Journal of Applied Ecology 2005
42, 901–909

Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities

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Summary

1. With the implementation of the European Water Framework Directive, the need for studies on European lake fish communities has increased to include lake type-specific fish community features. Although several standardized fish sampling methodologies are available, most previous fish community studies lack a simultaneous consideration of the littoral, benthic and pelagic habitats of lakes.

2. To compare habitat-specific fish communities, we sampled 67 lakes in the north-eastern German lowlands using Norden multimesh gillnets in the benthic and pelagic habitats, and electrofishing in the littoral zone.

3. Standardized catches and diversity of the fish community differed among the three habitats sampled. Species richness and Shannon diversity were higher in benthic and littoral habitats compared with pelagic habitats. Overall, the benthic habitat had the most homogeneous catches and contained the most diverse fish community.

4. Cluster analysis and subsequent indicator value analyses produced substantially different optimum cluster numbers for the three habitat-specific fish communities. Based on the significant differences in fish community composition among the habitats, a simultaneous consideration of numerical fish catches from all habitats was performed using standardized fish abundances.

5. The cluster analysis of the combined abundances resulted in three groups of lakes that were indicated by three fish species. Morphological descriptors (volume, area, maximum depth, mean depth) and descriptors related to the trophic situation (conductivity, total phosphorus) clearly distinguished the three lake groups.

6. All three habitats showed distinct characteristics with respect to either species diversity or relative species' abundances. Our results do not support a conceptual model for all lakes of a gradual succession of fish communities as a result of eutrophication.

7. *Synthesis and applications.* Only simultaneous consideration of all lake habitats will fulfil the requirements of the Water Framework Directive for evaluating the ecological integrity of lakes. A pre-separation into at least two community types according to lake morphology is necessary before the deviation of the present fish community relative to a reference state can be determined.

Key-words: indicator species analysis, lake fish communities, Norden multimesh gillnets, standardized fishing, Water Framework Directive

Journal of Applied Ecology (2005) **42**, 901–909
doi: 10.1111/j.1365-2664.2005.01068.x

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Introduction

The Water Framework Directive (WFD; EU 2000) released by the European Council (Brussels, Belgium) requires the ecological status of lakes with an area of ≥ 50 ha (0·5 km^2) to be assessed with respect to hydrological, morphological (structural) and chemical alterations using, among others, the biotic condition of pelagic phytoplankton, macrophytes, macroinvertebrates and fish. Søndergaard *et al*. (2005) have identified a number of useful indicators of lake quality in the context of the WFD. The WFD requires the comparison of current conditions with a type-specific reference state using standardized methods to obtain the data where available (EU 2000). Fish communities must be assessed using species composition, age structure and abundance data. However, it has not yet been defined how fish community data representing all relevant lake habitats should be obtained and incorporated into these analyses.

To determine the reference state for a community, the WFD recommends a comparison of a given waterbody with another of the same type and region from an undisturbed site, the analyses of historical data, or modelling and expert judgement (EU 2000). However, real reference state waterbodies are rare or unavailable in Europe (as shown for Scottish lakes; Bennion, Fluin & Simpson 2004). Historical data are scarce for most waterbodies and rarely include quantitative data such as species abundance. Modelling the reference state is appropriate only if there is a causal relationship between anthropogenic impact and consequences on biotic communities.

The number of studies that correlate anthropogenic degradation and the ecological state of waters based on fish communities has increased since the development of an index of biotic integrity (IBI) for warm-water streams in the mid-western USA (Karr 1981). In Europe, however, studies assessing the ecological quality of lentic waterbodies through their fish community composition are still surprisingly rare and restricted to Alpine and Scandinavian lakes (Appelberg, Bergquist & Degerman 2000; Gassner, Tischler & Wanzenböck 2003; Tammi *et al*. 2003) and waterbodies in Belgium (Belpaire *et al*. 2000).

General ecological studies on fish community composition of European lakes are more common (Eckmann 1995; Holmgren 1999; Tammi *et al*. 1999; De Leeuw *et al*. 2003), particularly in relation to the impact of (cultural) eutrophication (Hartmann & Nümann 1977; Persson *et al*. 1991; Eckmann & Rösch 1998; Jeppesen *et al*. 2000). These studies show that, with increasing productivity within the lakes, there is a shift from a numerical dominance by Salmoniformes (mainly coregonids) to a dominance by perch *Perca fluviatilis* L. and eventually by cyprinids (mainly roach *Rutilus rutilus* (L.)). More recently, several studies have questioned this conceptual model of fish community succession, and found a cyprinid dominance over a much wider trophic gradient than previously described (Holmgren & Appelberg 2000; Radke & Eckmann 2001; Olin *et al*. 2002; Mehner *et al*. 2005).

Unfortunately, most of the studies differ with respect to their sampling methodology. Some studies report fish biomass whereas others give data on both abundance and biomass. There has also been a broad diversity of fishing gears used, including gillnetting, electrofishing and trawling. Some information on species presence–absence has been obtained from fisheries' yield statistics and local inquiries. Furthermore, the available habitats in lakes have been sampled with differential effort, or incompletely, for example the near-shore zone has not been sampled at all. However, there is consensus that the three main habitats in lakes, namely the littoral, pelagic and profundal zones, contribute to the overall fish community. Littoral zones provide food and shelter for younger and small fish (Werner *et al*. 1983; Fischer & Eckmann 1997; Lewin, Okun & Mehner 2004). Pelagic habitats harbour the adult stages of those planktivores that often dominate the commercial fisheries' yields (Eckmann & Rösch 1998; Holmgren & Appelberg 2000). The deep benthic habitats support the top predators that regulate the biotic interactions over many trophic levels (Persson 1994; Jeppesen *et al*. 1997). In addition, all lake habitats are closely linked by the active migration of fish on diel or seasonal time scales, thus, matter and nutrient fluxes, and biotic interactions, cannot be separated spatially (Schindler & Scheuerell 2002). Therefore, as the fish community composition in the three habitats within one lake may differ substantially, simultaneous consideration of all habitats is needed to provide a reliable picture of the structure within fish communities.

A standardized fishing protocol that allows comparisons of fish communities in identical lake types is highly desirable under the WFD. Recommended methods include gillnets in benthic and pelagic habitats (Appelberg *et al*. 1995; Appelberg 2000) and electricity in the littoral habitats (Perrow, Jowitt & González 1996). However, there is no current method to compare the fish community composition in the three main lake habitats systematically. To this end, we sampled fish communities in 67 lakes of the German lowlands using standardized methods, and combined the protocols towards a simultaneous consideration of all three lake habitats. By comparing diversity and species dominance in all habitats, we aimed to determine whether differences among the habitats were always large enough to support the huge effort required to sample each habitat independently. We used cluster analyses in combination with species indicator analyses to evaluate whether the most appropriate characterization of the lake-wide fish community comes from sampling of certain single habitats, or from an integrated analysis. Finally, the validity of the resulting fish community types was tested independently by comparing several morphological and productivity-related variables of the lake groups.

Materials and methods

SAMPLING

Sixty-seven natural lakes in the north-eastern German lowlands were sampled between May and October 2001, 2002 and 2003 (Mehner *et al*. 2005). The study area corresponds to WFD ecoregion number 14 (Central plains), which is characterized by an altitude of up to 200 m.a.s.l. (EU 2000). The lakes differed strongly with respect to morphology and productivity (see the Appendix).

Fish community data were obtained from the benthic, pelagic and littoral habitats. The benthic habitat refers to the lake bottom in the profundal and near-shore areas with a depth of > 1·5 m. Shallower near-shore areas comprise the littoral zone, whereas the water column from the surface to the bottom represents the pelagic habitat in all lakes with a maximum depth > 6 m. Fish sampling was conducted using stratified random sampling (Appelberg 2000) with Norden multimesh gillnets (Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden) for benthic (length 30 m, height 1·5 m; 12 mesh-size panels, each being 2·5 m long, of 5, 6·25, 8, 10, 12·5, 16, 19·5, 24, 29, 35, 43 and 55 mm) and pelagic (length 30 m, height 3 m; 12 mesh sizes from 5 to 55 mm as given above) habitats, and daytime electrofishing, at six littoral locations per lake representing the major shoreline structures (e.g. reed belt and submerged macrophytes), using a boat and at least a two-person crew (details are given in Mehner *et al*. 2005).

All fish caught were identified and total body length (L_T) was measured to the nearest centimetre. Wet weight (±1 g) was also determined for fish caught by gillnets. Catch per unit effort (CPUE) for gillnet catch was determined as number per unit effort (NPUE) and weight per unit effort (WPUE), both standardized with respect to gillnet area (m^2) and fishing duration (h). NPUE for electrofishing catch was calculated as number of fish per dip.

In most cases, fish were determined to species. Exceptions were made only for coregonids (whitefish *Coregonus* spp. and vendace *Coregonus albula* s.l.; Table 1), as the systematic status of many German populations is still under study (Freyhof 2002). Within cyprinids, hybrids were frequently found, usually of bream *Abramis brama* (L.) and roach. They were considered as ‘species’ in further analyses.

STATISTICAL ANALYSES

The gear-specific NPUE data (littoral, pelagic and benthic habitats) and WPUE data (pelagic and benthic habitats) were arranged into five separate matrices of 58 (pelagic) and 67 (littoral and benthic) lakes × 23–30 species, depending on the total number of species caught in each habitat. The following catch data and diversity indices were calculated for each matrix: mean ± SD of NPUE or WPUE; coefficient of variation (CV; %) of lake totals; average species richness, S; Shannon diversity, H′; and evenness E [= H′/ln(S)] (McCune & Mefford 1999).

Comparisons of habitat-specific fish communities were performed by the multiresponse permutation procedure (MRPP) (McCune & Grace 2002). We used the MRPP with a rank-transformed distance matrix, based on the Sørensen coefficient of similarity distance measure (Legendre & Legendre 1998). The items per group were weighted by *n*/sum(*n*). Comparisons were either made between the three gears simultaneously in the case of NPUE, or between two methods in each possible combination for both NPUE and WPUE.

For further analyses, NPUE and WPUE data were transformed by:

$$x' = \log(x + d) - c \qquad \text{eqn 1}$$

where c is the order of magnitude constant, Int(log(min(x))), min(x) is the smallest non-zero value in the data, Int(x) is a function that truncates x to an integer by dropping digits after the decimal point, and d is the decimal constant, $\log^{-1}(c)$ (McCune & Grace 2002). This transformation tends to preserve the original order of magnitudes in the data and results in values of zero when the initial value was zero.

Grouping of similar lakes was based on hierarchical cluster analyses of each of the separate matrices from the log-transformed NPUE and WPUE data. Fish species caught in less than four lakes (< 5%) were deleted (McCune & Grace 2002). To avoid clustering of single lakes, an outlier analysis was performed within each matrix by using a cut-off value for the average distance of individual lakes of at least 2·3 SD away from the grand mean distance, based on the χ^2 distance measure. This procedure identified two to four extreme outliers in each matrix that were subsequently removed. These outlier lakes were in almost all cases extreme with respect to single morphological or limnological characteristics, such as Lake Rangsdorfer See, the shallowest lake, Lake Schmollensee, with the highest conductivity as a result of brackish water influence, and Lakes Schaalsee and Fleesensee, characterized by surface areas far above average and/or high mean depth with an overall low species number. Cluster analyses were performed by the Ward method using χ^2 distances (recommended in analyses with many zeros because it avoids calculating an incorrect high similarity between two lakes or habitats if both contain no fish of the same species, the double zero problem; Legendre & Legendre 1998).

Species that were most indicative of the cluster groups, and the optimum cluster number for each matrix, were determined by indicator species analyses (Dufrêne & Legendre 1997). The method combines information on the concentration of species abundance or biomass in a particular group (cluster) and faithfulness of occurrence of a species in a particular group. It produces indicator values (IV) of each species that are subsequently tested for statistical significance by a Monte Carlo technique. The optimum number of clusters can be found by maximizing

Table 1. The 33 fish species and one hybrid collected during the study, and the number of lakes in which they were caught in the three sampled lake habitats. A total of 67 lakes was sampled for benthic (gillnets) and littoral (electrofishing) habitats; 58 of these lakes with a maximum depth of > 6 m were sampled for the pelagic habitat (gillnets) as well. Names and authorities based on Freyhof (2002)

Scientific name	Common name	Total number of lakes	Benthic	Pelagic	Littoral
Anguillidae					
Anguilla anguilla (L.)	Eel	65	7		65
Cyprinidae					
Abramis bjoerkna (L.)	White bream	60	58	30	46
Abramis brama (L.)	Bream	67	66	31	61
Alburnus alburnus (L.)	Bleak	57	54	44	36
Aspius aspius (L.)	Asp	4	3	3	1
Carassius auratus (L.)	Goldfish	1			1
Carassius carassius (Bloch)	Crucian carp	2	1		1
Carassius gibelio (Bloch)	Prussian carp	1			1
Cyprinus carpio L.	Carp	10	6		6
Gobio gobio (L.)	Gudgeon	22	17	1	17
Hypophthalmichthys molitrix (Val.)	Silver carp	1	1	1	
Hypophthalmichthys nobilis (Rich.)	Bighead carp	2	1	1	
Leucaspius delineatus (Heckel)	Sunbleak	34	13	4	30
Leuciscus cephalus (L.)	Chub	1			1
Leuciscus idus (L.)	Ide	3			3
Rhodeus amarus (Bloch)	Bitterling	8	3		7
Rutilus rutilus (L.)	Roach	67	67	57	67
Scardinius erythrophthalmus (L.)	Rudd	65	45	16	65
Tinca tinca (L.)	Tench	44	35	2	43
Rutilus × *Abramis*	Hybrid	26	24	4	7
Cobitidae					
Cobitis taenia L.	Spined loach	29	25	1	24
Misgurnus fossilis (L.)	Weather loach	2	2		
Siluridae					
Silurus glanis L.	European catfish/wels	5	2	1	3
Salmonidae					
Oncorhynchus mykiss (Walbaum)	Rainbow trout	1	1		
Coregonidae					
Coregonus spp.*	Whitefish*	5	5	2	
Coregonus albula s.l.†	Vendace†	31	21	31	
Osmeridae					
Osmerus eperlanus (L.)	Smelt	14	12	11	
Esocidae					
Esox lucius L.	Pike	64	47	8	62
Gasterosteidae					
Gasterosteus aculeatus L.	Three-spined stickleback	17	11	5	15
Pungitius pungitius (L.)	Nine-spined stickleback	2	1		2
Lotidae					
Lota lota (L.)	Burbot	25	9	1	22
Percidae					
Perca fluviatilis L.	Perch	67	66	46	67
Gymnocephalus cernuus (L.)	Ruffe	67	67	14	45
Sander lucioperca (L.)	Zander/pikeperch	35	34	16	7

*Whitefish is listed as *Coregonus* spp. because the actual systematic status of each specimen could not be determined as a result of possible former stocking with different species, and because species status is still under study (Freyhof 2002).
†Vendace (*Coregonus albula* s.l.) included *C. albula* (L.) and endemic deepwater cisco for Lake Breiter Luzin (*C. lucinensis* Thienemann) and Lake Stechlin (*C. fontanae* Schulz & Freyhof).

the average significant indicator values per cluster. We performed the calculations on a range of three to 10 clusters.

Morphological and productivity-related variables of the lakes were compared between the resulting lake groups by separate non-parametric Kruskal–Wallis ANOVAS. All multivariate analyses were performed by PC-ORD version 4 (McCune & Mefford 1999) whereas the other calculations were done by SPSS version 9·0 (SPSS Inc., Chicago, Illinois, USA).

Results

A total of 33 species and one hybrid form was caught in the 67 lakes (Table 1). Bream, perch, roach and ruffe were the only species caught in all lakes (for Latin names and authorities see Table 1). Species present in less than four lakes were chub, goldfish, ide, nine-spined stickleback, Prussian carp, weather loach and the rare alien species rainbow trout, bighead carp and

Table 2. Summary of fish catches in the littoral, pelagic and benthic lake habitats and diversity indices (species richness S, evenness E, Shannon diversity H′) obtained from the standardized catches. Units: NPUE from electrofishing, individuals dip^{-1}; NPUE in gillnets, individuals gillnet m^{-2} h^{-1}; WPUE in g wet weight gillnet, m^{-2} h^{-1}

			CPUE			Mean		
Habitat	Lakes	Total species	Mean	SD	CV of totals (%)	S	E	H′
NPUE								
Littoral	67	27	0·172	0·534	122·1	10·4	0·611	1·418
Pelagic	58	23	0·003	0·009	108·6	5·8	0·583	1·020
Benthic	67	30	0·004	0·015	60·3	10·5	0·535	1·237
WPUE								
Pelagic	58	23	0·060	0·181	79·6	5·8	0·645	1·121
Benthic	67	30	0·115	0·341	54·8	10·5	0·623	1·443

silver carp (Table 1). Eel was considered for analysis only from electrofishing data.

Standardized catches and diversity of fish community differed among the three habitats. The species richness and Shannon diversity were higher in littoral and benthic habitats (Table 2) and the CV of CPUE was substantially lower in the benthic habitat. Thus, the benthic habitat had the most homogeneous catches with respect to total abundance and biomass, but contained the most diverse fish community.

The benthic fish community comprised several cyprinids such as bream, bleak, roach, rudd and white bream, which all occurred in at least 45 of the 67 lakes (Table 1). The main predators were frequently found in the benthic area and included perch (66 lakes), zander (34 lakes) and pike (47 lakes). Vendace was caught most often in the pelagic habitat (31 lakes) alongside bleak and roach. Fish found most often in the littoral areas included small species such as bitterling, gudgeon, rudd, spined loach, sunbleak and tench, and predators such as eel, pike and wels (Table 1).

These differences among the three habitats were significant with respect to NPUE (test statistics $t = -90{\cdot}6$, $n = 67, 58, 67$, observed $\delta = 0{\cdot}272$, expected $\delta = 0{\cdot}500$, effect size $A = 0{\cdot}455$, $P < 10^{-7}$). The differences were higher between the littoral and the pelagic ($t = -75{\cdot}2$, $n = 67, 58$, $A = 0{\cdot}437$, $P < 10^{-7}$) and the littoral and benthic habitats ($t = -81{\cdot}6$, $n = 67, 67$, $A = 0{\cdot}457$, $P < 10^{-7}$) than between the pelagic and the benthic habitats ($t = -29{\cdot}6$, $n = 58, 67$, $A = 0{\cdot}133$, $P < 10^{-7}$). The WPUE also differed significantly between pelagic and benthic habitats ($t = -32{\cdot}1$, $n = 58, 67$, observed $\delta = 0{\cdot}430$, expected $\delta = 0{\cdot}500$, effect size $A = 0{\cdot}139$, $P < 10^{-7}$).

In the cluster analyses the average species IV was maximized with 82·6% at six clusters for the WPUE in the benthic habitat. In the other habitats, for both abundance and biomass, the maximized average IV ranged between 54·3% and 74·6% (Fig. 1). Among the 20 species included in this analysis, five were found with significant IV, namely burbot (IV = 100%, $P = 0{\cdot}001$) for group 1, whitefish (IV = 100%, $P = 0{\cdot}001$) and vendace (IV = 43·1%, $P = 0{\cdot}028$) for group 2, carp (IV = 100%, $P = 0{\cdot}001$) for group 3, and sunbleak (IV = 69·1%, $P = 0{\cdot}02$) for group 4. For the remaining

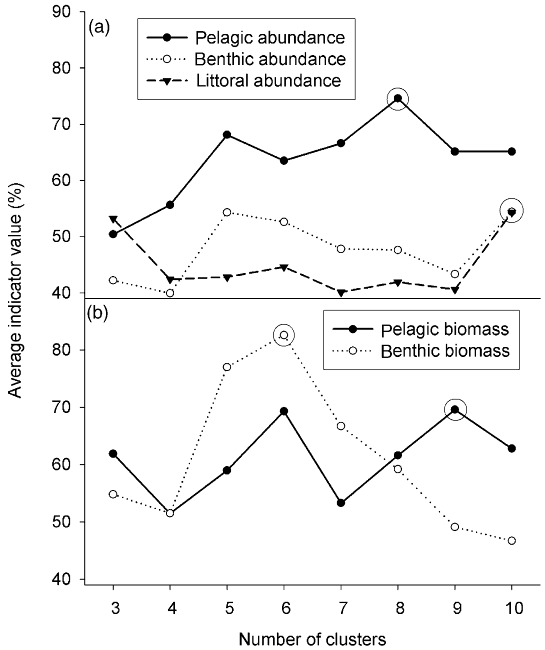

Fig. 1. Average significant indicator values (%) at 3–10 clusters from the fish catches in three habitats based on relative abundances (a) and in two habitats based on relative biomasses (b). The maximum average values per method are circled.

fifth and sixth clusters, no significant indicator species were found.

These results and the significant differences in fish community composition among the habitats indicated that a simultaneous evaluation of numerical fish catches from all habitats should be carried out to test the performance of any indicator values against the data from single habitats. However, the standardized catches from the three habitats were dimensionally different (see the Appendix; Mehner *et al*. 2005). Therefore, we standardized the three primary matrices of NPUE from the littoral, pelagic and benthic habitats by the row (= lakes) maximum, thus achieving dimensional comparability among the relative abundances without losing too much information on relative abundance differences among the fish species within one lake. These standardized NPUE were averaged over the

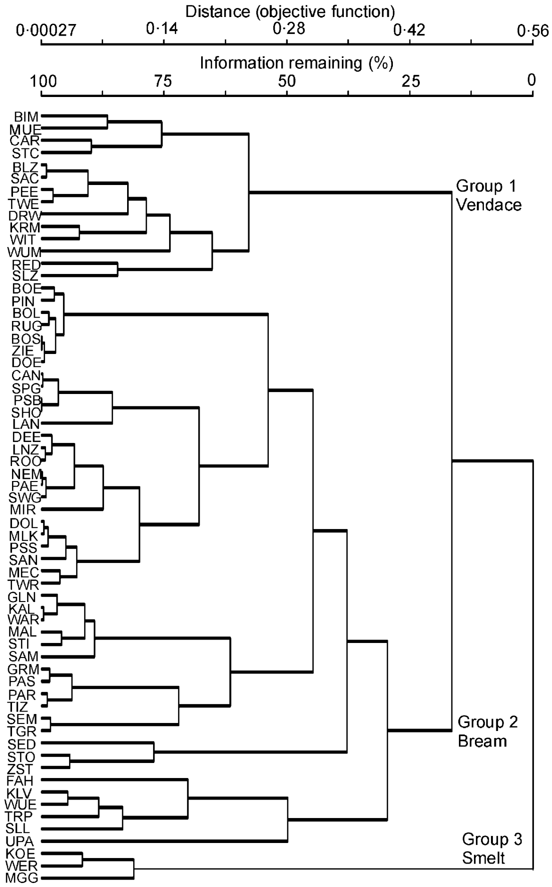

Fig. 2. Cluster dendrogram (χ^2 distance, Ward method) of 63 lakes based on a combination of standardized fish abundances from the littoral, pelagic and benthic habitats. The species characteristics of the three groups suggested by the indicator species analyses are given together with the cluster numbers. For lake codes, see the Appendix.

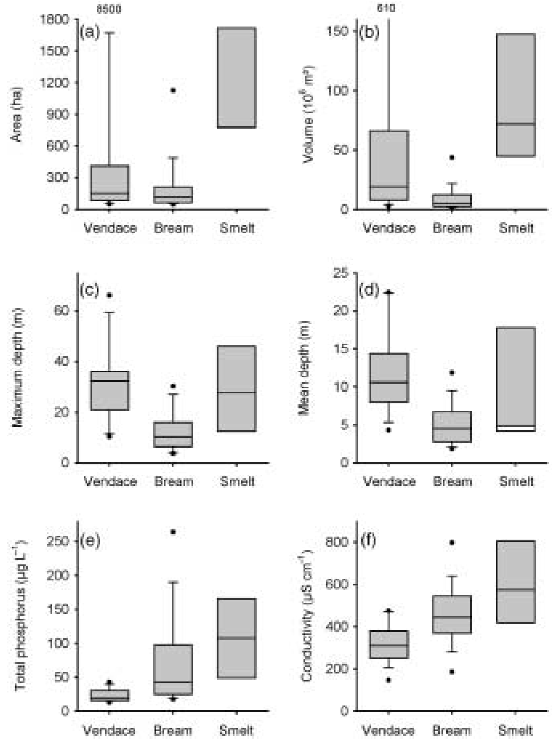

Fig. 3. Boxplots [50th, 75th (box), 90th (whisker) and 95th (dots)] showing the abiotic lake descriptors, separated into three groups according to the results of the cluster analyses in combination with the species indicator analyses. The three groups of lakes are named according to the indicator fish species.

three matrices, and placed into a new primary matrix that was subjected to similar outlier calculations and species removals as above. The final matrix was composed of 63 lakes × 24 species. Repeated cluster analyses in combination with indicator species analyses for three to 10 clusters revealed that the average significant IV was maximized with 87·2% at three clusters (Fig. 2). The resulting three groups of lakes were indicated by vendace (IV = 89·6%, $P = 0{\cdot}001$) for group 1, bream (IV = 78·1%, $P = 0{\cdot}001$) for group 2, and smelt (IV = 94·0%, $P = 0{\cdot}001$) for group 3 (Fig. 2). No significant IV could be calculated for the other 21 species.

The non-parametric Kruskal–Wallis ANOVAs on abiotic lake descriptors (see the Appendix) detected highly significant differences for the three clusters suggested by the IV from the combination of all three habitats. All morphological descriptors clearly distinguished the three lake groups (Fig. 3) (all d.f. = 2; area $\chi^2 = 8{\cdot}28$, $P = 0{\cdot}016$; volume, $\chi^2 = 16{\cdot}3$, $P < 0{\cdot}0001$; maximum depth, $\chi^2 = 18{\cdot}7$, $P < 0{\cdot}0001$; mean depth, $\chi^2 = 16{\cdot}4$, $P < 0{\cdot}0001$). In addition, both descriptors related to the trophic situation were significantly different between the three lake groups (all d.f. = 2; conductivity, $\chi^2 = 13{\cdot}8$, $P = 0{\cdot}001$; total phosphorus, $\chi^2 = 14{\cdot}2$, $P = 0{\cdot}001$).

Discussion

Our analyses clearly revealed that the littoral, benthic and pelagic habitats of lakes harboured substantially different fish communities. Consequently, the combination of catches from all habitats into one relative abundance estimate per species and lake was the best discriminator between groups of lakes. Based on our cluster analyses, the fish community in the 67 lakes sampled in north-eastern Germany could be classified into three main groups, named according to the indicator species as vendace, bream and smelt lakes. This classification was supported by the significant differences in morphological and productivity-related lake descriptors for the three clusters.

As the three main lake habitats contributed differently to the total fish community, we assume that food and refuge availability mirrored a variable degree of structural complexity in the habitats. In the near-shore littoral habitats, highly complex structures such as macrophytes, coarse woody debris and stones provide substrate for food resources for benthivorous species and refuge against predatory fish and birds (Werner *et al.* 1983; Jeppesen *et al.* 1997; Romare *et al.* 2003; Lewin *et al.* 2004). The littoral community diversity may be assumed to be high, as species richness is frequently coupled with habitat diversity (Eckmann 1995; Horppila *et al.* 2000). Indeed, the majority of the rare species, such as chub, goldfish, ide and Prussian carp, were caught exclusively by electrofishing in near-shore areas. Furthermore, many small species, such as bitterling, gudgeon, three- and nine-spined sticklebacks, sunbleak and spined loach, and also the larger rudd and tench, were caught in more lakes by littoral electrofishing than by the benthic gillnets. This was also true for the predators eel, pike and juvenile burbot. The immediate near-shore habitats therefore contributed substantially to the total fish species diversity, and sampling this zone by electrofishing (in addition to gillnet fishing) is strongly recommended if a reliable assessment of species numbers in lakes is required (cf. Eckmann 1995).

Recently, a number of studies have shown that human-made alterations of the riparian and near-shore areas may negatively impact fish species diversity and behaviour (Whittier, Halliwell & Paulsen 1997; Jennings *et al*. 1999; Schindler, Geib & Williams 2000; Scheuerell & Schindler 2004). The near-shore area of lakes is very sensitive to human modifications that may easily translate into shifts in fish community structure. Consequently, an explicit consideration of the near-shore zone is of critical value for correctly correlating anthropogenic degradation and biotic community structure in the context of the WFD.

The benthic habitat (deep littoral and profundal areas) harboured predators such as perch, zander and pike, suggesting a high predation risk in that lake area. Because of the substantially lower physical complexity in the benthic zones compared with the shallow littoral zone, the refuge function of the benthic habitat is limited to those depths where illumination strength is too low for visual hunting. The most abundant benthic species was the ruffe, whose adaptations of the visual apparatus allow it to feed under conditions of low illumination (Bergman 1988). Other potential benthic prey fish species normally grow to a rather large body size, such as bream and roach or the hybrids between them, which makes them less vulnerable to predators in the adult stage. Overall, species richness and diversity were highest in the benthic fish community in comparison with the other two habitats. Accordingly, the benthic community has most often been selected to develop predictive correlations between species composition or diversity and abiotic lake descriptors (Jeppesen *et al*. 2000; Radke & Eckmann 2001; Olin *et al*. 2002).

In the pelagic area, both species richness and diversity were low and catches were mainly confined to species of high commercial interest, such as vendace, perch and zander. However, only the vendace (31 lakes) and smelt (14 lakes) can be considered as typical pelagic species, which were caught most often by pelagic gillnets. The only species that was found in the pelagic area of all 57 lakes with > 6 m maximum depth was roach. Therefore, from the perspective of fish presence–absence studies, sampling in the pelagic habitat may not be necessary because no species was caught exclusively by pelagic gillnets. However, if abundance or biomass is to be correlated among fish species, or if fish data are to be correlated with abiotic descriptors, the inclusion of the pelagic habitat is required. Because of the large hypolimnetic volume of many vendace lakes (see below), vendace is often by far the dominant species (Mehner & Schulz 2002). Therefore, any exclusion of pelagic sampling in deeper lakes (≥ 6 m maximum depth) probably leads to unacceptable errors with respect to relative species abundance. Furthermore, it has been shown that coregonid abundance declines substantially in response to the eutrophication of lakes (Persson *et al*. 1991; Eckmann & Rösch 1998). Therefore, if the ecological integrity of lakes is to be evaluated, these pelagic species need to be adequately reflected in sampling programmes.

The cluster dendrogram obtained from the combined abundances from all habitats (Fig. 2) showed three clearly separated groups of fish communities, whose branches diverged early in clustering. In contrast, most other studies suggest that fish communities show a gradual transition from salmonids to perch towards cyprinid dominance with increasing trophic state (Persson *et al*. 1991; Jeppesen *et al*. 2000). It is possible that the vendace and bream community types found in our study reflect the endpoints of the described successions at either the oligo–mesotrophic or the highly eutrophic end, and that the smelt type deviates only by chance from the other two main types. Indeed, the two descriptors referring to the productivity of the lakes differed significantly if correlated to the fish community type. However, we also found that the morphological descriptors, such as area, depth and volume, differed significantly between all three fish community types, indicating that the fish communities correspond to a different lake morphology. In particular, both the maximum and mean depths only slightly overlapped between the lake groups, thus characterizing the vendace lakes with average depths of > 11 m, whereas the mean depth of bream lakes was *c.* 6 m. Furthermore, it is highly likely that there is a close correspondence between lake productivity and morphology, as most of the shallow lakes have on average higher productivity than deep lakes at comparable phosphorus concentrations (Mehner *et al*. 2005).

Because of this close correspondence between lake type morphology and fish community described by indicator species, clear gradients in fish community composition in response to eutrophication can be expected only within each lake type, and are less likely to be found across the types. This may explain why some Scandinavian and central European studies have found contradictorily results. Persson *et al*. (1991) observed a perch dominance at mesotrophic conditions, whereas Radke & Eckmann (2001) and Olin *et al*. (2002) found that roach dominated more often. It may be possible that perch dominance is characteristic for deep lakes at mesotrophy (Horppila *et al*. 2000; Radke & Eckmann 2001) whereas roach dominance occurs if the lake is of shallow to medium depth and mesotrophic.

The smelt lake community type was unexpected. The cluster analysis grouped only three lakes to this type; two other lakes where smelt numerically dominated in the pelagic catches were removed as outliers (SAA, FLE; see the Appendix for lake names). All five lakes where smelt was dominant in the pelagic (SAA, FLE, KOE, MGG, WER) were large (surface area ≥ 770 ha, in contrast to the median of 148 ha from all 67 lakes), connected with other waterbodies, and with an average water mean depth of between 4 and 22 m such that their volumes were always rather high. The total phosphorus concentration (average during the vegetation period) in the five smelt lakes ranged from 29 up to 185 µg L^{-1}. Many smelt populations spend most of their life as planktivores or piscivores in the pelagic area, but show spawning migrations into small rivers (Nyberg *et al.* 2001). As the morphological and productivity-related features described above do not belong completely to either the vendace or the bream lake types, we have to assume that the smelt type lake is indeed distinct, and characterized mainly by the connectivity.

The pre-separation of fish communities according to two or three morphological lake types in the German lowlands is also important for the WFD. The present ecological state of lakes must be assessed in comparison with a type-specific reference state that can be derived from unaltered natural sites, by modelling or by expert judgement. Following the conceptual models of gradual fish community successions without considering lake types, all lakes in ecoregion 14 would belong to one type and thus would have a similar reference state, indicated by a dominance of Salmoniformes (mainly coregonids) at oligotrophy. It is highly unlikely that all lakes were previously oligotrophic, and their trophic state has increased in response to the cultural eutrophication over the last decades. In contrast, we suggest that a different reference state should be determined for at least the vendace and bream lakes. Only the deep lakes can be characterized by vendace dominance at the reference state. The shallow and small bream lakes have a mesotrophic reference state at best, indicated by a codominance of perch and roach as found in many mesotrophic lakes in protected areas (i.e. almost undisturbed by humans, near the assumed reference conditions) of north-east Germany (Eckmann 1995; Radke & Eckmann 2001).

Our study provides evidence for a reliable description and assessment of lowland lake fish communities by combining fish catch data from all relevant lake habitats obtained by different sampling methods. Sampling time was chosen to cover activity periods of all species in all habitats but to exclude periods when fish concentrate in only one habitat (for example during winter seasons). Ideally, the WFD aims to provide comparable assessment of waterbodies on a pan-European scale. Thus, the use of standard methods (electrofishing and multimesh gillnets) is advisable for the assessment of lakes within the size and depth range recommended in the standards (up to *c.* 5000 ha in area and *c.* 75 m maximum depth; Appelberg 2000). However, for larger and much deeper lakes (e.g. pre-Alpine lakes), the methods used in our study might fail to reveal a realistic description of the fish community such that further comparisons are required that include lake types typical for areas outside the central European lowlands.

Acknowledgements

The study was financed by the German Federal Ministry of Education and Research (BMBF, grant No. 0330031). J. Köhler, R. Koschel, J. Matthes, U. Mischke, E. Rohde and J. Schönfelder provided abiotic data of the lakes.

We would like to thank T. R. Whittier and two anonymous referees for very helpful comments on the manuscript, and O. Prawitt for discussions during the application phase.

A. Baer, M. Böhm, R. Frenzel, F. Fust, S. Horn, C. Imholt, C. Kühn, D. Lill, T. Rohde, S. Schulz, A. Türck, C. Ubl, M. Valentin, F. Weichler and H. Weitcamp helped during the extensive sampling surveys.

Supplementary material

The following supplementary material is available for this article online:

Appendix. Summary of the abiotic characteristics and number of gillnets used at the 67 lakes sampled in this study.

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Received 7 September 2004; final copy received 17 May 2005
Editor: Paul Giller