer heating only (light grey bars) and all year round heating (dark grey bars). Significant results of repeated measures analysis of variance are indicated with asterisks (see Table 2 for details)

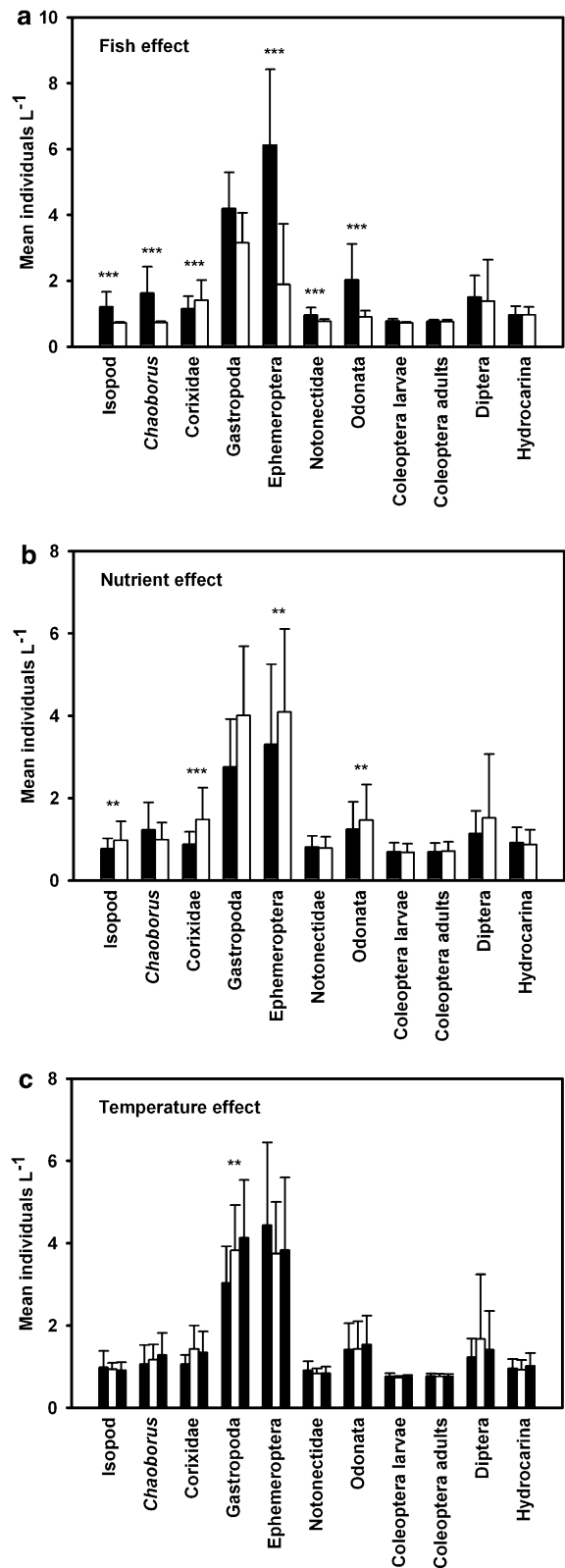


Table 2 Treatment effects determined by repeated measure analysis of variance of the various macroinvertebrate taxa

Effect	Isopoda	<i>Chaoborus</i>	Corixida	Gastropoda	Ephemeroptera	Notonectidae	Odonata	Coleoptera juveniles	Coleoptera adults	Diptera	Hydracarina
Fish (F)	12.9***	34.2***	13.4***	NS	21.5***	26.1***	22.9***	NS	NS	NS	NS
DF(1,36)											
Nutrients (N)	9.5***	NS	15.1***	NS	9.6**	NS	9.5**	NS	NS	NS	NS
DF(1,36)											
Warming (W)	NS	NS	NS	6.4**	NS	NS	NS	NS	NS	NS	NS
DF(2,36)											
F × N	NS	9.3**	NS	NS	NS	NS	NS	NS	NS	NS	NS
DF(1,36)											
F × W	NS	NS	NS	NS	7.5**	6.6**	NS	NS	NS	NS	NS
DF(2,36)											
N × W	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
DF(2,36)											
F × N × W	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
DF(2,36)											

Wherever effects were significant, F values are given and p values are indicated as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Degrees of freedom (DF) are given

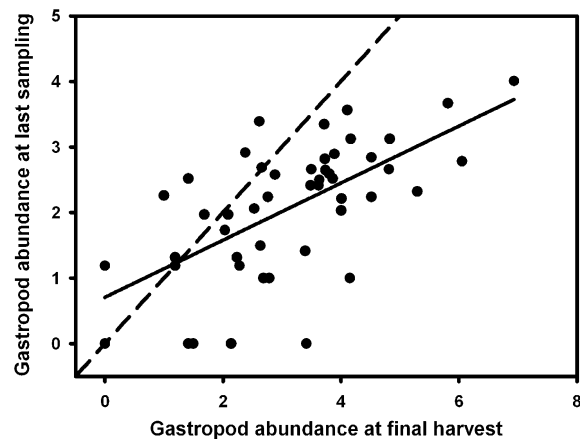


Fig. 2 Gastropod abundance at last net sweep sampling and from final harvest when all animals were removed from mesocosms. Data are shown for all 48 mesocosms and are fourth root transformed. The linear regression line is shown as a solid line (for details see Table 3). The 1:1 line is indicated as dashed line

weaker, but still significant results. Abundances determined by net sweep samples for Coleoptera larvae (*Dytiscus spp.*) and adults (*Dytiscus marginalis* L., *Dytiscus semisulcatus* Müll., *Halipus spp.*, *Agabus nebulosus* Forster, *Coelostoma orbiculare* Fabricius, *Colymbetes fuscus* L., *Laccophilus minutes* L. and other, undetermined, beetles), Diptera (Chironomidae, Tipulidae, Culicidae, Dixidae), Hydracarina and *Chaoborus* abundances were significantly different from abundances in the tanks at termination ($P > 0.05$, see Table 3).

Table 3 Results of regression analyses of abundance counts of the last sampling and the final harvest for each group

Group	Regression line equation	R^2	P-value
Isopoda	$y = 0.16x + 0.08$	0.22	0.001
<i>Chaoborus</i>	$y = 0.19x + 0.58$	0.04	0.21
Corixidae	$y = 0.30x + 0.37$	0.15	0.006
Gastropoda	$y = 0.43x + 0.71$	0.39	<0.0001
Ephemeroptera	$y = 0.60x + 1.15$	0.29	<0.0001
Notonectidae	$y = -0.18x - 0.03$	0.10	0.03
Odonata	$y = 0.49x + 0.03$	0.38	<0.0001
Coleoptera larvae	$y = -0.02x + 0.02$	0.001	0.84
Coleoptera adults	$y = 0.09x + 0.13$	0.03	0.21
Diptera	$y = 0.08x + 0.55$	0.2	0.34
Hydracarina	$y = -0.07x + 0.74$	0.004	0.65

Discussion

Effects of treatments

Macroinvertebrate taxa responded differently to treatments applied. Fish significantly reduced abundance of 6 out of 11 introduced groups as anticipated. Gastropods were not eaten: their shells are considered a defensive structure against predation by fish (e.g. Lewis & Magnuson, 1999), especially small sticklebacks. Surprisingly, numbers of corixids increased in the presence of predators, which might be due to invasion from outside the mesocosm tanks coupled with a high food supply as corixids are filter feeders and might have profited from the decline of filter feeding zooplankton (McKee et al., 2002a). Non-significant results of treatment effects on species are discussed in the section on sampling efficiency below.

Higher nutrient concentrations are likely to result in higher primary production and thus expected to support a greater number of invertebrates. Indeed, besides large effects caused by fish, nutrients had major impacts on the phytoplankton community (Moss et al., 2003) and zooplankton abundances were higher compared with tanks where no nutrients had been added when fish were not present (McKee et al., 2002a). However, only four macroinvertebrate groups showed significant increases in nutrient enriched tanks compared with tanks where no nutrients were added: isopods, mayflies, corixids and odonates. Ephemeroptera abundances were also found to be higher in streams when exposed to channels with high nutrients (Kiffney & Richardson, 2001). After one year of the mesocosm experiment, McKee & Atkinson (2000) determined the length of the mayfly *Cloeon dipterum* present in the tanks and reported larger nymphs to be found in tanks with high nutrients and no fish suggesting higher production in nutrient-rich tanks.

Heating had a small effect on the mesocosm communities of phytoplankton, zooplankton and macrophytes relative to predation and nutrient effects (McKee et al., 2002a; McKee et al., 2002b; McKee et al., 2003; Moss et al., 2003). This seems to also be the case for macroinvertebrates: tem-

perature increase only had a positive effect on gastropod abundance. In a stream experiment however, Hogg & Williams (1996) found a decrease in total animal densities as response to a temperature increase of 2–3.5°C, mainly due to a decrease in chironomid abundance, suggested to be caused by thermal limits. In general, ectotherms show increased development rates with higher temperatures (Atkinson, 1996). As macroinvertebrate taxa were affected by the presence of fish in our study, it could be assumed that the temperature effect might not be visible. However, there was no effect of temperature when analysis was restricted to fish-free tanks only (data not shown), in accordance with Baulch et al. (2005) who recorded no significant changes of Trichoptera, Diptera and Ephemeroptera abundances with warming. As Costil & Daguzan (1995) reported, sexual maturity of two *Planorbis* species was earlier at higher temperatures, and they began to lay eggs above a threshold temperature before spending most of their life span in reproduction. Thus higher temperature could have led to earlier reproduction of the gastropods. Embryonic development for *Bithynia tentaculata* was shown to be shortened with higher temperature (Kozminsky, 2003).

Effects of sampling

The four macroinvertebrate groups showing no response to any treatment were coleopteran adults and larvae, dipterans and mites. This however might result from inadequate sampling. The comparison between the last net sweep sampling for macroinvertebrate abundance and the total numbers of animals present in the mesocosms is an important step to determine taxon-specific representative sampling via sweep-netting. Net sweep sampling seems adequate for semi-quantitative sampling of some taxa, but not for others. If taxa were perfectly sampled by net sweeps, we would expect a regression line with an R^2 value of 1 and parallel to and below the 1:1 line. However most of the regression lines calculated in this study show a slope smaller than 1, under-representing high abundances, and over-representing low abundances. This, of course, could also have been caused by death between

the last sampling and final harvest or a sampling error at harvest.

Abundances in the last sampling and the final harvest of coleopteran larvae showed no correlation, which is not surprising as they were only found in three tanks in low numbers. Surprisingly, no representative sampling was achieved for adult beetles, regarded as optimally sampled with net sweeps by Humphries et al. (1998) as they are free swimming in the water. But, like larvae, abundance of beetles was very low during the experiment.

For *Chaoborus*, it could be argued that net sweeps are not an appropriate sampling method as the larvae hide in the sediment during the day when the sampling took place. However, in the case of *Chaoborus*, another factor could play a role. In 65% of the tanks where *Chaoborus* was found, abundances were greater in the last sampling than in the final harvest (data not shown), suggesting emergence from the tanks between the two sampling occasions. Therefore, predation effects shown in Fig. 1A and Table 2 on *Chaoborus* should be regarded with caution. Mites are the smallest of the sampled macroinvertebrates and their size might have prevented a representative sampling. Dipteran larvae are difficult to sample with net sweeps as most of them live in burrows in the sediment and might be easier to sample with sediment corers.

In conclusion, sweep netting in mesocosm tanks resulted in representative sampling of isopods, mayflies, gastropods, odonates, corixids and notonectids. We can recommend this sampling technique for obtaining semi-quantitative results for these taxa with water plants present. However, care has to be taken with truly benthic invertebrates (Diptera larvae) in pond sediment, as well as for beetles, mites and *Chaoborus*, for which the method yielded inadequate results. This may explain why no treatment effects were found for Diptera, mites and coleopterans. For the other groups, fish and nutrients had the strongest effects, while warming influenced only gastropod abundances. Nonetheless our conclusion that climate warming will only have a subtle influence on shallow lakes might be limited in a wider context. Some experimental effects could have been buffered by the presence of the plants,

mimicking clear water shallow lakes. Many lakes are already switched from a clear water stage to a turbid, phytoplankton dominated state (see Moss et al., 1996), where temperature impacts could be more severe.

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