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Moss, B; Stephen, D; Balayla, DM; Becares, E; Collings, SE; Fernandez-Alaez, C; Fernandez-Alaez, M; Ferriol, C; Garcia, P; Goma, J; Gyllström, Mikael; Hansson, Lars-Anders; Hietala, J; Kairesalo, T; Miracle, MR; Romo, S; Rueda, J; Russell, V; Ståhl-Delbanco, Annika; Svensson, Marie; Vakkilainen, K; Valentin, M; Van de Bund, WJ; Van Donk, E; Vicente, E; Villena, MJ

Published in:
Freshwater Biology

DOI:
10.1111/j.1365-2427.2004.01304.x

2004

Link to publication

Citation for published version (APA):
Moss, B., Stephen, D., Balayla, DM., Becares, E., Collings, SE., Fernandez-Alaez, C., Fernandez-Alaez, M., Ferriol, C., Garcia, P., Goma, J., Gyllström, M., Hansson, L.-A., Hietala, J., Kairesalo, T., Miracle, MR., Romo, S., Rueda, J., Russell, V., Ståhl-Delbanco, A., ... Villena, MJ. (2004). Continental-scale patterns of nutrient and fish effects on shallow lakes: synthesis of a pan-European mesocosm experiment. *Freshwater Biology*, *49*(12), 1633-1649. https://doi.org/10.1111/j.1365-2427.2004.01304.x

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Freshwater Biology (2004) **49,** 1633–1649 doi:10.1111/j.1365-2427.2004.01304.x

Continental-scale patterns of nutrient and fish effects on shallow lakes: synthesis of a pan-European mesocosm experiment

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SUMMARY

1. Results are analysed from 11 experiments in which effects of fish addition and nutrient loading on shallow lakes were studied in mesocosms. The experiments, five in 1998, six in 1999, were carried out in six lakes, distributed from Finland to southern Spain, according to a standard protocol.
2. Effects of the treatments on 29 standard chemical, phytoplankton and zooplankton variables are examined to assess the relative importance of bottom-up (nutrient enrichment) and top-down (fish predation) effects. For each year, the experiments in different locations are treated as replicates in a meta-analysis. Results of individual experiments are then compared in terms of the patterns of significant influences of nutrient addition and fish predation with these overall results (the baseline), and between years in the same location.
3. The overall meta-analysis gave consistent results across the 2 years, with nutrient loading influencing all of the chemical variables, and on average 31% of primary producer and 39% of zooplankton variables. In contrast, fish influenced none of the chemical variables, 11% of the primary producer and 44% of the zooplankton variables. Nutrient effects on the system were thus about three times greater than fish effects, although fish effects were not inconsiderable.
4. The relative importance of nutrients and fish in individual experiments often differed between years at the same location and effects deviated to varying degrees from the baseline. These deviations were treated as measures of consistency (predictability) of conclusions in repeat experiments. Consistency increased southwards and this is interpreted as a consequence of more variable annual weather northwards.
5. The influence of nutrient loading was greater southwards and this was probably manifested through naturally greater annual macrophyte abundance in warmer locations in consequence of the longer plant growing-season. There was no trend in the relative importance of fish effects with latitude but this may partly be an artefact of the simple fish

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community used. These findings suggest that nutrient control should be a greater priority than biomanipulation in the restoration of eutrophicated shallow lakes in warm temperate regions.
6. Starting conditions affected the outcome of experiments. High initial concentrations of total phosphorus and planktonic chlorophyll *a* concentration (created by local conditions prior to the experiment) led to de-emphasis of the importance of nutrient loading in the experiment.

Keywords: continental gradient, fish, meta-analysis, nutrients, weather variation

Introduction

Diversity in structure and function of ecosystems is considerable. There is concern that the functioning of ecosystems is being impaired by widespread destruction in a situation where there is still much to understand about fundamental patterns and processes in the systems. Such patterns in functioning may be driven by a range of environmental gradients. These include climate and variation in weather, geology and soil conditions and the accidents of past events that have led to distinctive biogeography. Because energy input in the form of solar radiation and its influence on production and water availability is fundamental to all ecosystem functioning and because it also controls processes such as soil formation and development, climate is often seen as the master driving variable in the establishment of terrestrial systems. In turn, freshwater systems are dependent on their surrounding terrestrial catchments, but because they are 'islands', their greater discontinuity may lead to patterns that are more locally controlled.

The gross differences between, say, Arctic tundra and tropical rain forest are substantial. The gross appearance of lake systems from poles to tropics is basically similar. Nonetheless there are still likely to be patterns among freshwater systems, although they may be subtle. Climate, for example, will have many effects on freshwaters, ranging from modifications within the system (changes in growth rates, timings of reproduction, balances of photosynthesis and respiration, rates of mineralisation) (Quayle *et al.*, 2002; McKee *et al.*, 2003; Moss *et al.*, 2003) to large-scale regional effects (Watson, 2002). These latter may be consequent on changes in the balance of rainfall in summer and winter, and effects induced by sea level rise on rivers and coastal lakes. However, geology, soil conditions and land use have been known for nearly a century to determine many details within freshwater lakes (Pearsall, 1921; Juday *et al.*, 1928). Linking the details to the drivers, however, is not easy. This is not because basic physiological effects of, say, temperature or phosphorus on individual processes are at all mysterious, but because the complexity of the systems, and the degree of stochasticity inherent in all ecological systems, leads to a likelihood of many possible outcomes in any individual system. Nonetheless, there must be some common denominators in effects on major system processes. The experiments considered here were conceived on this assumption.

Nitrogen and phosphorus loading determine many features of lakes (Vollenweider, 1975), but evidence has emerged of a more complex situation, especially in shallow lakes, where the nature of the fish community can influence the zooplankton and thus indirectly the phytoplankton communities and even water chemistry (e.g. Irvine, Moss & Balls, 1989; Scheffer *et al.*, 1993; Carpenter & Kitchell, 1994; Hansson *et al.*, 1998). These effects may also have impacts on aquatic plants, which in turn may counter-influence water chemistry and predator–prey relationships among fish and zooplankters (Jeppesen *et al.*, 1998). A consensus has emerged that nutrients remain very important in shallow lakes, but that the extent to which their potential influence may be realised is very much a function of food-web structure and how it can be modified by nutrient loading.

Understanding how continental- or greater-scale variations in environmental factors and food-web structure influence these complex shallow lake

systems is important because of the importance of these lakes to humanity as providers of diverse resources such as building materials, fisheries, water, and amenity (Dugan, 1994). They are also important reservoirs of conservation and biodiversity value, not least for migratory and other water birds. Many shallow lakes have become severely damaged by eutrophication in combination with other forms of pollution, recreational impact, changing salinity and introduced species. Both nutrient control and food web manipulation (biomanipulation) are used in combination in attempts to restore their biodiversity and other values (Moss, Madgwick & Phillips, 1996). The effectiveness of current restoration strategies could well be affected by climate as well as by local chemical conditions, but evidence from the subtropics and tropics is meagre in comparison with that from the north-temperate region. It is clear, however, that the differences in seasonality and in fish communities may have important consequences for warm lakes compared with cooler ones (Lazzaro *et al.*, 1992).

Investigation of how environmental drivers might affect these systems can be carried out through analysis of large data sets and the seeking of changing patterns along defined gradients. It can also be done by setting up highly controlled tank systems in which the environment, including factors like temperature can be closely regulated and their effects followed. Lack of data from low-latitude lakes, and the inherent problem that correlations do not imply causation, hampers the first approach; a degree of artificiality in the complexity of the systems and cost deter the latter. A compromise is to carry out comparable experiments with natural communities along a natural environmental gradient to investigate how major processes or controls change along this gradient. This was the approach used in the International Mesocosm Experiment (Stephen *et al.*, 2004a), whose overall results are presented here. The experiment involved carrying out a standardised experiment to a common design with fish addition and nutrient addition treatments, in mesocosms at five or six locations from Finland to Spain in each 2 years.

The founding hypothesis was that there would be shifts in the relative importance of top-down and bottom-up effects in shallow lakes across broad spatial scales. This hypothesis was based on the assumption that both macrophyte and algal growth would benefit from extended growing seasons at lower latitudes. However, nutrient shortage would be more likely to set in when temperature is higher and the growing season longer (Talling & Lemoalle, 1998), leading to greater importance of nutrient control in southerly locations. We also surmised that algal growth, being inherently faster than that of zooplankton (Fogg & Thake, 1987), would outstrip development of herbivorous zooplankton at higher temperatures. In turn, the influence of planktivorous fish on zooplankton populations would become less relevant for control of phytoplankton at higher temperatures. We thus anticipated a greater importance of nutrients in warmer locations and years and a greater importance of fish effects under cooler conditions.

Results of the individual mesocosm experiments at each location are reported in separate papers (Fernández-Alaez *et al.*, 2004; Hansson *et al.*, 2004; Hietala, Vakkilainen & Kairesalo, 2004; Romo *et al.*, 2004; Stephen *et al.*, 2004b; Van de Bund & Van Donk, 2004). Continental-scale patterns in zooplankton and phytoplankton community responses to fish and nutrient manipulations have also been examined (Vakkilainen *et al.*, 2004; Van de Bund *et al.*, 2004). Those papers aimed to provide pointers to understanding the functioning of shallow lake systems and to the interpretation in general of such experiments repeated across large spatial scales. In the overall synthesis provided here, we used the results for 29 standard chemical, phytoplankton and zooplankton variables from the eleven experiments and first treated them in a meta-analysis for each year at five (1998) or six (1999) locations. From this analysis we determined a baseline scenario against which the results from individual experiments could be compared. Our basis of comparison was the fractions of the 29 variables, divided into chemical, primary producer and zooplankton variables that were significantly influenced by either fish or nutrient treatments in the overall analysis and in individual experiments. We also made the comparison in relation to latitude, temperature and starting conditions. In contrast to the synthesis papers on phytoplankton and zooplankton (Vakkilainen *et al.*, 2004; Van de Bund *et al.*, 2004) we thus examine here not changes in communities or biomass but in the relative importance of processes.

Methods

Enclosure experiments

In 1998 and 1999, eleven replicated-mesocosm experiments were performed in six shallow, macrophyte-dominated lakes: Vesijarvi in Finland, Krankesjön in Sweden (1999 only), Little Mere in England, Naardermeer in the Netherlands, Sentiz in northern Spain near León, and Xeresa in southern Spain near Valencia. Background conditions in the lakes are given in Table 1 of Stephen *et al.* (2004a).

The mesocosms were polyethylene cylinders, 1 m in diameter, enclosing up to 750 L of lake water, with exposure to bottom sediment and with natural vegetation. Experimental treatments were identical between locations in a given year. Each experiment comprised 36 enclosures, with fish addition and nutrient addition treatments. In 1998 there were three zooplanktivorous fish levels (from 0 to 20 g fresh mass m^{-2}), and four nutrient additions (from no nutrient addition to weekly additions sufficient to create an additional immediate concentrations of up to 10 mg L^{-1} nitrate-N and 1 mg L^{-1} phosphate-P), with three replicates for each treatment. Fish treatments were the same in 1999 as in 1998, but there were six rather than four nutrient loadings (from no nutrient addition to weekly additions enough to create an additional immediate

Table 1 Results of overall analysis by two-way ANOVA on data from eleven mesocosm experiments carried out at six locations across Europe in 1998 and 1999

			Main effects					
	Transformation		1998			1999		
Dependent variable	1998	1999	Location	Fish	Nutrients	Location	Fish	Nutrients
TP	Log_{10}	Log_{10}	***	ns	***	***	ns	***
SRP	Log_{10}	Log_{10}	***	ns	***	***	ns	***
Nitrate	Log_{10}	Log_{10}	***	ns	***	***	ns	***
Ammonium	Log_{10}	Log_{10}	***	ns	***	***	ns	***
Alkalinity	Log_{10}	Log_{10}	***	ns	*			
pH	None	None	**	ns	***	***	ns	***
TSS	Log_{10}	Log_{10}	***	ns	*			
Planktonic chl-*a*	Log_{10}	Log_{10}	***	*	***	***	ns	***
Total phytoplankton	Log_{10}	Log_{10}	**	ns	*	**	ns	*
Chlorophycota	Log_{10}	Log_{10}	**	ns	***	**	ns	ns
Cryptophyceae	Log_{10}	Log_{10}	ns	*	**	***	ns	ns
Bacillariophyceae	Log_{10}	Sq rt	***	ns	ns	***	ns	ns
Cyanobacteria	Log_{10}	Log_{10}	***	ns	ns	***	ns	ns
Chrysophyceae	Log_{10}	Log_{10}	***	ns	ns	***	ns	ns
Dinophyceae	Log_{10}	Log_{10}	***	ns	ns	***	*	ns
Euglenophycota	Log_{10}	Log_{10}	***	ns	ns	***	ns	ns
Small algae (GALD<50 μm)	Log_{10}	Log_{10}	***	ns	**	***	ns	****
Large algae (GALD>50 μm)	Log_{10}	Log_{10}	*	ns	ns	***	ns	ns
Phytoplankton diversity index	None	None	***	ns	ns	***	ns	***
Periphytic chl *a*	Log_{10}	Log_{10}	***	ns	ns	***	ns	**
Total zooplankton	Sq rt	Sq rt	***	ns	*	***	*	*
Rotifers	Log_{10}	Log_{10}	***	***	ns	***	***	ns
Cladocera <500 μm	Log_{10}	Log_{10}	***	**	ns	***	ns	ns
Cladocera >500 μm	Log_{10}	Log_{10}	***	***	ns	***	***	ns
Cyclopoid copepods	Log_{10}	Sq rt	***	ns	ns	***	ns	**
Calanoid copepods	Log_{10}	Log_{10}	***	ns	ns	***	ns	**
Nauplii	Log_{10}	Sq rt	***	ns	ns	***	ns	ns
Raptorial zooplankters	Log_{10}	Sq rt	***	**	ns	***	Ns	***
Open-water filterers	Sq rt	Log_{10}	***	ns	**	***	*	**

Significances for main effects of fish and nutrient treatments are shown for up to 29 variables as: ns, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. There were no interaction effects.

Sq rt, square root; TP = total phosphorus, SRP = soluble reactive phosphorus, TSS = total suspended solids. Values for phytoplankton groups are biovolumes and values for zooplankton groups are biomasses.

concentration of 3 mg L^{-1} nitrate-N and 0.3 mg L^{-1} phosphate-P), with two replicates for each treatment. Appropriate zooplanktivorous fish species were used in different locations (Table 1 of Stephen *et al.*, 2004a).

Mesocosms were established several days before fish addition and the first nutrient addition; pre-existing fish were removed by electrofishing. The experiments lasted 5 weeks in 1998 and 6 weeks in 1999. Weekly samples were taken for water chemistry, phytoplankton and zooplankton. Details of sampling and methods are given in Stephen *et al.* (2004b). For the current analysis, 29 variables were selected. The chemical variables were: total phosphorus (TP; μg L^{-1}), soluble reactive phosphorus (SRP; μg L^{-1}), nitrate-N (mg L^{-1}), ammonium-N (μg L^{-1}), pH, alkalinity (meq L^{-1}), total suspended solids (TSS; mg L^{-1}), the latter two in 1998 only. Variables characterising primary production were phytoplankton chlorophyll *a* (μg L^{-1}), total phytoplankton biovolume and biovolumes of Chlorophycota, Cryptophyceae, Bacillariophyceae, Cyanobacteria, Chrysophyceae, Dinophyceae and Euglenophycota (μm^3 L^{-1}), Shannon–Wiener (Weaver) diversity index for the phytoplankton (bits per individual), biovolume of small algae with a Greatest Axial or Linear Dimension (GALD) <50 μm (μm^3 L^{-1}), biovolume of larger algae (GALD >50 μm) (μm^3 L^{-1}) and periphytic chlorophyll *a* (μg cm^{-2}). Zooplankton variables were biomasses (μg L^{-1}) of total zooplankton, total rotifers, Cladocera <500 μm, Cladocera >500 μm, cyclopoid copepods, calanoid copepods, nauplii, raptorial zooplankton, and open-water filterers.

Storms completely destroyed one of the Swedish experiments, but the data set was near complete for the eleven other experiments, although there was also severe damage to one Dutch experiment which led to a loss of data for some enclosures. In addition, there were omissions of single variables in a few experiments: Rotifers were not counted in the Netherlands experiments, and results of fish treatments with the two highest nutrient additions in 1998 in Finland were excluded from data analyses owing to the complete mortality of fish in those mesocosms. There was also high intermittent fish mortality in one experiment in northern Spain, but since the fish were replaced, the data were included. Likewise the data from the English 1999 experiment were included despite a 10-fold error in phosphorus loadings because available phosphate was so high in the lake water that phosphate was already present in substantial excess for algal growth.

Time-weighted averages of the 29 variables were calculated for each enclosure in each experiment in a standard way, with week number used as weighting factor. The rationale for this approach is given in Stephen *et al.* (2004a). Data were log-transformed or arcsine-transformed where necessary to meet ANOVA requirements. The five location experiments in 1998 and the six in 1999 were then combined for analysis as single experiments for each year with five and six blocks (i.e. location), respectively, and replications for each treatment of 15 in 1998 and 12 in 1999. The data were subjected to two-way analyses of variance (ANOVA) giving an overall baseline set of relationships against which the results from individual location experiments could be compared.

The threefold ratio of numbers of significant effects of nutrients on water chemistry: primary producers: zooplankton and the equivalent ratio for fish effects were determined. Data were analysed separately for 1998 and 1999 because the experimental set-up differed in detail between years. There were no interaction effects in the baseline results (and indeed rather few in the individual experiment results) so only main effects are treated. Where a variable was missing (for example, rotifer data in the Netherlands experiments) the ratios were normalised to the maximum possible ratio of variables measured to make them comparable. These ratios were then used as baselines for comparison with the parallel ratios obtained in the several locations for individual experiments. To do this, the numbers of variables, from the standard suite of 29 chemical, primary producer and zooplankton variables, significantly influenced by fish or nutrients were determined for the individual location experiments and expressed as ratios, as above. These ratios were calculated separately for fish and nutrient effects and were then compared by chi-square tests against the baseline ratios (the separate values for 1998 and 1999 being used because the number of chemical variables differed in the 2 years) for the experiment overall and between years in the same location. The latter calculation was not possible for Sweden where data were only available for 1999.

The experiment was conceived against a north-south gradient from Finland to southern Spain. This gradient is approximately indicated by latitude and

about 20° of latitude were embraced. However, other gradients were inevitably present. Weather differed and can be expressed as mean temperature during the experiments; initial conditions also inevitably differed because of weather and local circumstances prior to the experiments. We thus examined the data in terms of initial concentrations of chlorophyll *a*, TP and macrophyte density (on an arbitrary scale of abundance where 1 was negligible, 2 was sparse and 3 was abundant) as well as in terms of latitude and temperature gradients. The standard chemical, primary producer and zooplankton variables were grouped by year and the proportions of each group that were significantly influenced by fish or nutrients in each experiment were determined. The proportions of all biological and of all variables so influenced were then calculated. Linear regressions were made with latitude, temperature and initial conditions as driving variables and the percentages of significant influences as dependent variables.

Results

Overall analysis

The data used in the overall analyses are given in Appendices 1 and 2. In both years, block (i.e. location) significantly affected all variables with the one exception being Cryptophyceae biovolume in 1998 (Table 1). There were no interactions of fish and nutrients in either year. Fish influenced fewer variables than nutrients. Fish increased chlorophyll *a* concentration and biovolume of Cryptophyceae in 1998 but not in 1999, when instead fish increased dinoflagellate biomass. Fish also significantly increased rotifer biomass, but reduced biomass of large and small Cladocera and raptorial zooplankters in 1998. In 1999 they decreased the total zooplankton biomass, but increased the proportion of open-water filterers, increased the rotifer biomass and decreased that of large Cladocera. In 1998 fish significantly influenced none of the seven chemical variables, two of the 13 primary producer variables and four of the nine zooplankton variables. Comparable proportions in 1999 were 0 : 5, 1 : 13 and 4 : 9. The influence of fish was thus apparently greater on the upper levels of the food web than on the lower.

Nutrient loading influenced five of the seven chemical variables, always by increasing values and five of the primary producer variables in 1998. It increased chlorophyll *a* concentration, total phytoplankton biomass, and biomasses of Chlorophyceae and Cryptophyceae, and decreased the biomass of small algae (GALD <50 μm). Nutrients significantly increased total zooplankton biomass and that of open-water filterers in 1998, although the increases were small.

In 1999 nutrient additions positively influenced all chemical variables, and also increased chlorophyll *a* concentration, total phytoplankton biomass, the proportion of small algae and periphytic chlorophyll *a*, but decreased the diversity (Shannon–Wiener) index of phytoplankton. Nutrients increased total zooplankton biomass, both cyclopoid and calanoid copepod biomasses and in consequence decreased the biomass of open-water filterers in 1999 but increased that of raptorial species. They had no significant effect on other zooplankton variables.

Thus in 1998 nutrients significantly influenced five of seven chemical variables, five of 13 primary producer variables and two of nine zooplankton variables and in 1999 the proportions were, respectively: 5 : 5, 5 : 13 and 5 : 9. Chi-squared tests showed that the ratios of number of chemical: primary producer: zooplankton variables significantly influenced by either fish or nutrients did not differ between years for either fish effects (χ^2 for fish effects = 1, d.f. = 2, $P > 0.5$) or nutrient effects (χ^2 for nutrient effects = 2.6, d.f. = 2, $P > 0.2$) or all effects (fish and nutrient) taken together ($\chi^2 = 3.6$, d.f. = 5, $P > 0.5$). In percentage terms, the effects of nutrients on chemical, primary producer and zooplankton variables were, on average, 83, 39 and 39. The corresponding average effects for fish were 0, 12 and 44%. Nutrient additions thus had a much greater effect on water chemistry and about equal effects on primary producers and zooplankton, whilst fish addition had no effect on nutrients, modest effects on primary producers and the greatest effect on zooplankton. Overall the effects of nutrients might thus be assessed as greater than those of fish (Fig. 1; Table 2).

Comparisons with individual experiments

Ratios of significant effects of fish addition or nutrient addition or both added together differed significantly between years in all locations except southern Spain

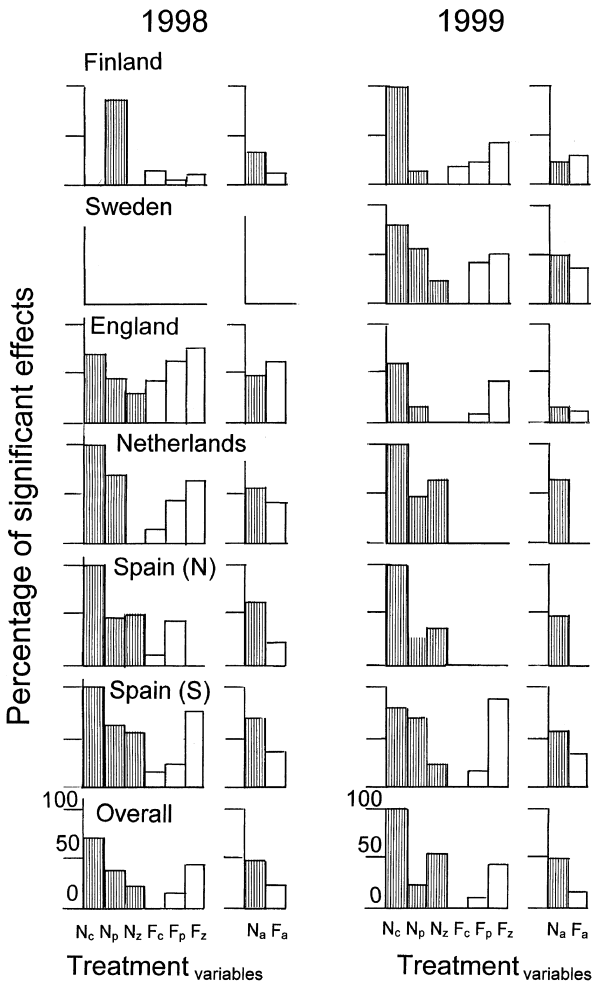

Fig. 1 Percentages of variables, all together (a) or grouped as chemical (c), primary producer (p) or zooplankton (z) that were significantly affected by nutrient (N) or fish (F) treatments in mesocosm experiments carried out in 1998 and 1999 at six European locations. Similar results from a meta-analysis of all locations (overall) are also shown.

(Table 3). The combined ratios (fish and nutrient effects together, ratio of six items) differed between years in the three more northerly locations but not in the two more southerly ones.

Compared with the overall baseline ratios for each year, there were again differences in fish or nutrient effects, or both, in both years at three locations. Of the four possibilities for significant differences (fish and nutrients, 2 years) there was a tendency for a greater proportion to be significantly different towards the north and this trend was also shown for the combined ratios (ratio of six items). For the total number of comparisons (both between years and against the baseline) the proportion that showed significant differences can be calculated. There was a greater tendency for stability (predictability) of effects (lower proportion of significant differences in the chi-squared comparisons) with decreasing latitude (Fig. 2; $r^2 = 0.41$, $n = 22$, $P < 0.005$).

Table 2 Ratios of numbers of significant fish effects on all variables to the sum of significant fish effects plus significant nutrient effects in mesocosm experiments carried out at five locations in 1998 and 1999

Location	1998	1999
Finland	0.21 (14)	0.54 (15)
England	0.56 (32)	0.49 (10)
The Netherlands	0.42 (28)	0 (15)
Northern Spain	0.29 (25)	0 (13)
Southern Spain	0.36 (31)	0.38 (25)
Overall	0.31 (18)	0.25 (19)

In parentheses are shown the absolute total numbers of significant effects (the denominator).

There were similar relationships between stability of effects with mean temperature during the experiment ($r^2 = 0.33$, $P < 0.05$), although this was strongly conditioned by one data point from southern Spain, and with initial macrophyte density ($r^2 = 0.32$, $P < 0.01$), which was not so conditioned. There were no relationships between stability of effects and initial concentrations of chlorophyll *a* or TP.

Regression analyses

Among the drivers tested, temperature and latitude were inversely related and initial macrophyte density increased with temperature and decreased with latitude (Table 4). Initial concentrations of chlorophyll *a* and TP were positively related. There were no significant relationships among any of the drivers and the percentage of variables influenced by fish. However, there were significant relationships with the percentages of variables influenced by nutrients. The percentages of significantly-influenced zooplankton variables, and that of all variables significantly influenced by nutrients, increased southwards (Fig. 3) There was also a pattern with initial TP and chlorophyll *a* concentrations. High initial values of these led to a decreased proportion of the variables being influenced by nutrients. Finally, initial macrophyte density was positively correlated with the proportion of the chemical variables significantly influenced by nutrient addition.

Table 3 Numbers of significant effects of fish and nutrients on chemical, primary producer and zooplankton variables among a series of mesocosm experiments in six European locations; differences between 2 years of experimentation (1998 and 1999) at each location (chi-squared test, 2 d.f. for fish and nutrient effects separately, 5 d.f. for combined effects); and differences from the overall ratios in each year derived from combination of the entire data set (chi-squared test, 2 d.f. for fish and nutrient effects separately, 5 d.f. for combined effects)

		Number of effects of						χ^2					
		Fish on			Nutrients on			Between years			Compared with baseline		
Location	Year	Chemistry	Primary producers	Zooplankton	Chemistry	Primary producers	Zooplankton	Fish	Nutrients	Combined	Fish	Nutrients	Combined
Finland	1998	1	1	1	0	11	0	3.5 (ns)	45.5***	***	11.0**	16.2**	***
	1999	1	3	4	5	2	0				5.0 (ns)	7.3*	*
Sweden†	1999	0	5.4	5	4	7.6	2				19.6***	3.4 (ns)	***
England	1998	3	8	7	5	6	3	10.4**	6.5*	**	8.8*	1.3 (ns)	ns
	1999	0	1	4	3	2	0				0 (ns)	7.6*	ns
The Netherlands†	1998	1	5.4	5.6	7	8.7	0	12.0*	11.9*	***	3.6 (ns)	4.7 (ns)	ns
	1999	0	0	0	5	4	5.6				5.0 (ns)	0.3 (ns)	ns
Northern Spain (Leon)†	1998	0	6	1.1	7	6	4.5	7.1*	1.89 (ns)	ns	10.1**	3.3 (ns)	*
	1999	0	0	0	5	4.3	3.4				5.0 (ns)	6.0 (ns)	ns
Southern Spain (Valencia)†	1998	1	3	7	7	8	5	1.4 (ns)	5.5 (ns)	ns	2.6 (ns)	2.9 (ns)	ns
	1999	0	2	7.9	4	9	2.3				2.4 (ns)	4.9 (ns)	ns
Overall	1998	0	2	4	5	5	2	1.0 (ns)	2.6 (ns)	ns			
	1999	0	1	4	5	5	5						

ns, not significant ($P > 0.05$); *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

†Indicates that data for one variable were unavailable and that the ratio calculated has been normalised to allow for the missing data.

The maximum values for chemical, primary producer and zooplankton variables were 7 : 13 : 9 in 1998 and 5 : 13 : 9 in 1999.

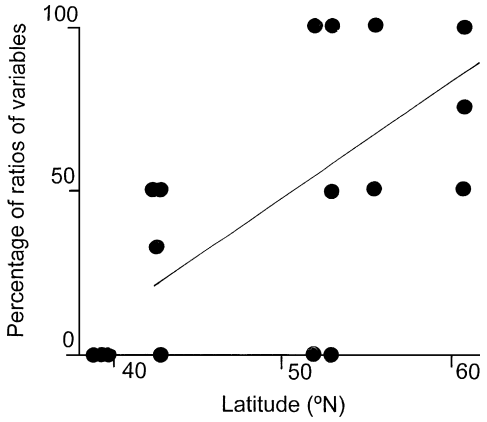

Fig. 2 Percentage of ratios of numbers of significantly-influenced (by fish or nutrients) variables that significantly differed (chi-square test) either between years at a single location or significantly differed (chi-square test) from the equivalent ratio obtained as a baseline in the overall meta-analysis. Values are plotted against latitude of the location of the experiment in a series of mesocosm experiments carried out in 1998 and 1999. The relationship was significant ($r^2 = 0.41$, $P < 0.005$, $n = 18$) and the equation for the regression line is $y = 3.44x - 124$.

Discussion

Despite differences in weather in 1998 and 1999, the overall analyses of the collections of five and six experiments, respectively, gave similar results in terms of the balance of importance of top-down and bottom-up processes (Fig. 1; Table 2). The effects of nutrient loading were, inevitably, strongest on water chemistry whilst effects of fish were greatest on zooplankton but were absent for water chemistry. There were no interaction effects so the picture that emerges is of a strong effect of nutrients on which are superimposed lesser but still substantial effects of fish. The zooplankton are pivotal in that both nutrients and fish have about equal effects and it is the balance of these zooplankton effects that could explain much of the variation in individual experiments.

The baseline scenario that emerged from overall analysis of the experiments is consistent with much other information (Jeppesen *et al.*, 1998). Nutrient loading increased phytoplankton growth, often selectively increasing the proportions of green algae and cryptomonads, and decreasing the proportions of small algae and phytoplankton diversity. Through food availability, it sometimes increased zooplankton biomass but had lesser influence on community composition. Fish tended to remove the Cladocera,

Table 4 Relationships between latitude, mean temperature, initial chlorophyll *a* concentration (Chl-*a*), initial total phosphorus (TP) concentration and initial macrophyte abundance and the percentages of a suite of chemical, primary production and zooplankton variables significantly influenced by nutrient and fish treatments in 11 mesocosm experiments carried out in six locations in 1998 and 1999 across Europe

					Effects of fish on					Effects of nutrients on				
Variable	Latitude	Chl-*a*	TP	Macrophytes	Chemistry	Primary producers	Zooplankton	Biological variables	All variables	Chemistry	Primary producers	Zooplankton	Biological variables	All variables
Temperature	0.48*–	ns	ns	0.36*+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Latitude		ns	ns	0.49*–	ns	ns	ns	ns	ns	ns	ns	0.40*–	ns	0.42*–
Chl-*a*			0.72**+	ns	ns	ns	ns	ns	ns	ns	0.47*–	ns	0.46*–	0.39*–
TP				ns	ns	ns	ns	ns	ns	ns	0.37*–	ns	0.42*–	0.43*–
Macrophytes					ns	ns	ns	ns	ns	0.39*+	ns	ns	ns	ns

ns, not significant; *$P < 0.05$; **$P < 0.01$.
+, indicates a positive relationship; –, an inverse relationship.
Values are given for separate groups of chemical, primary producer and zooplankton variables, for all biological (non-chemical) variables and for all variables. Values are coefficients of determination (r^2) with probabilities and direction of the effects.

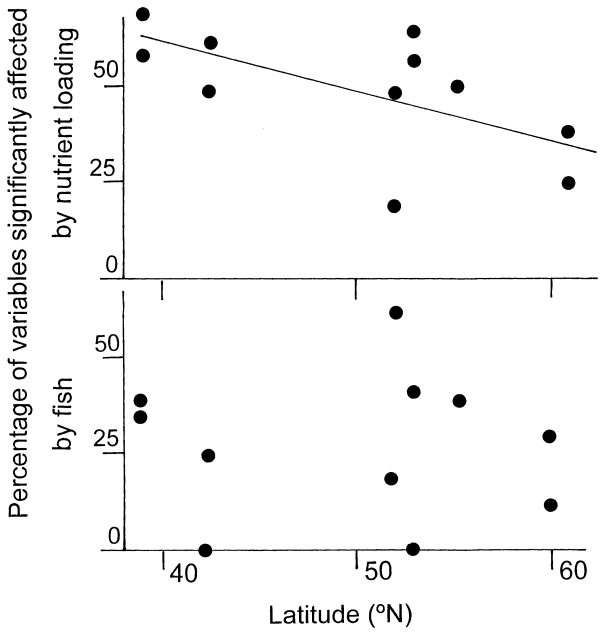

Fig. 3 Percentage of variables from a standard set of 29 chemical, primary producer and zooplankton variables that were significantly influenced by experimental nutrient (upper) and fish (lower) additions, plotted against latitude of the experimental sites in a series of mesocosm experiments carried out across Europe in 1998 and 1999. The relationship for nutrients was significant ($r^2 = 0.42$, $P < 0.05$, $n = 11$) with a regression equation, $y = 112 - 1.27x$. The relationship for fish was not significant at $P = 0.05$.

particularly the larger ones (Gliwicz, 2004) and increase the rotifer biomass and sometimes increase the chlorophyll *a* concentration. These conclusions are not new (Hrbácek, 1962; Brooks & Dodson, 1965); their significance lies in their consistency with current understanding. This gives confidence in the further analysis of the patterns of differences obtained in different years and from the overall analysis.

Differences between years are very important in that large-scale, relatively expensive experiments are often only carried out once, the presumption being that major processes should be consistently important from year to year. The results of our highly standardised, continent-wide experiment illustrate that this may not typically be the case (Table 3). At two locations there were no effects of fish in one year and many effects in the other. There were also differences in individual experiments from the baseline scenario derived from the meta-analysis. By comparing the ratios of significant effects between years and with the baseline ratios, two measures of such inconsistency are apparent.

The y axis of Fig. 2, in which the percentage of significantly different ratios of significant effects on the test variables obtained from comparisons between years or with the baseline, is plotted against latitude, can be taken as a measure of consistency (predictability) of results in individual experiments. There is apparently a pattern, with greater inconsistency northwards. This is understandable as weather patterns are more unpredictable in cold-temperate climates than in warm-temperate climates (Watson, 2002). The implication is that there is greater stability of processes between years with decreasing latitude. This can be understood in terms of longer growing seasons for plants (initial macrophyte density also increased with decreasing latitude). There would also be less likelihood, for example, of poor summer plant growth resulting from cold spring weather and failure of the overwintering plants to grow, or perhaps for turions to be damaged by bird grazing before full establishment of the new growth (Pokorny & Kvet, 2004). Warm, dry winters in the north may also be more likely to give advantages to the phytoplankton, which may establish a strong foothold before macrophytes have started to grow. Plants are more likely to overwinter at relatively high biomass in the south. The result suggests that experiments need to be repeated more frequently in northern temperate regions than in warm temperate regions for good understanding of the relative importance of different processes determining community structure in shallow lakes.

Our planned intention was to investigate the effects of broad-scale variation in site characteristics on the balance of importance of top-down and bottom-up controls of plankton biomass and community structure. One of the evident differences at continental scales is temperature along a north-south gradient. We thus analysed the proportions of variables influenced by fish and nutrients against latitude and mean temperature (during the experiments). We were, however, unable to control some initial conditions for the experiments. It was thus crucial to examine the effects of potentially important initial conditions (e.g. macrophyte density and concentrations of TP and chlorophyll *a*) on the results (Table 4).

Strikingly, the influence of fish had a relationship with neither latitude nor temperature. We may partly

have predetermined this lack of effect by selecting ecologically equivalent fish and being unable to incorporate whole fish communities into small mesocosms. The picture emerging from other observations is that of a more diverse, more omnivorous fish community in warmer regions, feeding year around and imposing severe predation pressure on the zooplankton (Crisman & Beaver, 1990). In turn this means continual, severe top-down effects on zooplankton and a phytoplankton thus effectively released from grazer control. We were unable to test this, however, with a monospecies fish community.

What did emerge in our analysis is a relationship between the influence of nutrient loading and latitude. Nutrient effects were more frequent southwards and this was not a trend manifestly conditioned by the effects of the southernmost Valencia experiment. It may be linked with the greater macrophyte density southwards (itself correlated with temperature, and thus probably length of growing season). Macrophytes are very effective at stripping nutrients, particularly nitrogen, from the water (Howard-Williams, 1985) and thus nutrient loading can be expected to have a greater effect on phytoplankton. The positive relationship between nutrient effects on water chemistry variables and initial macrophyte density (Table 4) is consistent with this. Northwards, greater inconsistency in plant communities, dependent on weather fluctuations between years, may result in less tight nutrient cycling and greater nutrient availability. There is certainly a prominent increase in nutrient concentrations in winter prior to growth in spring at high latitudes that is not so much a feature of lower latitudes where growth continues in winter (Talling, 1986). Towards the Equator, inputs from runoff are also lesser owing to high evaporation rates even in winter, which is also frequently relatively drier than at high latitudes. This too is likely to increase emphasis on nutrients.

Temperature did not produce the correlation that latitude did. Latitude integrates many climatically related variables, including weather over the longer period prior to the experiment that might greatly influence starting conditions and therefore potentially the outcome of experimental manipulations. Mean temperature during the experiment, although inversely correlated with latitude has not such a comprehensive influence.

Results of relatively short-term mesocosm experiments are certainly influenced by starting conditions, and this apparently underlies many of the differing pictures obtained at the same location in the two years of our experiments. The influence of macrophyte density was referred to above. Initial concentrations of chlorophyll *a* and TP, however, are probably not latitude-related, but depend more on local conditions and weather just previous to the experiment. Initial TP and chlorophyll *a* concentrations were strongly correlated and when an experiment began with high values of both, there was a lesser importance of nutrients (Table 3). Inevitably therefore, choice of lakes for experiments such as ours is important. Ideally only pristine lakes should be used, but the reality is that most lakes are impacted to greater or lesser extents by eutrophication. For example, the lake used in the U.K. experiments was recovering from previous eutrophication but still had residual high phosphorus levels in summer owing to release from the sediments (Beklioglu, Carvalho & Moss, 1999). It was a pragmatic choice and helped reveal important effects of variability between years and the importance of starting conditions, but conversely it may have obscured or weakened other relationships that less extreme nutrient concentrations would have revealed.

In spite of several unavoidable imperfections of our study, some important general conclusions emerge from our experiments: (i) in shallow lakes nutrient effects on the plankton community are greater than fish effects, although fish effects are not inconsiderable; (ii) predictability of the importance of different processes increases with decreasing latitude and this is probably a consequence of more variable weather polewards; (iii) the influence of nutrient loading is greater with decreasing latitude and this is probably manifested through the effects of longer plant growing seasons and greater macrophyte abundance (averaged over the year) in warmer locations. Do these conclusions suggest that the simple biomanipulations (primarily removal of zooplanktivorous fish) found to be effective in northern lakes (e.g. Hansson *et al.*, 1998; Mehner *et al.*, 2002) may be less successful in warmer climates? They do, but indirectly because biomanipulation of shallow lakes is carried out when they are dominated by phytoplankton and thus turbid. The lakes of our experiments were specifically chosen to be macrophyte-dominated and clear. The relatively greater importance of nutrients southwards,

however, does suggest that nutrient control of eutrophicated southern lakes may be a greater priority than it is for northern lakes where biomanipulation alone may clarify the water.

Acknowledgments

We are very grateful to the European Union for providing funds (Contract ENV4-CT97-0420, SWALE) for this project, to a very large number of people, including a fleet of referees, who have given valuable help and to Mark Gessner, who provided rigorous editing and contributed greatly to the quality of the papers. It has been a considerable but largely pleasurable experience over 8 years. Now that it is completed, we are reminded of Huckleberry Finn's (Twain, 1884) final sentiments: 'and so there ain't nothing more to write about, and I am rotten glad of it, because if I'd 'a' knowed what a trouble it was to make a book I wouldn't 'a' tackled it, and ain't a-going to no more'.

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(Manuscript accepted 15 September 2004)

Appendix 1

Appendix 1A Treatment mean values ($\bar{x}$) and standard deviations (SD) of time weighted averages for chemical variables in the combined data set derived from five mesocosm experiments in five locations in 1998 ($n = 15$)

		Treatment											
Variable	Statistic	F0N0	F0N1	F0N2	F0N3	F1N0	F1N1	F1N2	F1N3	F2N0	F2N1	F2N2	F2N3
TP	$\bar{x}$	65	136	595	1106	99	153	428	804	108	185	473	775
	SD	58	70	442	873	96	98	241	326	94	128	206	426
SRP	$\bar{x}$	25	39	341	802	34	26	175	524	35	42	212	425
	SD	44	52	370	843	52	32	152	357	60	43	175	268
NO_3-N	$\bar{x}$	0	0	6	14	0	0	4	14	0	0	4	12
	SD	0	0	5	9	0	0	2	3	0	0	2	7
NH_4-N	$\bar{x}$	60	158	231	308	54	118	187	348	54	133	274	315
	SD	60	115	184	180	60	122	117	237	62	118	167	250
Alkalinity	$\bar{x}$	1.95	1.88	2.01	2.31	1.91	1.83	2.11	2.72	1.76	1.75	2.37	2.74
	SD	1.89	1.54	1.25	1.95	1.73	1.54	1.55	0.54	1.36	1.21	1.56	2.04
pH	$\bar{x}$	8.0	8.7	9.4	9.3	8.0	8.9	9.4	9.3	8.0	9.0	9.4	9.4
	SD	0.6	0.6	0.5	0.4	0.7	0.7	0.3	0.6	0.5	0.6	0.3	0.3
TSS	$\bar{x}$	4.26	9.95	13.3	17.3	7.26	10.2	11.1	14.2	6.61	9.71	14.3	10.8
	SD	2.47	10.9	16.9	28.6	4.94	7.05	14.7	18.7	3.01	6.28	15.8	10.8

F, fish treatment; N, nutrient treatment. Numbers refer to successive levels of treatment. Units are: μg L^{-1} for total phosphorus (TP), soluble reactive phosphorus (SRP), NH_4-N and chlorophyll *a*; mg L^{-1} for NO_3-N and total suspended solids (TSS); and meq L^{-1} for total alkalinity.

Appendix 1B Treatment mean values ($\bar{x}$) and standard deviations (SD) for primary producer variables in the combined data set derived from five mesocosm experiments in five locations in 1998 ($n = 15$)

		Treatment											
Statistic	Statistic	F0N0	F0N1	F0N2	F0N3	F1N0	F1N1	F1N2	F1N3	F2N0	F2N1	F2N2	F2N3
Planktonic chl-*a*	$\bar{x}$	10	52	126	146	23	57	125	140	23	64	154	127
	SD	5	56	182	270	24	32	176	204	18	45	147	108
Total phytoplankton	$\bar{x}$	12.00	19.9	18.1	14.4	46.9	34.3	35.9	20.9	37.3	35.7	31.3	37.1
	SD	21.5	15.3	18.7	14.0	91.4	44.4	31.0	9.35	69.6	46.1	24.1	42.2
Chlorophycota	$\bar{x}$	0.87	8.69	9.84	7.32	3.33	7.63	12.9	13.5	3.88	3.68	19.3	12.78
	SD	0.87	11.0	8.65	6.34	5.78	8.41	13.0	14.2	5.39	2.15	15.2	41.9
Cryptophyceae	$\bar{x}$	0.46	4.06	1.88	0.74	0.44	2.68	7.74	2.47	0.78	5.17	3.19	9.37
	SD	0.29	7.82	2.01	0.63	0.30	3.28	11.3	0.93	0.68	9.67	2.44	2.29
Bacillariophyceae	$\bar{x}$	0.25	3.59	0.16	0.19	1.36	0.58	0.55	0.32	0.69	2.19	1.27	0.253
	SD	0.48	2.85	0.14	0.16	2.67	0.60	0.48	0.30	1.12	4.08	1.77	0.157
Cyanobacteria	$\bar{x}$	10.2	3.37	6.05	6.05	41.5	23.1	14.5	4.53	31.2	24.4	7.47	14.93
	SD	22.0	4.53	9.25	8.58	92.3	46.6	18.6	5.15	69.5	52.3	8.70	5.02
Chrysophyceae	$\bar{x}$	0.086	0.195	0.086	0.065	0.074	0.19	0.001	0	0.242	0.070	0.001	0.002
	SD	0.172	0.361	0.17	0.128	0.148	0.23	0.001	0	0.280	0.125	0.001	0.002
Dinophyceae	$\bar{x}$	0.017	0.021	0.037	0.023	0.030	0.035	0.031	0.02	0.111	0.093	0.030	0.054
	SD	0.022	0.032	0.066	0.035	0.038	0.043	0.042	0.026	0.139	0.130	0.044	0.078
Euglenophycota	$\bar{x}$	0.083	0.063	0.082	0.050	0.192	0.145	0.148	0.074	0.444	0.115	0.047	0.065
	SD	0.103	0.086	0.117	0.076	0.035	0.238	0.171	0.142	0.599	0.160	0.078	0.126
Diversity index	$\bar{x}$	2.55	2.30	2.30	2.20	2.47	2.39	2.00	1.87	2.60	2.11	1.74	1.70
	SD	1.13	1.10	1.21	1.21	1.22	0.74	0.81	0.83	1.20	0.74	0.56	0.49
Small algae (GALD <50 μm)	$\bar{x}$	9.7	9.91	12.43	8.99	40.2	11.3	27.6	15.9	33.7	34.4	28.4	30.8
	SD	21.6	8.51	9.52	6.58	90.9	43.9	17.8	3.72	69.2	47.3	23.2	34.3
Large algae (GALD >50 μm)	$\bar{x}$	2.44	10.0	5.67	5.18	6.70	23.0	8.29	5.00	3.24	1.28	2.90	6.32
	SD	6.35	5.54	6.98	7.47	15.7	45.8	14.8	2.45	59.7	2.1	6.15	6.00
Periphytic chl-*a*	$\bar{x}$	21.3	87.4	8.3	5.8	24.8	35.6	5.2	4.4	25.3	39.1	4.2	5.9
	SD	44.5	188.5	9.1	3.3	54.2	71.2	1.8	2.2	55.1	80.4	2.1	3.1

F, fish treatment; N, nutrient treatment. Numbers refer to successive levels of treatment. Units are: μg L^{-1} for chlorophyll-*a*; millions of μm^3 mL^{-1} for total phytoplankton biovolume, the component algal biovolumes and the biovolume of algal size classes (GALD); bits per individual for diversity; and μg cm^{-2} for periphytic chlorophyll *a*.

Appendix 1C Treatment mean values ($\bar{x}$) and standard deviations (SD) of time-weighted averages for zooplankton variables in the combined data set derived from five mesocosm experiments in five locations in 1998 ($n = 15$)

		Treatment											
Variable	Statistic	F0N0	F0N1	F0N2	F0N3	F1N0	F1N1	F1N2	F1N3	F2N0	F2N1	F2N2	F2N3
Total zooplankton	$\bar{x}$	447	826	1110	709	431	801	666	1029	492	649	991	512
	SD	345	676	426	341	445	1035	361	824	489	560	689	208
Total rotifers	$\bar{x}$	103	87	186	208	159	281	158	157	228	367	369	402
	SD	73	71	178	278	153	271	81	92	180	305	336	93
Cladocera <500 μm	$\bar{x}$	15	40	49	22	11	49	26	99	11	12	51	22
	SD	20	47	82	22	15	90	44	183	15	18	101	44
Cladocera >500 μm	$\bar{x}$	182	393	577	226	57	174	211	112	3	8	59	6
	SD	176	386	721	233	70	265	296	156	5	9	115	12
Cyclopoid copepods	$\bar{x}$	112	252	216	203	127	160	137	464	166	227	436	59
	SD	115	240	347	274	129	219	129	734	226	407	840	110
Calanoid copepods	$\bar{x}$	8	6	14	8	29	46	35	80	53	4	5	12
	SD	10	9	27	13	48	88	60	139	101	7	8	21
Nauplii	$\bar{x}$	27	48	69	42	48	91	99	57	31	31	71	11
	SD	20	55	104	53	49	70	136	48	36	27	79	6
Raptors	$\bar{x}$	155	385	451	224	177	247	140	465	173	229	441	74
	SD	145	463	495	259	188	413	132	734	237	406	837	104
Open-water filterers	$\bar{x}$	202	353	610	347	235	463	349	325	241	312	392	261
	SD	197	265	561	274	262	431	291	355	250	338	311	210

F, fish treatment; N, nutrient treatment. Numbers refer to successive levels of treatment. Units are μg L^{-1}.

Appendix 2

Appendix 2A Treatment mean values ($\bar{x}$) and standard deviations (SD) of time-weighted averages for chemical variables in the combined data set derived from six mesocosm experiments in six locations in 1999 ($n = 12$)

		Treatment																	
Variable	Statistic	F0N0	F0N1	F0N2	F0N3	F0N4	F0N5	F1N0	F1N1	F1N2	F1N3	F1N4	F1N5	F2N0	F2N1	F2N2	F2N3	F2N4	F2N5
TP	$\bar{x}$	396	466	579	478	639	930	187	384	636	671	660	1499	234	388	468	855	888	1245
	SD	865	1043	1266	984	1279	1859	370	846	1439	1485	1363	3076	486	845	1004	1916	1916	2506
SRP	$\bar{x}$	207	328	448	320	363	627	134	234	507	443	354	1314	128	273	344	763	639	886
	SD	485	771	1035	705	778	1271	315	540	1198	1027	772	2951	298	624	785	1821	1429	1869
NO_3-N	$\bar{x}$	2	8	25	163	222	993	2	11	40	94	239	762	2	26	29	53	300	745
	SD	4	14	41	304	352	1585	3	17	63	148	397	1381	4	48	44	86	582	1168
NH_4-N	$\bar{x}$	208	104	183	186	136	209	127	55	119	183	173	485	96	112	81	321	205	262
	SD	427	159	326	288	178	238	219	41	174	280	231	767	146	157	81	642	266	271
pH	$\bar{x}$	8.3	8.5	8.6	9.0	8.9	8.9	8.2	8.5	8.6	8.7	9.0	9.0	8.3	8.4	8.6	8.6	8.9	8.9
	SD	0.7	0.9	0.8	1.1	0.9	0.9	0.8	1.0	1.0	0.9	0.9	0.9	0.7	1.0	0.8	0.9	1.0	0.9

Treatments and units as in Appendix 1A.

Appendix 2B Treatment mean values ($\bar{x}$) and standard deviations (SD) of time-weighted averages for primary production variables in the combined data set derived from six mesocosm experiments in six locations in 1999 ($n = 12$)

		Treatment																	
Variable	Statistic	F0N0	F0N1	F0N2	F0N3	F0N4	F0N5	F1N0	F1N1	F1N2	F1N3	F1N4	F1N5	F2N0	F2N1	F2N2	F2N3	F2N4	F2N5
Planktonic chl-*a*	$\bar{x}$	82	60	56	98	115	99	22	67	58	80	126	137	55	60	65	55	105	125
	SD	170	104	75	174	167	126	25	120	79	117	177	142	100	84	91	33	142	104
Total Phytoplankton	$\bar{x}$	31.3	42.3	38.0	28.0	251	56.0	9.73	26.2	17.8	141	39.3	59.7	24.6	20.5	70.1	46.6	43.3	32.5
	SD	60.3	85.7	58.3	23.3	485	101	10.3	39.7	18.2	264	47.6	64.8	35.7	23.1	82.6	50.2	55.0	40.9
Chlorophycota	$\bar{x}$	4.62	1.83	3.11	7.01	207	14.0	3.11	2.84	2.70	115	3.49	4.81	18.6	5.00	21.6	20.9	3.23	4.88
	SD	5.78	2.43	2.57	11.4	503	19.8	4.09	2.65	3.80	275	3.36	3.43	32.7	6.00	49.6	46.5	2.29	5.93
Cryptophyceae	$\bar{x}$	1.43	1.88	1.05	5.4	9.00	4.00	0.74	2.08	1.71	3.16	5.98	10.4	0.521	0.679	0.748	1.84	4.04	4.34
	SD	2.95	3.25	1.53	10.5	19.3	6.52	1.04	4.03	1.88	5.95	12.4	18.9	0.523	0.601	0.519	2.99	8.00	6.89
Bacillariophyceae	$\bar{x}$	0.27	0.23	0.16	0.23	0.21	0.15	0.51	0.33	0.22	0.166	0.265	0.23	0.67	0.319	0.259	0.396	0.376	0.337
	SD	0.29	0.29	0.16	0.26	0.23	0.14	1.00	0.53	0.20	0.134	0.278	0.21	1.16	0.361	0.210	0.400	0.457	0.470
Cyanobacteria	$\bar{x}$	24.7	38.1	33.3	15.1	34.7	37.8	5.09	20.7	12.6	22.7	28.8	43.8	4.12	14.1	47.8	22.6	34.6	22.3
	SD	52.5	80.3	55.6	16.8	38.5	63.5	6.70	33.6	13.3	28.5	43.5	58.7	4.10	17.9	78.1	35.8	52.4	38.5
Chrysophyceae	$\bar{x}$	0.00	0.00	0.02	0.05	0.08	0.01	0.009	0.009	0.016	0.022	0.03	0.093	0.33	0.043	0.035	0.027	0.021	0.376
	SD	0.00	0.00	0.03	0.10	0.16	0.01	0.015	0.015	0.016	0.030	0.048	0.176	0.60	0.055	0.065	0.038	0.026	0.825
Dinophyceae	$\bar{x}$	0.10	0.14	0.13	0.21	0.15	0.07	0.254	0.156	0.411	0.34	0.526	0.34	0.35	0.303	0.31	0.77	0.997	0.288
	SD	0.14	0.28	0.21	0.33	0.26	0.12	0.454	0.203	0.701	0.66	0.096	0.63	0.63	0.444	0.638	1.67	2.16	0.620
Euglenophycota	$\bar{x}$	0.12	0.06	0.23	0.03	0.07	0.05	0.022	0.042	0.115	0.025	0.184	0.053	0.052	0.098	0.014	0.078	0.035	0.024
	SD	0.20	0.12	0.34	0.04	0.08	0.07	0.018	0.062	0.191	0.031	0.280	0.049	0.049	0.141	0.022	0.157	0.051	0.022
Diversity index	$\bar{x}$	3.37	2.74	2.89	2.65	2.79	2.44	3.06	2.91	2.79	2.50	2.35	2.45	3.15	3.12	2.85	2.61	2.83	2.37
	SD	1.05	1.07	1.10	1.03	1.22	1.11	1.29	0.99	0.88	1.24	0.77	1.29	1.25	1.21	1.12	0.97	1.23	1.05
Small algae	$\bar{x}$	4.06	2.70	4.47	14.6	21.8	13.1	3.85	8.22	9.4	18.0	17.7	30.7	2.73	6.44	8.86	20.2	16.8	28.1
(GALD <50 μm)	SD	7.58	5.55	6.84	17.2	25.0	17.5	4.65	9.07	9.4	28.8	16.2	41.7	3.73	6.57	8.29	28.5	19.6	41.8
Large algae	$\bar{x}$	27.4	39.6	33.5	13.4	230	43.1	5.73	18.1	8.27	123	21.6	29.1	21.9	14.1	61.7	26.4	26.5	4.42
(GALD >50 μm)	SD	58.5	89.3	60.2	12.5	535	67.1	7.48	38.3	13.8	297	43.0	60.7	36.6	20.5	88.9	48.4	53.1	4.74
Periphytic chl-*a*	$\bar{x}$	34.9	29.8	60.5	78.9	142.0	100.0	40.9	41.5	73.4	62.6	105.2	154.0	29.3	43.0	47.1	60.6	65.2	140.4
	SD	76.7	65.4	134.0	175	317.0	223.0	89.0	91.8	162.6	138.6	233.5	342.5	64.4	94.7	104.2	133.9	142.3	311.0

Treatments and units as in Appendix 1B.

Appendix 2C Treatment mean values ($\bar{x}$) and standard deviations (SD) of time-weighted averages for zooplankton variables in the combined data set derived from six mesocosm experiments in six locations in 1999 ($n = 12$)

		Treatment																	
Variable	Statistic	F0N0	F0N1	F0N2	F0N3	F0N4	F0N5	F1N0	F1N1	F1N2	F1N3	F1N4	F1N5	F2N0	F2N1	F2N2	F2N3	F2N4	F2N5
Total zooplankton	$\bar{x}$	624	1440	1314	1237	1143	1506	757	787	733	1357	790	926	1404	1368	1319	1621	1036	1343
	SD	568	1904	1361	985	1115	1298	882	821	762	1142	370	630	2089	1929	1334	1405	606	1175
Total rotifers	$\bar{x}$	326	941	636	432	555	817	156	369	351	714	350	463	1049	1012	766	767	595	798
	SD	532	1860	1194	650	732	1303	182	564	409	1154	213	483	1941	1636	1043	730	633	1028
Cladocera <500 μm	$\bar{x}$	20	22	177	27	62	20	324	86	62	67	43	31	61	84	142	347	45	74
	SD	26	14	269	21	62	19	684	116	59	48	45	36	100	107	261	593	80	99
Cladocera >500 μm	$\bar{x}$	106	207	224	411	347	255	58	56	48	85	42	35	26	13	36	33	48	39
	SD	165	251	305	671	638	438	81	93	109	198	98	75	54	24	64	61	113	78
Cyclopoidd copepods	$\bar{x}$	114	132	166	232	122	327	101	148	149	309	210	261	97	135	204	365	178	268
	SD	115	115	171	228	144	424	82	132	120	287	199	260	85	110	267	444	178	288
Calanoid copepods	$\bar{x}$	27	66	48	53	10	13	51	66	60	77	69	12	91	50	76	24	74	8
	SD	57	117	83	110	13	15	97	130	117	153	146	19	183	91	157	45	158	11
Nauplii	$\bar{x}$	31	72	63	82	47	74	67	62	63	105	76	124	80	74	95	85	96	156
	SD	16	80	53	80	38	69	107	93	90	154	104	207	138	94	147	117	110	209
Raptors	$\bar{x}$	123	140	180	247	143	374	105	155	161	316	218	267	102	165	221	216	177	273
	SD	116	115	176	218	144	407	84	134	121	282	197	260	86	143	267	185	177	286
Open-water filterers	$\bar{x}$	413	1064	871	796	884	887	529	523	539	795	405	453	1108	1012	862	948	579	760
	SD	471	1774	1109	872	995	1173	788	716	693	1042	369	499	2047	1880	1288	1303	619	1113

Treatments and units as in Appendix 1C.