

Relationships between fish feeding guild and trophic structure in English lowland shallow lakes subject to anthropogenic influence: implications for lake restoration

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Received: 25 October 2004 / Accepted: 27 February 2006 / Published online: 9 May 2006
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Abstract The shallow lakes of Eastern England have been subject to intense anthropogenic pressures including nutrient enrichment and fish stocking. We sought to determine the relationships between fish community structure and other ecosystem characteristics in 28 of these lakes through classification of fish species into piscivorous, zooplanktivorous and benthivorous feeding guilds according to the literature. Canonical correspondence analysis produced clear associations between fish and ecosystem characteristics that generally agreed with other theoretical (e.g. the alternative stable states hypothesis) and empirical studies, but with some important differences. There was a striking lack of relationships between nutrients and other variables, indicating the importance of top-down rather than bottom-up processes as a structuring force in the generally eutrophic study lakes. The

presence of submerged (and shoreline) vegetation was associated with a diverse assemblage of apparently co-existing piscivorous (principally pike *Esox lucius*) and zooplanktivorous species. Perch *Perca fluviatilis*, a significant predator in other studies, was unimportant and argued to be limited by water quality in the extremely shallow lakes. In contrast, the benthivorous fish guild (principally carp *Cyprinus carpio*, bream *Abramis brama* and tench *Tinca tinca*) essentially represented the inverse of the potential pelagic associations between piscivores/zooplanktivores and vegetation. The introduction of large benthivores to many study lakes could have precipitated a loss of submerged vegetation through direct uprooting during foraging, with the effect of simplifying the fish community being most acute where littoral vegetation was limited by other anthropogenic factors. It is implied that attempts to promote or restore submerged vegetation in these lakes would best target benthivorous species.

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Keywords Feeding guild · Trophic interactions ·
Submerged macrophytes · Benthivorous fish ·
Zooplanktivorous fish · Piscivorous fish ·
Lake management and conservation

Introduction

The composition of the fish community has great bearing on lower trophic levels in shallow lakes through both top-down and bottom-up processes

(Brönmark and Weisner 1992; Scheffer 1998; Jeppesen et al. 2000). Different functional groups of fishes have particular impacts. For example, through selective predation on zooplankton a high density of zooplanktivorous fish may significantly reduce or even eliminate large-bodied zooplankton with a consequent reduction in grazing pressure on phytoplankton (Perrow et al. 1999a). A comparable cascade mechanism is generated by predation on grazing invertebrates, which would otherwise regulate densities of plant-associated periphyton (Jones and Sayer 2003). Through foraging amongst bottom sediments benthivorous fish may uproot submerged plants (Zambrano and Hinojosa 1999) or cause significant resuspension of fine material, thereby increasing water turbidity and enhancing the release of nutrients into the water column (Breukelaar et al. 1994). Piscivorous fish may reduce the density and biomass of prey species (Skov et al. 2002), or change their behaviour and habitat use with a potential impact on lower trophic levels (Jacobsen and Perrow 1998).

As a consequence of these processes, the structure of the fish community is of key importance in attempts to restore eutrophic shallow lakes from a turbid to a clear water, submerged macrophyte-dominated state. An ideal community is comprised of a high proportion of piscivorous fish with a corresponding low density of zooplanktivorous and low biomass of benthivorous fish (Perrow et al. 1997). However, it has proved difficult to generalise on the boundaries of stability of different fish communities along gradients of nutrient concentration, macrophyte cover, salinity and even latitude and altitude (Perrow et al. 1999b). An analysis of 71 lakes in Denmark by Jeppesen et al. (2000) showed that at low nutrient concentrations, the fish community was dominated by piscivores whereas benthivorous fish dominated in lakes with higher nutrient concentrations concomitant with a shift to smaller organisms within the zooplankton community. In the UK, there have been very few multi-lake analyses, although those that have been conducted illustrate the importance of fish community structure in determining trophic relationships. For example, in 12 Norfolk Broads a significant portion of the variance in fish community composition was explained by macrophyte cover, total phosphorus (TP) and the limnetic:littoral ratio

respectively (Perrow et al. 1999b). Moreover, in 11 lakes, Smith (2001) suggested a fish biomass threshold between 150 and 250 kg ha⁻¹ above which a submerged macrophyte community could no longer be sustained. Many lakes in the UK have an unnaturally high biomass of fish as a result of stocking for the purposes of recreational angling, to the detriment of water quality and conservation value (Carvalho and Moss 1995; Smith 2001; Moss et al. 2002).

There is a clear need to understand the relationships between fish and lower trophic levels from the perspectives of science, management and conservation. Given the lack of multi-lake studies in the UK especially, we sought to elucidate the key relationships and possible interactions between fish community structure and other trophic levels and system characteristics in 28 shallow lakes in the intensively managed lowland landscape of Eastern England. This was undertaken with an ultimate view to prospective management of particular lakes to maintain and/or enhance conservation value and biodiversity. We chose to use fish feeding guild as a descriptor of general patterns rather than a species-based approach, which in our case was likely to be prone to variation in the abundance of individual species as a result of introduction, exploitation and other management activities.

Study sites

The 28 study lakes are located in Norfolk in Eastern England, a low-lying (<100 m O.D.) arable agricultural region underlain by a mixture of Cretaceous chalk deposits and Pleistocene and Pliocene sands and clays. All sites but one (Saham Mere, a glacial kettle hole) were artificially created through either flooding of medieval peat diggings from the fourteenth century (so-called 'Broads'—Moss 2001) or damming of small streams since the mid-eighteenth century. Sites were chosen from a larger training set of 74 standing waters, to represent a range of nutrient conditions and likely fish abundances. The lakes are small (0.2–22.5 ha.), shallow (<3 m max. depth), flat bottomed and have a variety of current uses including wildfowling, angling and nature conservation, as well as being of integral landscape value to large country estates containing historic houses.

Methods

Fish sampling

Point-abundance sampling by electric fishing (PASE) (Copp and Peñáz 1988; Perrow et al. 1996a; Skov and Berg 1999) was selected to provide quantitative estimates of the fish stock in the study lakes. With this technique, both the limnetic and littoral zones may be effectively sampled even where the former contains dense emergent vegetation and the latter contains dense submerged vegetation (Perrow et al. 1996a). These factors tend to preclude the effective use of standard techniques such as seine netting. The routine use of other sampling methods such as fyke-nets and gill-nets is not allowed on recreational fisheries by the statutory authorities in the UK. Sampling was conducted in late summer/autumn (between 16th August and 25th October) of 1999 in daylight hours, with one lake surveyed over the course of one day. Each survey was conducted from a 3 m fibreglass dinghy manoeuvred by 'push-rowing', with the electrofishing operator positioned at the stern of the vessel. High frequency (600 Hz) pulsed DC electric fishing equipment, powered by a 1.1 KVa generator was used. This gear induces effective galvanotaxis of fish towards the anode at a higher voltage gradient than conventional frequencies of 50–100 Hz, yet has the advantage of decreasing recovery time (Bird and Cowx 1993), and is thought to be less physiologically damaging (Lamarque 1990). The anode used was 3 m in length with a 40 cm ring, which reduced the danger zone close to the anode and thus fish mortality (Novotny 1990). The area of influence (thus allowing a quantitative estimate of density—see Copp and Peñáz 1988) was calculated to be 1.3 m^{-2} , according to the standard two-dimensional area measure adopted in fish density estimation.

At each sample point the anode was rapidly immersed and a lightweight, long handled net was swept through the point collecting all stunned fish even where none were seen. Small catches of a few small specimens were processed in a few seconds before being returned to the water. Larger catches and individuals were temporarily retained in large water-filled containers before being processed. The latter involved identification and the measurement of fork length to the nearest mm of all fish. Large individuals

were weighed using a spring balance, but otherwise the biomass of each fish was estimated using length-weight regression relationships derived from previous extensive sampling (involving around 1000 individuals) in similar water bodies carried out during the same season. Following processing, all fish were returned unharmed to the water.

Samples were taken in a systematic fashion at equidistant intervals (determined by the number of oar strokes) along parallel transect lines covering the entire water surface in the limnetic habitat. The littoral zone, taken as the extent of overhanging or emergent vegetation, was separately but similarly sampled at equidistant sample intervals around the entire perimeter of the lake including bays and small channels. At each point, the width of the littoral was estimated (see macrophyte sampling) in order to allow calculation of its area. The spacing between samples was partly determined by the size of the lake, with the aim to take at least 90 samples overall (average=60 samples ha^{-1}). Separate sampling of the proportionally small littoral zone allowed at least 40 samples to be taken in what may be a structurally diverse habitat that is of considerable importance for many species. Estimates of fish density by number and biomass (wet weight) for both limnetic and littoral zones were combined to produce whole lake estimates by determining the relative area of the littoral to the limnetic zones and adjusting the figures accordingly.

Water chemistry, transparency and chlorophyll-*a* sampling

Water chemistry variables were measured on a monthly or bi-monthly basis ($n=10$) between May 1999 and May 2000. Given the likelihood of low patchiness of water chemistry in small, well-mixed, shallow lakes such as those studied, samples were taken from one central lake location. Water transparency was measured at this location in the principal growth period for submerged macrophytes from May to September using a Secchi disc. Water samples for analysis of TP, nitrate nitrogen (NO_3^- -N) and chlorophyll-*a* were collected in acid-rinsed polyethylene bottles dipped just below the water surface. Samples for NO_3^- -N and chlorophyll-*a* determination were coarse filtered just after collection using Whatman® GF/C (1.2 m) and GF/F (0.7 m) filter papers

respectively. TP was determined by the persulphate microwave digestion method (Johnes and Heathwaite 1992) and NO_3^- -N by the procedure given in Wetzel and Likens (1991). Chlorophyll-*a* was estimated spectrophotometrically by grinding filter papers in c. 90% acetone following Talling and Driver (1961).

Macrophyte sampling

The cover of each submerged macrophyte species in each lake was estimated in early and late summer (June and August) by the plant volume infested (PVI) method (Canfield et al. 1984) calculated as:

$$\text{PVI} = \frac{\%C \times M}{D}$$

where %C is percentage coverage of macrophytes within the lake, *M* is the mean height of macrophytes within the water column and *D* is water depth. On both occasions measurements were made at 25–60 randomly located points covering all parts of the lake. Depending on visibility and water depth, the vegetation was surveyed either using an underwater viewer (bathyscope) or by snorkelling with a PVI point corresponding to an area of approximately 1 m². Average PVI for each lake was estimated by averaging the data for all points on each sampling occasion. The change in mean PVI between June and August (August PVI divided by June PVI) was used to determine the rate of increase/decrease in plant cover (termed macrophyte permanence), over the summer period. The mean width (m) of the littoral margin was estimated from measurements (*n*>40) taken during the fish sampling (see above).

Zooplankton sampling

Zooplankton abundance were determined for both the littoral (Zlm) and open water (Zow) zones of each lake once in August, by which time fish are likely to have exerted any effect of predation (Cryer et al. 1986). The littoral zone was sampled by making three approximately 1 m sweeps in three different parts of the lake edge with a 40 µm plankton net attached to a long-handled pole. In the open water, five samples were taken along a transect from the centre to the edge of the littoral zone. Each sample was comprised of an entire column of water taken by immersing a perspex tube (2.5 m length, 7.5 cm internal diameter)

to the lake bed. Water was fixed in the tube by inserting one plastic bung in the top prior to lifting with another at the bottom just prior to removal from the water. All zooplankton samples were filtered through a 40 µm mesh and pooled for each zone before being preserved with isopropanol. Zooplankters were enumerated using a Sedgewick-Rafter cell on a compound microscope at 40–100× magnification. A known volume of sample was examined until at least 100 individuals of the dominant species were counted.

Statistical analysis

Fish species diversity for each lake was estimated with the Shannon-Wiener index: $H = -\sum p_i \ln(p_i)$ (Hayek and Buzas 1997), where *p_i* is the proportion of biomass of each species found in the fish community. Minimum square linear correlations were performed to determine the relationships between nearest trophic levels (e.g. nutrients vs. phytoplankton, phytoplankton vs. zooplankton, zooplankton vs. fish biomass), as well as TP and fish biomass and water transparency vs. chlorophyll-*a* and PVI.

Fish assemblages were partitioned into benthivorous (B), zooplanktivorous (Z) and piscivorous (P) guilds as specified in the literature (Table 1). Many species are omnivorous and are known to be flexible in terms of diet, switching between different prey items and foraging modes (e.g. perch—Persson 1986) as well as undergoing ontogenetic shifts. For example, perch is reputed to switch from zooplankton to invertebrates and finally to fish as it grows (Persson et al. 1991). However, other studies document very young (<30 mm) (Spanovskaya and Grygorash 1977; Borcherdig et al. 2000) and even larval perch (c.10 mm) (Brabrand 1995) routinely preying on fry of their own and other species. Many species may thus exhibit different diets in different circumstances and accurate classification of the diet of different sizes of fish will rely on detailed dietary studies in each lake sampled. This was beyond the scope of this study and we opted to place fish in feeding guilds that resembled them most, as has been adopted in other studies (e.g. Jeppesen et al. 2000).

Canonical correspondance analysis (CCA) was used to determine the relationships between the biomass of the fish guilds and selected environmental and trophic level variables including lake area (ha.),

Table 1 Classification of fish species recorded according to their principal feeding guild (MFG)

Name	Scientific name	MFG	OFS	Reference
Eel	<i>Anguilla anguilla</i> (L.)	P	I	Golani et al. (1998); Provan and Reynolds (2000)
Common Bream	<i>Abramis brama</i> (L.)	B	Z,O	Bohl (1982); Breukelaar et al. (1994); Vasek and Kubecka (2004)
Common Carp	<i>Cyprinus carpio</i> (L.)	B	O	Scott and Crossman (1973); Adamek et al. (2003); Flik and Vijverberg (2003)
Common Gudgeon	<i>Gobio gobio</i> (L.)	B	Z	Michel and Oberdorff (1995); Declerck et al. (2002)
Common Roach	<i>Rutilus rutilus</i> (L.)	Z	O	Bohl (1982); Williams and Moss (2003); Vasek and Kubecka (2004)
Common Rudd	<i>Scardinius erythrophthalmus</i> (L.)	Z	H	Bohl (1982); Garcia-Bethou and Moreno-Amich (2000)
Northern Pike	<i>Esox lucius</i> (L.)	P	Z,I	Bucke (1971); Skov et al. (2003); Hyvärinen and Vehanen (2004)
Tench	<i>Tinca tinca</i> (L.)	B	O	Michel and Oberdorff (1995); Perrow et al. (1996b); Adamek et al. (2003); Flik and Vijverberg (2003)
Three-spined Stickleback	<i>Gasterosteus aculeatus</i> (L.)	Z	I	Scott et al. (1973); Larson (1976)
Ruffe	<i>Gymnocephalus cernuus</i> (L.)	B	Z	Collette et al. (1977); Bergman (1991)
European Perch	<i>Perca fluviatilis</i> (L.)	P	Z,I	Dörner et al. (2003); Flik and Vijverberg (2003); Svanbäck and Persson (2004)

Other potential food sources (OFS) as a result of potential ontogenetic shifts and/or local conditions are also mentioned. B=Benthivorous, P=Piscivorous, Z=Zooplanktivorous, I= Insectivorous, H= Herbivorous and O=Omnivorous

nutrient level (average TP and NO_3^- -N), zooplankton in the open water (Zow) and littoral margin (Zlm), phytoplankton abundance as average chlorophyll-*a* (Cha), average water transparency from June to September (Tra), macrophyte permanence (PVIP), submerged plant species richness (SpM) and littoral margin width (LM). Initial data exploration demonstrated that no variable showed collinearity and the fish community response to most of the explanatory variables was generally unimodal, reinforcing the selection of CCA. Moreover, there was no discernible effect upon the results of CCA of assigning all small (<5 g) individuals of every species to the zooplanktivorous guild. Those variables that failed normality were transformed with logarithmic, square or cubic root transformations depending of the type of dispersion they presented. To test the explanatory significance of individual variables *F* tests were applied using forward selection and 1000 permutations. Multiple linear regressions were used to determine which variables were best related to fish guild biomass. This included the relationships between the different fish feeding guilds and fish diversity (DI). A backward selection procedure was performed to produce a parsimonious model. Starting with the full model including all explanatory variables, Akaike's Information Criterion (AIC) was used to assess the change in model performance resulting from excluding individual explanatory variables. At each

step in this procedure the change in AIC compared to the current model was evaluated and the model that results in the lowest AIC was selected. Validation tests for each equation were produced by QQ plots, and Cook's distance test. All statistical analyses were undertaken using Brodgar 2.4.2 (2004).

Results

Lake characteristics

All lakes were small (maximum of 22.5 ha. for Narford), with the majority between 1–8 ha. and only three exceeding 10 ha. (Table 2). The lakes were generally of rather high transparency with a mean value of 1.06 m (i.e. close to the mean depth of 1.27 m). The more turbid lakes still had mean values in the range 0.5–0.6 cm including Big Wood, Burntfen, Cromes, Decoy and Haveringland. These contrasted with Lowes Pond, Narford, Wolterton and Green Plantation where the Secchi disc was consistently visible on or near to the lake bed. This was to nearly 3 m in Green Plantation, one of the deeper lakes. The water quality of the lakes varied considerably with TP ranging between 30–489 $\mu\text{g l}^{-1}$, NO_3^- -N from non-detectable to 3.6 mg l^{-1} , and chlorophyll-*a* from 2.9–63.9 $\mu\text{g l}^{-1}$ (Table 2). Saham was an outlier with the highest TP (around

Table 2 Limnological data for the twenty-eight Norfolk shallow lakes

Site	Key	Area Ha.	Depth cm	TP mg l ⁻¹	NO ₃ ⁻ -N mg l ⁻¹	Chl μg l ⁻¹	Tra cm	PVI June %	PVI Aug. %	PVIP	LM m	SpM	Zow Ind l ⁻¹	Zlm Ind l ⁻¹
BAYFIELD	BY	2.7	108.8	241	2.4	7.1	108.8	21.4	18.7	0.9	3.4	14	446	2168
BEESTON	BE	2.6	87.3	105	0.8	19.0	87.3	46.3	25.2	0.5	3.9	14	122	613
BIG WOOD	BW	2.0	109.4	113	2.6	50.9	64.8	7.3	8.5	1.2	16.4	5	269	264
BLICKLING	BL	10.1	137.3	102	0.8	45.4	53.5	13.7	0.8	0.1	3.1	9	149	1113
BLUESTONE	BU	3.6	152.0	41	0.7	12.7	152.0	15.2	21.5	1.4	17.2	9	82	297
BUCKENHAM	BK	0.4	132.8	87	1.2	41.4	132.8	7.6	10.4	1.4	1.8	14	453	1284
BURNTFEN	BR	4.7	138.1	116	1.0	63.9	53.3	10.2	10.2	1.0	4.0	4	543	1692
COCKSHOOT	CS	5.1	88.6	72	0.1	21.3	88.5	11.3	4.6	0.4	2.2	7	471	170
CROMES	CM	4.4	75.2	249	0.6	33.4	59.0	20.6	16.0	0.8	4.1	7	200	2658
DECOY	DC	9.4	170.9	120	1.2	36.3	65.5	0.0	0.0	0.0	2.4	4	324	328
FELBRIGG	FL	2.7	117.5	107	1.3	14.9	89.3	47.9	0.0	0.0	7.2	8	288	73
GREEN PLANTATION	GP	1.6	303.3	31	0.9	2.9	303.3	44.6	21.9	0.5	4.6	13	64	999
GUNTHORPE	GN	1.7	124.8	65	0.7	44.1	124.8	19.4	17.5	0.9	1.9	7	475	121
HAVERINGLAND	HV	4.7	78.5	65	2.2	36.6	52.8	0.0	0.0	0.0	2.2	1	619	5529
HOLKHAM 1	HK	0.8	119.0	44	3.6	3.9	99.0	27.3	2.1	0.1	1.7	9	220	2912
HOLKHAM 2	HK2	14.7	94.1	58	1.9	14.4	84.0	6.2	0.8	0.1	3.6	6	369	1576
LILY	LI	8.1	149.2	148	0.3	5.2	136.0	0.0	0.0	0.0	7.3	9	1311	1121
LOWES	LP	0.5	162.1	40	2.8	8.1	162.3	2.2	0.0	0.0	4.5	6	1053	21994
MELTON CONSTABLE	MC	7.4	145.8	154	0.1	32.1	145.8	24.4	2.9	0.1	4.4	8	172	4356
NARFORD	NR	22.5	177.8	34	2.5	3.7	177.8	9.7	9.6	1.0	2.4	6	27	4034
PEDHAM	PD	3.1	114.1	165	1.7	45.4	61.0	3.8	3.8	1.0	5.0	3	159	2266
SAHAM	SM	5.3	160.4	490	0.0	49.2	60.8	0.0	0.0	0.0	13.6	2	382	14365
SALHOUSE LITTLE	SL	1.2	100.1	76	2.1	22.1	92.8	31.2	31.2	1.0	4.0	10	304	145
SCOTTOW	SC	1.0	103.0	72	0.1	9.1	103.0	52.9	38.6	0.7	13.0	6	296	150
SELBRIGG	SB	1.0	112.5	35	0.1	8.0	90.0	37.3	23.8	0.6	27.6	13	673	2452
STRADSETT	ST	8.3	128.5	166	1.1	12.5	128.3	64.0	5.2	0.1	2.2	8	618	1148
STRUMPSHAW	SP	2.8	96.0	174	0.1	21.5	96.0	27.4	40.7	1.5	3.0	12	801	2319
UPTON	UP	6.9	99.9	32	0.1	7.4	90.3	6.2	53.2	8.5	4.9	6	421	6104
Mean		5.0	127.2	114	1.2	24.0	105.8	19.9	13.1	0.8	6.1	7.9	404	2938
Min.		0.4	75.2	30	0.0	2.9	52.8	0.0	0.0	0.0	1.7	1	27	73
Max.		22.5	303.3	489	3.6	63.9	303.3	64.0	53.2	8.5	27.6	14	1311	21994

TP=mean annual total phosphorus, NO₃⁻-N=mean annual nitrate nitrogen, Chl=mean annual chlorophyll-*a*, Tra=summer transparency measured as Secchi-disc depth, PVI = macrophyte percentage volume infested score, PVIP=PVI permanence (June PVI/August PVI – see text), LM=mean width of littoral margin, SpM=plant species richness, Zow=open water zooplankton, Zlm=littoral zooplankton

double the concentration of the second highest) but the lowest NO_3^- -N concentration. There were only two significant correlations amongst water quality variables both involving chlorophyll-*a* (*Cha*): with phosphorus ($Cha=15.91+0.07 (TP)$; $r^2=0.14$, $p<0.05$) and with transparency ($Tra=144.3-1.6 (Cha)$; $r^2=0.29$, $p<0.01$).

The width of the littoral zone occupied by macrophytes (LM) was around 3 m on average, with only five lakes having a mean value in excess of 10 m. A total of 39 species of submerged and emergent macrophyte were recorded, with 26 species found in the limnetic zone and 21 submerged species. The maximum number of macrophyte species recorded in a lake was 14 (Buckenham, Bayfield and Beeston) with only one species recorded at Haveringland. Four lakes (14%) supported no submerged macrophytes at all and of the remaining 24, 15 (62.5%) showed a reduction in macrophyte density between June and August (PVI permanence) (Table 2). Fourteen lakes (50%) supported PVI values $>20\%$ at peak and three lakes (Scottow, Stradsett and Upton) had a PVI of $>50\%$. Zooplankton abundance was generally lower in the open water than in the littoral margin (Table 2).

Fish species and densities

Eleven species (with one hybrid) of fish were recorded (Table 3). The highest species richness in any one lake was nine (Bayfield and Burntfen). In contrast, both Holkham lakes each contained only two species. Accordingly, Bayfield had the highest Shannon diversity index for fish and the two Holkham lakes the lowest (Table 3). There was no relationship between the number of fish species and lake area. Overall mean fish biomass in the lakes was 17.35 g m^{-2} but this varied considerably with Holkham 1 and Blickling having mean values of $>60 \text{ g m}^{-2}$, whilst Green Plantation and Narford had below 1 g m^{-2} of fish. This was not explained by nutrient status as neither biomass (g) nor numerical density were related to TP.

Roach and bream were the most numerically abundant species overall with a mean value around 0.2 ind m^{-2} . However, this was partly caused by the high abundance of these species in a few lakes (especially Haveringland and Selbrigg). Tench and rudd were next numerous at 0.15 ind m^{-2} , with the

rest of the fish species much less abundant with mean values $<0.07 \text{ ind. m}^{-2}$. Piscivorous species were the most widespread, with pike present in 78% of lakes, followed by eel in 75% and perch in 61%. Almost 30% of the species were considered uncommon through presence in three or less ($<11\%$) of the lakes (Table 3).

Relationships between fish and other trophic levels

The first two axes in the CCA explain almost 50% of between-lake variation in the fish community with the majority of this (45%) explained by axis one. Parameters related to macrophytes (LM, SpM and PVIP) appear to explain most of the variance within the analysis, with littoral margin width significant as a conditional effect ($F=3.92$, $P=0.05$; 4.792 , $P=0.04$ respectively). Plots show a clear separation between those lakes dominated by benthivorous fish (Felbrigg and Holkham 1) and those dominated by zooplanktivorous (Big Wood, Scottow and Gunthorpe) and piscivorous fish (Narford and Buckenham) (Fig. 1).

Lakes dominated by piscivorous and zooplanktivorous fish showed similar trends with the former especially related to macrophyte permanence and the number of macrophyte species, whilst the latter was most closely related with chlorophyll-*a* and water transparency. The benthivorous guild was thus negatively related with all aforementioned variables but appeared to be positively related to NO_3^- -N and zooplankton in the littoral margin (Fig. 1).

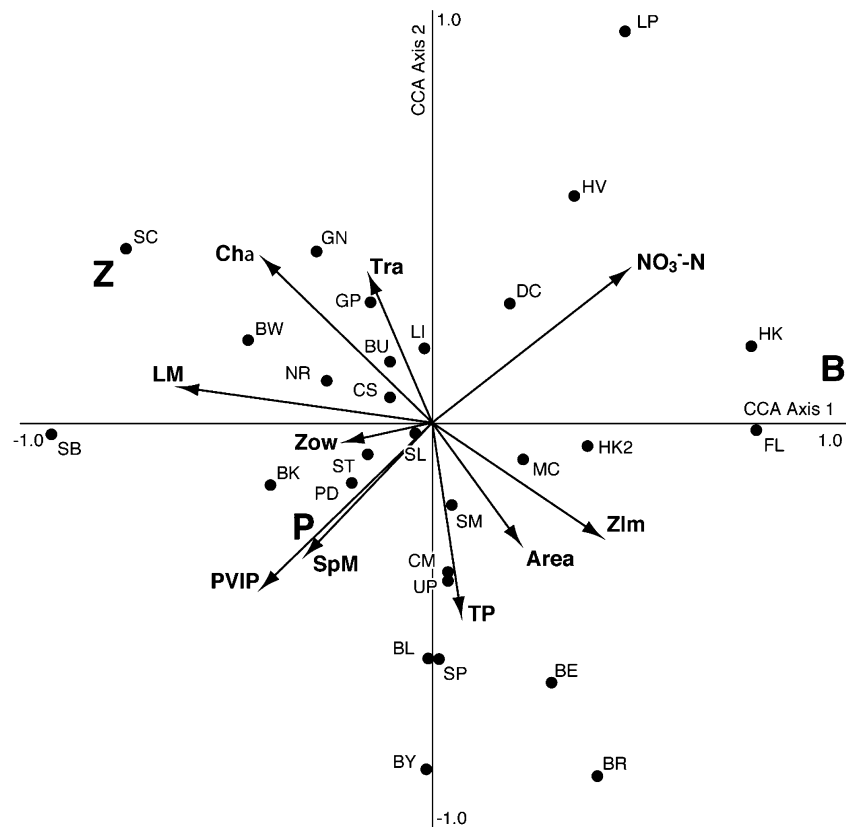
Backwards selection with AIC in the multiple linear regressions gave four to six different explanatory variables for the biomass of each fish guild with all equations significant. The majority of the variables in the *t*-test were also significant (Table 4). Validation with Cook's distance test gave values below 0.6 in the three regressions, and QQ plots did not show any significant trends. The zooplanktivorous guild was positively related to littoral margin width, chlorophyll-*a*, zooplankton abundance in the open water and negatively related to zooplankton abundance in the littoral margin. The piscivorous guild was positively related to the same variables, but including the number of submerged macrophyte species, and negatively related to water transparency as well as zooplankton abundance in the littoral margin. The piscivorous and zooplanktivorous guilds thus appeared

Table 3 Fish biomass (as wet weight in g m^{-2}) and diversity in the twenty-eight study lakes

Species & feeding guild	Gudgeon	Carp	Tench	Bream	Ruffe	Rudd	Roach	Roach× Rudd	3 spined stickleback	Perch	Eel	Pike	Total Biomass	Shannon diversity	Species richness
	Benthivorous					Zooplanktivorous					Piscivorous				
	Site														
BAYFIELD*	0.01	0.01	0.00	0.00	0.03	0.00	0.15	0.00	0.01	0.09	1.00	3.14	4.43	0.85	9.00
BEESTON	0.00	0.00	1.65	0.00	0.00	0.31	0.01	0.00	0.00	2.18	10.29	0.54	14.98	0.98	6.00
BIG WOOD*	0.00	0.00	0.00	0.00	0.00	5.63	6.74	0.30	0.00	0.00	0.00	28.97	41.64	0.85	4.00
BLICKLING	0.00	5.77	0.01	0.32	0.00	0.00	0.16	0.00	0.00	0.13	6.15	51.03	63.57	0.68	7.00
BLUESTONE	0.00	0.00	0.00	0.00	0.00	3.74	4.76	1.16	0.00	0.00	0.00	1.01	10.67	1.19	4.00
BUCKENHAM	0.00	0.00	0.00	0.03	0.00	0.15	4.64	0.00	0.00	2.99	2.24	1.06	11.10	1.34	7.00
BURNTFEN	0.01	0.00	0.00	0.00	0.02	0.63	3.28	0.00	0.00	3.21	2.59	6.36	16.12	1.45	9.00
COCKSHOOT	0.00	0.00	0.02	0.00	0.54	0.12	1.59	0.00	0.00	0.74	0.59	1.28	4.88	1.62	8.00
CROMES	0.00	0.00	0.88	0.26	0.04	0.87	0.27	0.00	0.00	1.29	0.00	0.25	3.86	1.63	7.00
DECOY	0.01	0.00	0.00	0.01	0.01	0.00	0.74	0.00	0.00	0.13	1.12	0.12	2.13	1.11	8.00
FELBRIGG*	0.00	0.00	8.04	0.00	0.00	1.97	0.00	0.00	0.00	0.00	0.00	21.52	31.53	0.78	3.00
GREEN PLANTATION	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.28	0.04	3.00
GUNTHORPE	0.00	0.00	0.06	0.07	0.00	0.00	4.48	0.00	0.00	0.63	0.88	2.23	8.36	1.20	6.00
HAVERINGLAND*	0.00	0.00	0.00	37.66	0.00	0.20	0.33	0.00	0.00	0.34	0.13	3.37	42.04	0.42	8.00
HOLKHAM 1 *	0.00	64.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	64.80	0.04	2.00
HOLKHAM 2	0.00	0.00	20.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00	20.71	0.09	2.00
LILLY	0.00	0.00	0.00	0.15	0.12	0.05	0.00	0.00	0.00	0.65	0.15	2.84	3.96	0.95	7.00
LOWES POND	0.00	0.00	0.00	0.00	0.00	0.04	0.46	0.00	0.00	4.01	0.11	0.00	4.61	0.48	4.00
MELTON CONSTABLE	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	1.10	0.04	3.00
NARFORD*	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.74	0.00	0.88	0.53	3.00
PEDHAM*	0.00	0.42	0.00	0.00	0.00	0.12	1.60	0.00	0.00	0.16	0.70	6.67	9.66	1.00	6.00
SAHAM*	0.00	6.86	0.00	0.06	0.00	0.05	0.16	0.00	0.00	0.00	3.29	0.63	11.05	0.93	6.00
SALHOUSE LITTLE	0.01	0.00	0.00	0.02	0.07	0.01	1.95	0.00	0.00	0.90	0.00	33.46	36.43	0.35	7.00
SCOTTOW*	0.00	0.00	7.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.71	8.73	16.82	0.84	4.00
SELBRIGG	0.00	0.00	0.02	0.00	0.00	0.00	7.43	0.00	0.00	2.07	0.00	29.90	39.42	0.68	4.00
STRADSETT*	0.00	0.00	0.00	8.15	0.00	0.00	0.01	0.00	0.00	0.00	1.21	3.45	12.83	0.87	4.00
STRUMPSHAW	0.00	0.00	0.00	0.00	0.00	0.00	1.32	0.00	0.00	0.27	2.26	2.87	6.71	1.18	5.00
UPTON*	0.00	0.00	0.24	0.08	0.13	0.00	0.00	0.00	0.00	0.27	0.45	0.00	1.17	1.46	6.00

Lakes where fish introduction is known to have occurred or that are subjected to recreational angling are marked (*)

Fig. 1 Canonical correspondence analysis plot (axes 1 and 2) showing relationships between the biomass of piscivorous (P), benthivorous (B) and zooplanktivorous (Z) fish guilds and selected environmental and trophic variables. For lake's names (given in *italics*) and lake's variables (represented with lines) refer to Table 1



to be similarly coupled to the pelagic phytoplankton-zooplankton food chain. In accordance with the results from CCA, the benthivorous guild showed a different trend with only negative relationships to fish diversity, littoral margin width, water transparency and zooplankton abundance in the open water.

Discussion

Value of the feeding guild classification

To the best of our knowledge the current study represents the most extensive attempt to classify fish communities in shallow lakes in the UK, which have been subject to intense anthropogenic pressures, particularly eutrophication and manipulation of fish communities. Despite the potentially complicating issues of dietary flexibility and switching between different prey items and foraging modes, our approach of assigning fish to feeding guilds as an approximation of functional group produced clear, ecologically meaningful divisions. The use of fish

biomass is likely to have buffered the potential effect of any size-related dietary shifts. For example, assigning all small individuals of the benthivorous and piscivorous guilds to the zooplanktivorous guild made no discernible difference to the results of CCA, as the contribution of small individuals to the biomass of the population of large benthivores or piscivores was negligible (as each adult of 1.5 kg weighs >250 small individuals). Consequently, it is suggested that the approach adopted may prove valuable in datasets with large numbers of functionally similar species and allow comparison of patterns and trends between datasets from different eco-regions with different, but ecologically similar species, as well as disturbed lakes. In our case, the approach helped clarify the potential interactions between fish and other ecosystem characteristics.

Fish feeding guild and trophic structure

In contrast to other studies (e.g. Persson et al. 1991; Jeppesen et al. 2000), there was a notable lack of relationships between nutrients and other trophic

Table 4 Statistics of multiple regressions analyses undertaken using fish guild as an independent variable

<i>F</i>	DF	<i>P</i>	<i>R</i> ₂	Var	<i>t</i>	<i>P</i>
<i>Piscivorous fish</i> : $P=4.64 + \text{Cha} (0.02) - \text{Tra}(2.6) + \text{LM} (0.26) + \text{SpM} (0.1) + \text{Zow} (0.05) - \text{Zlm} (0.1)$						
3.661 on 6	20	0.01	0.38	Intercept	2.55	0.02
				Cha	1.7	0.1
				Tra	2.94	0.01
				LM	1.7	0.1
				SpM	1.95	0.06
				Zow	2.33	0.03
				Zlm	2.192	0.04
<i>Zooplanktivorous fish</i> : $Z=-0.2 + \text{Cha} (0.01) + \text{LM} (0.24) + \text{Zow} (0.03) - \text{Zlm} (0.1)$						
5.244 on 4	22	0.004	0.4	Intercept	0.44	0.66
				Cha	2.13	0.04
				LM	2.13	0.05
				Zow	1.94	0.06
				Zlm	2.64	0.01
<i>Benthivorous fish</i> : $B=7.2 - \text{DI} (0.96) - \text{Tra} (1.91) - \text{LM} (0.37) - \text{Zow} (0.04)$						
2.558 on 4	22	0.067	0.19	Intercept	2.83	<0.001
				DI	2.37	0.03
				Tra	1.78	0.08
				LM	2.06	0.05
				Zow	1.62	0.11

DI=Fish Diversity Index. The remainder of the variable definitions are given in Tables 1 and 2

levels in the study lakes, including overall fish abundance, biomass and community composition. The fish feeding guild classification thus operated somewhat independently of nutrient concentrations. Whilst we accept that sampling for nutrients and primary producers was not undertaken exhaustively, given the substantial nutrient range across the lake set it was anticipated that at least gross patterns would have been discernible. Nutrient concentrations were generally high as illustrated by the occurrence of 75% of the most lakes in the moderate to poor TP classes (i.e. $>50 \mu\text{g l}^{-1}$) derived by S ndergaard et al. (2005a) to describe lake quality. The fact that intensive agriculture dominated the catchments of almost all lakes, few of which could be considered isolated from their potential catchments (as indirectly shown by the widespread presence of the catadromous European eel) with many lakes connected to natural streams as well as artificial drainage channels, may have been ultimately responsible for the generally eutrophic nature of the lakes.

Despite high levels of nutrients, submerged macrophytes were rather well distributed amongst the lakes with half of them containing a moderate PVI (20%). This may be explained by the alternative stable state hypothesis for shallow lakes whereby at intermediate nutrient concentrations, either a turbid

algal-dominated state or a clear-water submerged macrophyte-dominated state may occur (Scheffer et al. 1993). Br nmark and Weisner (1992) postulated that changes in fish community structure, specifically a selective loss of piscivores (e.g. through winter-kill), could precipitate changes in both pelagic (piscivore \rightarrow zooplanktivore \rightarrow zooplankton \rightarrow phytoplankton) and benthic (benthivore \rightarrow grazing invertebrate \rightarrow epiphyte \rightarrow macrophyte) food chains, both combining to reduce macrophyte growth and vigour ultimately leading to their loss. Conversely, the introduction of piscivores and/or the removal of zooplanktivorous/benthivorous species (biomanipulation) are now widely used to induce a shift from the turbid state to the clear water submerged macrophyte dominated state (Jeppesen and Sammalcarpi 2002).

In general, the fish communities of the study lakes were characterised by two types of dominant fish: either piscivorous and zooplanktivorous species, or benthivorous species. At face value, this seems to agree with the differences expected in fish communities between turbid and clear-water lakes (Br nmark and Weisner 1992; Perrow et al. 1997). However, the clear separation between zooplanktivorous and benthivorous species in the study lakes is opposed to grouping them as ‘plankti-benthivorous

species' (typically cyprinids), which tend to increase with nutrient concentrations (Jeppesen et al. 2000; Mehner et al. 2005).

In the study lakes, the similarity of relationships of the zooplanktivorous and piscivorous guilds with trophic variables such as zooplankton abundance, chlorophyll-*a*, water transparency and submerged macrophyte abundance/permanence, suggests that both groups were linked to the pelagic chain of interactions (Brönmark and Weisner 1992). The propensity of zooplanktivorous fish to occur and seemingly co-exist with piscivores in the presence of submerged macrophytes, may be explained by the influence of both submerged macrophytes and the size of the littoral margin (comprised of emergent and overhanging vegetation) upon the resource base and predator-prey interactions. In simple terms, increased cover of vegetation provides more niches for zooplankton (Jeppesen et al. 1998) and macroinvertebrates (Diehl and Kornijów 1998) and thereby prey for a greater diversity of fish species (Persson and Crowder 1998; Scheffer and de Boer 1995). In our small study lakes, the proportionally large littoral zone appeared to complement the effect of submerged macrophytes upon fish diversity and the structure of the fish community. This closely agrees with Perrow et al. (1999b) who showed that the littoral:limnetic ratio along with macrophyte cover were important descriptors of fish community structure in the Norfolk Broads, but contrasts with the findings of Mehner et al. (2005) in substantially larger lakes (50–10531 ha.) where the littoral zone is proportionately small and where modifications to the lake shore environment were of minor importance.

The presence of structure increases the prospects of co-existence between species across trophic levels, stabilising trophic interactions. For example, submerged macrophytes are known to offer refuges for zooplankton against fish predation, allowing grazing cladoceran zooplankton to persist at even moderate to high fish density, depending on the nature of the refuge (Schriver et al. 1995; Stansfield et al. 1997; Perrow et al. 1999b). The emergent vegetation in the littoral margin may also accumulate large concentrations of zooplankton undertaking diel migration to escape predation in the open water (Jeppesen et al. 1998). Such a phenomenon appeared to be in operation in the study lakes with massive density of zooplankton (mostly cladocerans) in some lakes

(Table 2). In turn, large densities of grazing cladocerans in the presence of refuges may partly explain the weak relationship between nutrients and chlorophyll-*a*. Even though chlorophyll-*a* concentrations were influenced water transparency, the latter was generally not thought to be limiting with most lakes having rather clear water.

Moreover, submerged vegetation may also provide a refuge for small zooplanktivorous species such as roach from attack from piscivorous pike promoting their co-existence (Jacobsen et al. 1997). However, in general, pike are likely to benefit both from the presence of zooplanktivorous fish and vegetative cover: small zooplanktivorous soft-bodied cyprinids being the preferred prey (Beyerle and Williams 1968), and vegetation providing cover in which to operate its typical ambush hunting strategy as well as supporting the invertebrate food supply of very young individuals (Bry 1996). The emergent zone of lakes is also known to be of critical importance in mediating cannibalism of young pike by older conspecifics (Grimm, 1983).

Overall, our results concur with those of Jeppesen et al. (2000) in their empirical study of Danish lakes classified along a phosphorus gradient, where pike were also associated with zooplanktivorous fish in more nutrient-rich lakes. In contrast, in nutrient-poor lakes perch was the dominant piscivore. Although several of the lakes in our study fell into the lower two phosphorus categories of Jeppesen et al. (2000) (25% in $<0.05 \text{ mg l}^{-1} \text{ TP}$ and 25% in $0.05\text{--}0.1 \text{ mg l}^{-1} \text{ TP}$), perch only truly dominated (87% of biomass) in one lake (Lowes Pond) and only exceeded 20% of biomass in a further three lakes (11%). This is despite the fact that perch was relatively well distributed (61%) amongst the study lakes, as expected from what is a common fish in the UK. Using anecdotal evidence from catches, Perrow et al. (1999b) suggested perch was formerly more common in the Norfolk Broads comprising some of the study lakes, and that decline occurred as a result of eutrophication and competition with cyprinids in accordance with standard models (e.g. Persson et al. 1991). Interestingly, this does not explain their low biomass in many of the study lakes, which generally offered structured environments in which perch have a competitive advantage over roach as a result of more efficient foraging on plant-associated invertebrates (Diehl 1988). Moreover, there was no correlation

between perch and roach (using lakes in which at least one species occurred; Spearman rank correlations; by number, $n=22$, $r^2=0.19$, $P=0.4$; by biomass, $n=19$, $r^2=0.30$, $P=0.2$) and no clear relationship with nutrients (see above). In another study, Mehner et al. (2005) showed that lake depth was an important factor in explaining the structure of fish communities in German lakes, with perch prevalent in a cold-water community in deeper lakes in excess of 6–8 m. Perch biomass also increased with depth in the lakes studied by Jeppesen et al. (2000) which averaged 3.4 m, again rather deeper than in our study where no lake exceeded 3 m and where mean depth was below 1.3 m. However, there is no obvious mechanistic effect of depth itself and we suggest its interaction with temperature and related variables such as oxygen and ammonia concentrations may be more important. In keeping with the perception of perch as a 'cool-water' species relative to the 'warm-water' cyprinids (Mehner et al. 2005), we postulate that in our very shallow, often enriched study lakes, perch may be more susceptible to fish kills than co-existing cyprinids. This could lead to their reduced abundance despite the presence of apparently suitable habitat.

The potential impact of introduction of benthivorous species

In agreement with Jeppesen et al. (2000) and Mehner et al. (2005), benthivorous fish comprised a distinct community in our study lakes. In contrast to these studies however, there was no link between benthivorous fish and nutrient concentrations or abundance of phytoplankton (chlorophyll-*a*). This is surprising given that a lake dominated by benthivorous fish might be expected to have an increased concentration of suspended solids, nutrients and chlorophyll-*a* (Meijer et al. 1990; Breukelaar et al. 1994; Scheffer et al. 2001, 2003), as a result of the foraging action of the fish and processing within their bodies (Zambrano et al. 1999). Part of the explanation may be that external loading of nutrients from agricultural or human sources may be far more important than internal loading related to a high biomass of benthivorous fish (Søndergaard et al. 2005b) (see above).

A lack of strong links with other trophic levels in regression analyses may be interpreted as suggesting that benthivorous fish did not contribute to important

trophic interactions in our study lakes. However, such was the separation between benthivorous fish and piscivorous/zooplanktivorous fish in CCA that, in general, benthivorous fish represented the inverse of the relationships between piscivorous/zooplanktivorous fish and variables relating to macrophytes. Indeed, closer inspection showed that all lakes with $>5 \text{ g m}^{-2}$ of benthivorous fish ($n=8$) were characterised by few macrophyte species and although 75% contained some macrophytes, these were typically not sustained over the entire summer with permanence values from 0 to 0.7, all below the mean value (Table 2). Some of these lakes exhibited a quite dramatic collapse of aquatic vegetation between June and August. For example, in Stradsett, cover declined from an overall PVI of 64% in June (the highest value recorded in the study) to just 5% by August. Similarly, in Felbrigg, there was no macrophyte cover in August compared to 48% in June.

Whilst the presence and nature of any impact of benthivorous fish upon submerged macrophytes can only be truly assessed through experimental studies, it seems most likely that any effect they may have (given the lack of strong effects on transparency and nutrients-see above) is through direct uprooting when foraging amongst bottom sediments as in the study of Zambrano and Hinojosa (1999). Here, the introduction of carp had a significant negative impact upon submerged macrophytes in small ponds. Introduction of carp is recognised as one of the main causes of loss of biodiversity and water clarity in lakes worldwide (Crivelli 1983; Roberts et al. 1995; Zambrano et al. 2001; Moss et al. 2002). The presence of carp in 21% of our study lakes all result from purposeful introduction of this alien species. Overall, 39% of lakes were known to have been stocked with fish and/or currently subject to intensive recreational 'coarse' (for cyprinids/pike) angling, which typically involves introduction of large benthivorous species (carp, bream and tench) (Table 3). In theory, a decline in submerged vegetation following the introduction of benthivorous fish may precipitate a shift to a turbid state once a critical threshold is exceeded (Zambrano et al. 2001), assuming piscivorous control does not operate. As benthivorous fish are typically introduced at large size, this may be beyond the capability of gape-limited piscivores as even the largest piscivorous species in our study, pike, typically consumes small prey (in the range 5–25 cm —van Densen, 1994).

Any loss of submerged vegetation as a result of the impact of benthivorous fish may be buffered by the alternative presence of a structured littoral fringe of emergent and overhanging vegetation. Where both submerged and littoral habitat is limited, an extremely simple fish community with few or no piscivores may result. It may be no coincidence that of the six study lakes with three species or less, five had benthivorous fish as a major component of fish biomass and a below average mean littoral width of 4 m. We attributed the generally small extent of littoral vegetation in the study lakes (despite the potential for colonization of large areas of these shallow lakes by emergent vegetation), to the cultivation or management of the lakeshore or extensive grazing by cattle, sheep and introduced geese (Mangnall and Crowe 2002).

To conclude, classification of the fish communities into feeding guilds provided clear associations between the different groups and ecosystem characteristics that offered insight into the potential trophic interactions in the shallow lakes of the study region. Considerable variation in submerged vegetation in the typically eutrophic study lakes implied the existence of alternative stable states, which were independent of nutrients and were characterised by two distinct fish communities. Piscivorous and zooplanktivorous guilds appeared to co-exist in diverse communities in the presence of submerged (and shoreline) vegetation. In contrast, the benthivorous fish guild largely represented the inverse of the potential pelagic associations between piscivores/zooplanktivores and macrophytes. It is plausible that the introduction of large benthivores to many study lakes could have precipitated a loss of submerged vegetation through direct uprooting during foraging. The effects of the loss of submerged vegetation on the fish community (as well as other aspects of biodiversity) is likely to be most acute where littoral vegetation was also limited by other anthropogenic factors. It is thought that any attempt to promote or restore submerged vegetation in the study lakes would do well to focus on removal of benthivorous species where they occur or to prevent their introduction where they are currently absent.

Acknowledgements We are thankful for the kind permission of many landowners, land managers/gamekeepers who gave us access to lakes on their property. Thanks also to Eduardo Pérez

García and several anonymous referees for their comments on the manuscript. This research was funded by a NERC fellowship (GT5/98/21/CB) and a NERC small grant (GR8/4350) awarded to C. Sayer.

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