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

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SUMMARY

1. Shallow lake ecosystems are normally dominated by submerged and emergent plants. Biological stabilising mechanisms help preserve this dominance. The systems may switch to dominance by phytoplankton, however, with loss of submerged plants. This process usually takes place against a background of increasing nutrient loadings but also requires additional switch mechanisms, which damage the plants or interfere with their stabilising mechanisms.
2. The extent to which the details or even major features of this general model may change with geographical location are not clear. Manipulation of the fish community (biomanipulation) has often been used to clear the water of algae and restore the aquatic plants in northerly locations, but it is again not clear whether this is equally appropriate at lower latitudes.
3. Eleven parallel experiments (collectively the International Mesocosm Experiment, IME) were carried out in six lakes in Finland, Sweden, England, the Netherlands and Spain in 1998 and 1999 to investigate the between-year and large-scale spatial variation in relationships between nutrient loading and zooplanktivorous fish on submerged plant and plankton communities in shallow lakes.
4. Comparability of experiments in different locations was achieved to a high degree. Cross-laboratory comparisons of chemical analyses revealed some systematic differences between laboratories. These are unlikely to lead to major misinterpretations.
5. Nutrient addition, overall, had its greatest effect on water chemistry then substantial effects on phytoplankton and zooplankton. Fish addition had its major effect on zooplankton and did not systematically change the water chemistry. There was no trend in the relative importance of fish effects with latitude, but nutrient addition affected more variables with decreasing latitude.
6. The relative importance of top-down and bottom-up influences on the plankton differed in different locations and between years at the same location. The outcome of the

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experiments in different years was more predictable with decreasing latitude and this was attributed to more variable weather at higher latitudes that created more variable starting conditions for the experiments.

Keywords: alternative stable states, community structure, eutrophication, fish, large-scale variation, nutrients

Introduction

Shallow lakes constitute the bulk of the world's freshwater area (Wetzel, 1990); they have great importance in providing productive fisheries in Asia, Africa and South America (Dugan, 1994); they are of great conservation value, often for the migratory bird communities they support in the temperate world. Shallow lakes are also very vulnerable to change. Many have lost the dominance of their submerged plants in clear water to a take-over by phytoplankton communities in turbid water with consequences for their biodiversity and fish communities (De Nie, 1987; Carvalho & Moss, 1995; Jeppesen *et al.*, 1998, 1999).

Shallow lake plant communities are resistant to change at low nutrient loadings, and may survive considerable increase in nutrients (Irvine, Moss & Balls, 1989), with changes in community composition from short-growing species through taller, more vigorous pondweeds and lilies, to semi-floating and floating species like hornwort (*Ceratophyllum demersum* L.) and duckweeds (*Lemna* spp.). As nutrient loading increases further, however, submerged plants become increasingly vulnerable to the action of switch mechanisms. These include damage to the plants by cutting or boat propellers, disturbance and grazing by ducks, geese or benthic fish, especially exotic species that increase to large populations (Cahn, 1929; Crivelli, 1983), or changes in the water level or in the fish community to favour zooplanktivory (Brönmark & Weisner, 1992).

One mechanism that helps stabilise plant communities is the harbouring of large numbers of daphnids and other Cladocera, that graze phytoplankton from adjacent waters, in and around the plant beds (Timms & Moss, 1984). Similar relationships exist among molluscs, periphyton and plants (Brönmark, 1985). These mechanisms are particularly influenced by fish predation, particularly on zooplankton, but also on periphyton grazers (Lauridsen *et al.*, 1996). Another mechanism for maintaining stability is restriction of

the nitrogen availability in the water (Ozimek, Gulati & Van Donk, 1990), both through plant uptake and denitrification in the often-deoxygenated conditions within plant beds.

Much of the information on these processes has been pieced together into a general hypothesis of alternative stable states (Irvine *et al.*, 1989; Scheffer *et al.*, 1993; Jeppesen *et al.*, 1998) from experiments and observations at many locations, although mainly in northern Europe. However, limited amounts of information from elsewhere suggest that there is a further level of complexity dependent on differing natures of macrophyte and fish communities. The macrophyte communities of South America, for example, have a greater proportion of large floating plants and the fish communities of warm temperate and tropical regions are more diverse than those impoverished in the north, particularly in Europe, by the recent glaciation. Spatial effects of background geology, soil development and land use may also complicate the core hypothesis.

Much effort has also gone into development of techniques for restoration of plant-dominated clear-water lakes through combinations of nutrient control and manipulation of fish communities (Shapiro, Lamarra & Lynch, 1975; Hosper, 1989; Moss, Madgwick & Phillips, 1996; Mehner *et al.*, 2002). It is not yet clear, however, how appropriate these might be outside the northern locations in which largely they have been developed. Understanding of the wider context is thus important, not least because in an analysis of the contribution of natural systems to the cash economy of the Earth, wetland systems, including shallow lakes, provided the greatest contribution to a very large sum (Costanza *et al.*, 1997).

The overall hypothesis tested here was that the balance of importance of top-down (predation) controls and bottom-up (nutrient) controls on the planktonic community would change across Europe, with greater importance of top-down effects at higher latitudes. We reasoned that both macrophyte

and algal growth would benefit from extended growing seasons and that therefore nutrient shortage would be more likely to set in at southern sites, leading to a greater relative importance of nutrient control. We reasoned also that algal population growth, being inherently faster than that of zooplankton (on considerations of average size of organisms) would be more likely to outstrip development of herbivorous zooplankton populations at the higher temperatures characterising southern sites. Therefore, control, no matter how substantial, of zooplankton populations by fish would be less likely to impact phytoplankton growth. We thus expected a greater importance of bottom-up effects (nutrients) in warmer, southern sites and a greater importance of top-down effects (fish predation) in cooler, northern lakes.

Eleven individual experiments, collectively the International Mesocosm Experiment (IME), were carried out, five in summer, 1998, six in summer, 1999 at locations in Finland, Sweden, England, the Netherlands, northern Spain (Leon) and southern Spain (Valencia). This introduction gives an overview of the locations, the common experimental design, data analysis and major outcomes. Information on sites and methods is also briefly outlined in papers on component experiments (Fernández-Aláez *et al.*, 2004; Hansson *et al.*, 2004; Hietala, Vakkilainen & Kairesalo, 2004; Romo *et al.*, 2004; Van de Bund & Van Donk, 2004) with some finer detail given in Stephen *et al.* (2004) for reference.

Sites, experimental design and data analysis

The lakes (Table 1) were chosen for their comparability. Key criteria included an immediate history of dominance by submerged plants at the height of summer and a depth over extensive areas or over the whole lake of about 1 m. However, particular species of macrophytes were present at different sites and the fish used in the experiments reflected local conditions.

Sets of 36 mesocosms of a standardised design were established in the six lakes in each year. The Swedish experiment in 1998, however, was destroyed by storms after 2 weeks and was abandoned. Mesocosms were made of polyethylene (125 µm thick) cylinders mounted top and bottom on plastic hoops, 1-m in diameter, so that the enclosed area was 0.79 m² and depth about 1 m. The bottom hoop was weighted or

staked so that it was firmly buried in sediment. Thus the water in the mesocosms was in contact with the sediment, and at the top was exposed to the atmosphere. Mesocosms were held on a fixed or floating wooden or plastic framework such that there was provision sufficient for expected water level increases in the lake without ingress of new water. In 1998, they were constructed in three blocks of 12, and in 1999 in two blocks of 18, situated randomly within the area dominated by submerged plants the previous year. The location was moved within the area between years.

Samples were taken in all mesocosms, before fish and nutrients were added, to test for homogeneity of water chemistry and plankton variables with results checked by one-way analysis of variance. There were three fish density treatments (0, 4 and 20 g fresh mass m⁻²) and four (1998) or six (1999) nutrient additions in a randomised block design. Treatments for both nutrients and fish are referred to as levels 0, 1, 2, 3 etc. with level 0 the control. The fish used were small (approximately 5 cm total length) individuals of locally important zooplanktivorous species, such that at least two fish were used in the 4 g m⁻² treatment. Inevitably, different species had to be used in different locations, but previous studies (Lazzaro *et al.*, 1992; Williams & Moss, 2003) suggest that in zooplanktivory, total biomass and individual size rather than taxon are the key features.

Nutrients were added as mixtures of either calcium or sodium nitrate (dependent on the major ion chemistry of the water, to minimise change to major ion chemistry) and potassium dihydrogen phosphate, at weekly intervals. In 1998, additions caused theoretical immediate increases in concentration of zero P and N, 100 µg L⁻¹ P and 1 mg L⁻¹ N, 500 µg L⁻¹ P and 5 mg L⁻¹ N, and 1000 µg L⁻¹ P and 10 mg L⁻¹ N, based on the initial volume. Six loadings were similarly used in 1999 to give: zero N and P; 30 µg L⁻¹ P and 0.3 mg L⁻¹ N; 60 µg L⁻¹ P and 0.6 mg L⁻¹ N; 90 µg L⁻¹ P and 0.9 mg L⁻¹ N; 150 µg L⁻¹ P and 1.5 mg L⁻¹ N; and 300 µg L⁻¹ P and 3.0 mg L⁻¹ N. Loadings were kept constant irrespective of water level changes, which were generally small. Exceptions were made in the experiments in Spain, where evaporation was so intense that volume changes were allowed for so as to keep the added concentrations in line with those in other locations.

Table 1 Characteristics of lakes used in the International Mesocosm Experiment and pretreatment conditions in mesocosms

Lake	Location	Altitude (m a.s.l.)	Water temperature		pH	NH ₄ -N (µg L ⁻¹)	NO ₃ -N (mg L ⁻¹)	SRP (µg L ⁻¹)	TP (µg L ⁻¹)	Chl- <i>a</i> (µg L ⁻¹)	Plant density	Plants present	Fish added
			Year	(°C) [mean (range)]									
Vesijärvi	Finland (61°00'N, 25°30'E)	81.4	1998	17.5 (15.4–20.6)	7.5	9	<0.005	<5	50	4	Negligible	<i>Lemna trisulca</i> L. <i>Elodea canadensis</i> Michx., <i>Ceratophyllum demersum</i> L. <i>Lemna trisulca</i> , <i>Elodea canadensis</i> , <i>Ceratophyllum demersum</i>	<i>Rutilus rutilus</i> L.
Krankesjön	Sweden (55°42'N, 28°19'E)	19	1999	21.1 (18.6–23.0)	7.9	9	<0.005	6	62	18	Sparse	<i>Lemna trisulca</i> , <i>Elodea canadensis</i> , <i>Ceratophyllum demersum</i>	<i>Perca fluviatilis</i> L.
Little Mere	England (53°20'N, 2°24'W)	60	1998	17.8 (16.5–19.4)	7.3	400	0.06	99	184	3	Negligible	<i>Myriophyllum spicatum</i> L., <i>Chara tomentosa</i> L. <i>Ceratophyllum demersum</i> , <i>Potamogeton berchtoldii</i> Fieb.	<i>Gasterosteus aculeatus</i> L.
Naardermeer	The Netherlands (52°30'N, 5°01'E)	0	1999 1998	20.8 18.6 (17.7–21.9)	8.0 8.5	74 13	<0.005 0.03	295 <2	470 30	91 5	Negligible Sparse	<i>Ceratophyllum demersum</i> <i>Chara aspera</i> Deth ex Willd.	<i>Gasterosteus aculeatus</i> <i>Scardinius erythrophthalmus</i> L.
Sentiz	Northern Spain (42°33'N, 5°22'W)	930	1999 1998	22.4 23.0 (19.0–22.5)	9.6 8.4	19 30	0.01 0.05	3.5 2	30 100	9 nd	Abundant Sparse	<i>Chara aspera</i> <i>Myriophyllum alterniflorum</i> DC. <i>Myriophyllum alterniflorum</i> , <i>Ceratophyllum demersum</i>	<i>Scardinius erythrophthalmus</i> <i>Chondrostoma arcasii</i> Steindachner <i>Chondrostoma arcasii</i>
Xeresa	Southern Spain (39°6'N, 0°20'W)	10	1998	28.7 (28.4–29.2)	8.9	27	0.0014	1	17	3	Abundant	<i>Chara hispida</i> L., <i>C. vulgaris</i> L. C. <i>aspera</i> <i>Chara hispida</i> , C. <i>vulgaris</i> , C. <i>aspera</i>	<i>Gambusia holbrooki</i> Girard (ex Agassiz) <i>Gambusia holbrooki</i>

SRP, soluble reactive phosphorus; TP, total phosphorus; nd, not determined.

Initial density of submerged plants was estimated visually as: negligible = very few plants present, more than 75% of the bottom bare; sparse = between 25 and 75% of the bottom covered with plants; abundant = all of the bottom covered, confluent growth.

Samples were taken a week after the treatments had begun, and subsequently every week, just prior to the nutrient addition. The open lake was sampled on the same dates. Dead fish in mesocosms were replaced where this involved occasional individuals, but not in one instance (Finland, 1998) where the mortality was complete and associated with the treatment. The inside walls were lightly brushed in 1998 whenever the mesocosms were visited (several times each week, but not on days when nutrients were added) to minimise periphyton build-up. Water temperature was determined on a random subset of mesocosms during the weekly sampling.

A common set of 29 chemical, primary producer and zooplankton variables was determined. Chemical variables were: total phosphorus ($\mu\text{g L}^{-1}$), soluble reactive phosphorus ($\mu\text{g L}^{-1}$), nitrate-N (mg L^{-1}), ammonium-N ($\mu\text{g L}^{-1}$), pH, alkalinity (meq L^{-1}), total suspended solids (mg L^{-1}), the latter two in 1998 only. Primary producer variables were largely phytoplanktonic, except for periphyton chlorophyll *a* ($\mu\text{g cm}^{-2}$) and included chlorophyll *a* ($\mu\text{g L}^{-1}$), total phytoplankton biovolume ($\mu\text{m}^3 \text{L}^{-1}$; equivalent to biomass in $\mu\text{g} \times 10^{-6} \text{L}^{-1}$, if a specific gravity of 1 is assumed), and biovolumes of Chlorophycota, Cryptophyceae, Bacillariophyceae, Cyanobacteria, Chrysophyceae, Dinophyceae and Euglenophycota ($\mu\text{m}^3 \text{L}^{-1}$), Shannon–Wiener (Weaver) diversity index (bits per individual), biovolume of small algae with their Greatest Axial or Linear Dimension (GALD) $<50 \mu\text{m}$ ($\mu\text{m}^3 \text{L}^{-1}$), and biomass of larger algae (GALD $>50 \mu\text{m}$) ($\mu\text{m}^3 \text{L}^{-1}$). Zooplankton variables were biomasses ($\mu\text{g L}^{-1}$) of total zooplankton, total rotifers, Cladocera

$<500 \mu\text{m}$, Cladocera $>500 \mu\text{m}$, cyclopoid copepods, calanoid copepods, nauplii, raptorial zooplankton, and open-water filterers.

Methods were standardised and results were analysed in uniform ways so that comparisons could be made across sites. Workshops and written, agreed protocols ensured that almost all analyses and procedures were completed in each laboratory in the same way. Inter-laboratory comparisons for water-chemical analyses were made to promote uniformity of results. The observed deviations in samples preserved with mercuric chloride (Table 2) were small enough to make misleading interpretations unlikely, but were greater than is commonly assumed. Inter-comparability generally improved with increasing experience. Similar conclusions have been drawn in other, more extensive inter-comparisons (Marchetto *et al.*, 1997).

Professional advice was taken in the selection of statistical analyses and an agreed outcome arrived at. Pretreatment data sets were tested for uniformity by one-way analysis of variance (ANOVA). The experiments were designed to be analysed by repeated-measures ANOVA. However, the distributions obtained for many variables proved not to meet the requirements of parametric tests, even after various transformations. A variety of mixed models applied to the same data sets gave disparate results when applied to data sets that did meet the conditions of repeated-measures ANOVA. Uniformity among results was obtained, however, when time-weighted averages (with log, square root, or arcsine transformations to achieve normal distributions of some data that were

Table 2 Cross-laboratory comparisons of analyses on standard water samples for some water chemistry variables. Common samples were taken from the indicated lakes and analysed in the laboratories of each of the six participants in the International Mesocosm Experiment by largely common methods.

Variable	Source of water											
	Little Mere, England (27 April 1998)			Vesijarvi, Finland (9 July 1998)			Xeresa, southern Spain (10 October 1998)			Zwemlust, Netherlands (17 December 1998)		
	Mean	Range	CV (%)	Mean	Range	CV (%)	Mean	Range	CV (%)	Mean	Range	CV (%)
SRP ($\mu\text{g L}^{-1}$)	7.2	5–13	41	15	9–18	22	5.2	2–10	60	360	320–396	8.1
TP ($\mu\text{g L}^{-1}$)	53	34–139	79	58	45–74	17	20.7	9–42	57	483	345–502	15
NH ₄ -N ($\mu\text{g L}^{-1}$)	49	14–87	55	22	0–50	105	29	15–50	45	2150	1060–2800	32
NO ₃ -N (mg L^{-1})	1.3	0.4–1.8	46	0.06	0.006–0.19	117	0.115	0.002–0.39	139	0.112	0.1–0.13	8.9
Total alkalinity (meq. L^{-1})	1.19	1.0–1.5	17	0.59	0.49–0.7	12	3.3	3.2–3.4	2.7	4.3	4.13–4.39	2.3

TP, total phosphorus; SRP, soluble reactive phosphorus; TSP, total soluble phosphorus.

skewed) were used in ANOVAS and results compared with those of repeated-measures ANOVA on data sets that met its requirements. Time-weighted averages were calculated by multiplying the values measured in each week by the week number (e.g. 1–6 in 1999) and dividing the sum of these by the sum of week numbers (i.e. by 21 in 1999) (Hansson *et al.*, 2004). These weighted averages thus give greater emphasis to data points obtained with increasing time after the start of experiments.

Outcome

The results of the eleven individual experiments at first sight appeared random with respect to any obvious pattern based on likely geographical gradients. The occurrence of significant effects of fish addition or nutrient addition frequently differed between years in a given location. For example, in Finland, both nutrient addition and fish addition resulted in a turbid state in 1998 whilst fish had little effect in 1999, yet a clear-water state was maintained even with high nutrient additions (Hietala *et al.*, 2004). The difference appeared because of differing starting conditions, with sparse aquatic plants in 1998 and abundant in 1999 when they provided refuges for zooplankton grazers.

In contrast, in England (Stephen *et al.*, 2004), a clear-water state was destroyed in 1998 owing to fish predation on the zooplankton, but nutrients were not important. In 1999, fish addition had no effect in a system that began turbid and continued so. In neither year did the macrophyte community develop as anticipated, but starting nutrient concentrations were high in 1998 and very high in 1999. The experiments in the Netherlands (Van de Bund & Van Donk, 2004) likewise showed differences between years, fish addition being important in 1998 in creating turbid conditions but such conditions occurring in 1999 irrespective of fish addition, and resulting in loss of macrophytes. Temperatures were higher in 1999 than in 1998 in four sites, including all the northern ones. Results of experiments in northern Spain (Fernández-Aláez *et al.*, 2004) also differed between years, both fish and nutrients having significant effects in 1998, but not in 1999 when plant density began much higher and was maintained during the experiment. Nutrients had major effects on phytoplankton turbidity in southern Spain (Romo *et al.*, 2004) but fish

addition, despite major impacts on zooplankton, did not affect the phytoplankton biomass.

Despite the apparent randomness of these effects between years, quantification of the relative importance of fish and nutrient additions through an inspection of the numbers of their effects on the common suite of 29 chemical, primary producer and zooplankton variables, did reveal patterns (Moss *et al.*, 2004). There were relationships with temperature, latitude, and starting macrophyte density that could be explained in terms of greater and more consistent over-wintering biomass of macrophytes, and their sequestering of nutrients, with decreasing latitude. Moreover, comparison with a baseline set of results obtained from treating the separate experiments as blocks of a meta-experiment, and of results between years in the separate locations, showed a pattern of increasing unpredictability with increasing latitude and this could be related to more variable weather and its impact on starting conditions.

We also sought patterns in the communities of phytoplankton (Van de Bund *et al.*, 2004) and zooplankton (Vakkilainen *et al.*, 2004). Phytoplankton biomass was influenced much more by nutrients than fish, with increases being found with increasing nutrient loading in all locations, although fish shifted the community composition towards smaller algae, especially chlorophytes and cyanobacteria, presumably by removing large grazers that would otherwise have fed on these small species. The contribution of cyanobacteria also increased with increasing temperature.

Fish had their greatest effect on zooplankton communities (increasing the biomasses of smaller cladocerans and rotifers and decreasing that of large cladocerans) and little effect overall on water chemistry. However in contrast to the patterns obtained for phytoplankton, there was no latitudinal gradient in zooplankton communities, only a strong and consistent reduction in large crustacean grazers in southern Spain. This might hint at a latitudinal gradient in which fish predation is so severe in low latitude lakes that effective zooplankton grazer communities cannot persist, but our experiment had insufficient low latitude lakes to confirm this. Analysis of one experiment (Hansson *et al.*, 2004) particularly at different taxonomic levels, showed considerable predictability of effects from food web theory at the levels of zooplankton and phytoplankton biomass but not at finer taxonomic levels. This

does not necessarily imply that community details are of little concern, for our experiments were established to manipulate variables at the biomass level. We were able to perceive some order in phytoplankton community response at the level of algal Division or family but not at all at finer levels such as species. The degree of variability in relative effects between years, however, does suggest that attempts to use community composition to reflect ecological quality of shallow lakes, as might be proposed for monitoring for the purposes of the European Water Framework Directive, may be doomed to failure.

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