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No differences between littoral fish community structure of small natural and gravel pit lakes in the northern German lowlands

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ABSTRACT

Habitat loss has been identified as a major contributor to declining freshwater biodiversity, resulting in a high threat level among European fishes. Non-natural ecosystems such as pit lakes may compensate habitat loss by providing new habitat for aquatic organisms. We compared the structure of the littoral fish communities of 18 natural and 19 gravel pit lakes located in the northern German lowlands to evaluate whether artificial lakes managed by angling clubs host similar communities as typically observed in natural lakes. The fish community structure was analyzed between the lake types and along gradients of lake morphometry, productivity and littoral complexity. Although the gravel pit lakes differed in morphology (characterized by steeper littoral slopes and less structured littoral habitat), differences in fish community structure between the natural and gravel pit lakes were weak and mainly related to differences in the abundance of the dominant species perch, roach and rudd. Both lake types had similar species richness, community diversity and hosted several small-bodied and endangered species. To conclude, fish communities characteristic of small natural lakes may serve as reference for the development of gravel pit lakes. Moreover, our study reveals that recreational-fisheries management of gravel pit lakes does not result in artificial communities that deviate strongly from the communities present in natural lakes. Therefore, nature conservation and fisheries management goals can be reconciled in relation to fish in small artificial lakes managed by angling clubs.

Introduction

Lentic freshwaters are among the world's most threatened ecosystems experiencing a disproportionate rapid biodiversity decline over recent times (Sala et al., 2000; Abell, 2002). Habitat loss has been identified as one of the major threats, which has contributed to the present-day freshwater biodiversity crisis (Dudgeon et al., 2006). Today, about 41% of all native freshwater fish species have been classified as threatened or are considered as near threatened, one of the highest threat level for any major taxonomic group in Europe (Freyhof and Brooks, 2011). Particularly, species that depend on small and temporary stagnant waters have declined in abundance and distribution throughout central Europe (Freyhof, 2002; Aarts and Nienhuis, 2003).

Lentic freshwater ecosystems of natural and non-natural origin (such as reservoirs, gravel pits and ponds) provide valuable habitat for many European fish species. In particular large, deep lentic ecosystems support diverse fish communities (e.g., Irz et al., 2002; Brucet et al., 2013). Such ecosystems have attracted scientific attention for generations (Wetzel, 2001), and also recent legal demands stemming from the European Water Framework Directive (European Union, 2000) safeguard repeated sampling of fish communities in natural lakes and reservoirs larger than 50 ha. Surprisingly, only few studies have compared the structure of fish communities between natural and non-natural large lakes, and the few available studies have been mainly confined to reservoirs (e.g., Whittier et al., 2002; Irz et al., 2006; Launois et al., 2011). As would be expected due to variation in genesis, morphology, hydrology and water chemistry among natural lakes and non-natural systems (Thornton et al., 1990; Castro and Moore, 2000; Schultze et al., 2010), reservoirs have been found to host different fish communities with a greater number and proportion of non-native and tolerant species (Whittier et al., 2002; Launois et al., 2011). Despite these differences also many commonalities in fish community structure including the number of common and rare species

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and the same dominating species have been observed among natural lakes and reservoirs in Europe (Godinho et al., 1998; Irz et al., 2006).

Compared to large lentic systems, much less research effort on fish community structure has been devoted to small European and German lakes (for exceptions see Tonn et al., 1990; Eckmann, 1995). Across the world, small lakes <10 ha are numerically dominant (Oertli et al., 2002; Downing et al., 2006), and small artificial lakes stemming from soil extraction have become main elements of the landscape in many water-scarce areas (Gee, 1978; Schagerl et al., 2010) such as the west German lowlands. The lack of dedicated attention to fish communities in small non-natural lakes has been repeatedly noted (Gee, 1978; Bartmann et al., 1990) and is surprising given its importance for recreational fisheries and its potential to host relevant aquatic biodiversity. Small lentic surface waters may potentially compensate for the loss of natural habitat for many aquatic biota as shown for several aquatic invertebrates, amphibians and macrophytes (Biggs et al., 1994; Gee et al., 1997; Williams et al., 2008). The degree to which non-natural water bodies provide refuges for diverse fish communities and the question how fish communities in small non-natural lakes differ from natural lakes has hitherto not been studied.

Recreational fishing is a popular pastime in Germany, with about 3.3 million active anglers living in the country (Arlinghaus, 2004). In Germany many artificially created lakes are managed by about 10,000 angling clubs who are obliged, according to state-specific inland fisheries laws, to maintain and support natural fish communities in terms of species and age/size structure commensurate with the ecological conditions of a given water body (Daedlow et al., 2011). Legal terminology in German fisheries legislation acknowledges that many aquatic ecosystems have been heavily modified or are entirely artificially created. Accordingly, fishing rights holders are demanded to maintain near-natural ("*naturnah*") fish communities while using and managing fish stocks for recreational purposes. However, a near-natural status for fish communities in small non-natural lakes has as yet not been defined. In the absence of comparative studies, fish communities in small natural lakes have served as reference communities and targets for non-natural lakes, but whether this agrees with ecological reality is an open empirical question.

The lake littoral is a zone of high productivity and essential in the life-cycle of most fish species (e.g., Winfield, 2004). Shallow and diversely structured littoral habitats provide spawning and nursery grounds, foraging areas and shelter against predation (reviewed in Winfield, 2004; Smokorowski and Pratt, 2007; Strayer and Findlay, 2010). The high meso- and microhabitat diversity of the littoral zones in lakes promotes higher species diversity and fish abundances compared to profundal and pelagic habitats (Diekmann et al., 2005; Menezes et al., 2013). Littoral sampling is therefore particularly important for the characterization of fish communities and the assessment of biodiversity in lakes (Diekmann et al., 2005; Menezes et al., 2013).

The fish species composition of littoral zones is influenced by a range of abiotic (e.g., morphometry, productivity) and biotic factors (e.g., predator–prey dynamics), which often interact simultaneously in non-linear ways. For example, with increasing lake productivity and water turbidity littoral fish abundance may increase (Jeppesen et al., 2006; Lewin et al., 2014) but only up to a maximum point after which it decreases due to oxygen limitations (Hartmann, 1977). The presence of macrophytes and coarse woody debris is thought to increase species richness and abundance of juvenile fishes (Lewin et al., 2004, 2014; Helmus and Sass, 2008) by providing refuges against predation by piscivorous fish and birds and by elevating feeding opportunities (Eklöv, 1997; Russell et al., 2005). Although this statement is rarely questioned, experimental manipulations of littoral zones have either strongly affected fish communities (Sass et al., 2006; Helmus and Sass, 2008) or have no measurable impact at all (Sass et al., 2012). In US ecosystems, correlations among shoreline development and fish communities have been reported (Scheuerell and Schindler, 2004), while no such strong impacts were detected across lakes studied in northern Germany, which have typically less structurally degraded shorelines (Mehner et al., 2005; Lewin et al., 2014). More studies on lentic fish communities in systems, which have less structural elements in the littoral (e.g., non-natural waterbodies), are needed to further improve our understanding of the abiotic and biotic factors that structure lake fish communities in littoral zones.

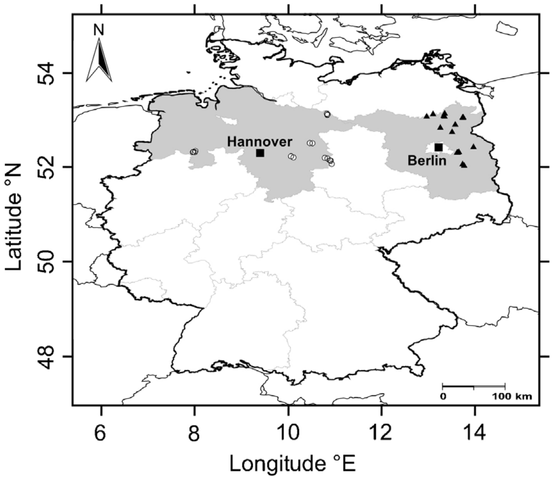

Fig. 1. Location of the 37 study lakes in northern Germany. Triangles indicate location of the natural lakes in Brandenburg (grayish area); open circles indicate location of the gravel pit lakes in Lower Saxony (grayish area).

In this study we compared the structure of littoral fish communities in small and relatively shallow natural and non-natural lowland lakes (hereafter called gravel pit lakes) located within northern Germany along gradients of lake morphology, productivity and littoral complexity. We aimed at identifying to what extend fish communities in gravel pit lakes that are managed by local angling clubs differ from fish communities in natural lakes in terms of fish community composition, species richness, community diversity, proportion of predators, and the abundance of threatened and alien species. The results were meant to inform whether small gravel pit lakes can provide valuable habitat that support diverse fish communities similar to those observed in small natural lakes. We further wanted to elucidate whether fish communities in natural lakes can serve as management targets for the rehabilitation and management of non-natural systems by angling clubs and other stakeholders. Due to the younger age of gravel pit lakes and the potentially more intensive fisheries management via stocking we hypothesized that gravel pit lakes would host less threatened species but a greater proportion of non-native and predatory fishes due to their importance for recreational fisheries. We also expected gravel pit lakes to be less structured in terms of the habitat diversity in the littoral zone with steeper littoral zones, and hence that fish communities should be different compared to natural lakes of similar size.

Methods

Study lakes

Littoral fish communities of 37 small (mean surface area: 17 ha, SD = 22.9, range = 0.4–61.4 ha) lakes located in the lowlands of northern Germany (<200 m a.s.l., European "Central Plains" Ecoregion, Illies, 1978) were analyzed (Fig. 1). A total of 18 lakes located in the state of Brandenburg (Fig. 1) were of natural origin formed by glaciation and deglaciation processes at the southern edge of the Weichselian ice shield, which covered north-east Germany between 25,000 and 13,000 years BP. The 19 non-natural gravel pit lakes were located in previously unglaciated regions in the state of Lower Saxony at comparable latitudes (Fig. 1). They originated from excavation of sand, gravel and clay, were younger than 100 years of age and were managed by local angling clubs. The natural lakes were also accessible to anglers but not managed by angling clubs.

Variables known to shape natural fish community composition in large central European lakes (Mehner et al., 2005, 2007; Brucet et al., 2013; Lewin et al., 2014; Mehner et al., 2014) were assessed for their relation to the fish community composition in the small lakes. It has recently been documented that spatial separation between lakes can effect fish community composition even across relatively small distances (Mehner et al., 2014). Our study lakes covered a latitudinal gradient of 1.2° (~132 km) and a longitudinal gradient of 6.1° (~419 km). We therefore initially considered lake location in the statistical analysis (CAP procedure, see section Data analysis) to test for spatial effects on fish community compositions. However, spatial predictors were ranked lowest and were not associated to differences in fish community composition and were therefore removed from the analysis. Variables of stronger predictive power were associated with lake morphometry and lake productivity. Lake morphometry was characterized by area (ha), maximum depth (m), and littoral depth (cm). Littoral depth was measured at the back of the electrofishing boat, which was moved parallel to the shoreline in a distance of approximately 2–3 m. The variables related to lake productivity were total phosphorus concentration (TP; $\mu g\,L^{-1}$) and water transparency measured as Secchi depth (cm). Both variables were measured at least twice per year (in spring and autumn) according to standardized protocols (DIN EN ISO 6878). For statistical analyses, mean values were calculated. Total phosphorus and Secchi depth were sampled in the year of fish sampling for most lakes. In case of five natural lakes, however, measurements were taken up to three years prior to the year when the fish sampling took place.

Morphological (maximum depth, area) and productivity data of the natural lakes were provided by state authorities (Ministry of Environment, Health and Consumer Protection of the Federal State of Brandenburg, Potsdam). Littoral depth was recorded during fish sampling. Maximum depth and littoral depth of the gravel pit lakes were measured during the fishing campaigns using a Humminbird Sonar (Type 788ci). Lake area was extracted from digital maps using ArcGIS software by ESRI (Version 10.1). Secchi depth was measured in the field, and TP was measured in the laboratory using the identical protocol as for the natural lakes (see above).

The variables characterizing the littoral complexity included the degree of shadowing, the coverage of macrophytes (emersed and submersed pooled) and submerged woody structures. All of these variables were recorded in late summer or early autumn when the abundance of aquatic vegetation typically peaks. However, the recordings of littoral complexity differed between lake types because the pit lakes and the natural lakes were sampled as part of separate projects following different sampling guidelines. The littoral complexity of the gravel pit lakes was estimated quantitatively (percentage cover data). By contrast, littoral complexity of the natural lakes was estimated in three categories (1 = none/rare, 2 = medium, 3 = dominant). To generate comparable data, the littoral complexity of the natural lakes was converted into three categories with none/rare = 0–33.3%, medium = 33.4–66.6% and dominant >66.6% coverage. Categorical data were then converted into continuous synthetic variables using multiple correspondence analysis (see below).

Fish sampling

Fish communities in shallow, structured littoral habitats are most efficiently sampled by electrofishing (e.g., Diekmann et al., 2005; Menezes et al., 2013). The fish sampling took place between 2001 and 2011 using daytime point abundance electrofishing. Sampling was performed by a two-person crew by boat using an EFG4000 or EFGI4000 electrofishing aggregate (4–8 A, Bretschneider Spezialelektronik, Germany) with one anodic handnet of 40–45 cm ring diameter and 6 mm mesh size, and a copper cathode. Pulsed direct current was used. Most lakes were sampled in early autumn (end of August–early October) but eight natural lakes were sampled in summer (end of May–June).

Littoral fish sampling in the larger natural lakes (>10 ha) was conducted at six transects, which represented all habitat structures relative to the whole lakes' littoral zones. Each of the six transects in the larger lakes was sampled by 15 dips with approximately 10 m distance between each dip resulting in a total of 90 dips per (natural) lake. Because many of the gravel pit lakes were smaller (<10 ha, Fig. 2) and hence coverage of the entire shorelines was feasible in one sampling day, electrofishing was conducted along the entire shoreline in transects of 50–100 m resulting in 6–13 transects (mean = 8, SD = 2.4) and a total of 235 dips per lake on average (range: 107–439, SD = 83.4). All captured fishes within each transect were placed in a tank identified to species level, measured to the nearest cm total body length and released at the end of each transect. Fish abundance was calculated as catch per unit effort (CPUE) for each transect by dividing the number of fishes caught per transect with the number of dips conducted in each transect. Total lake CPUE was then averaged across all transect CPUE values of each lake.

Fish community descriptors

Nine biotic metrics were derived from the littoral fish catches and compared among the natural and gravel pit lakes. Total lake CPUE was calculated as a measure of littoral fish density. Community diversity was characterized using species richness, the Shannon index (Shannon, 1948) and Pielou's evenness (Pielou, 1966). We further compared the proportion of piscivorous fish, which are regularly stocked to support recreational fisheries (Cowx and Gerdeaux, 2004). Because high predator densities can cause substantial reduction or disappearance of small-sized prey fish (He and Kitchell, 1990; Trumpickas et al., 2011) the species number (richness) and proportion of small-bodied non-game fish was compared. We further compared the species number and the proportion of threatened and near-threatened species. Classification of threat status followed the red list of fish species reproducing in German freshwaters (Freyhof, 2009). Accordingly, the catadromous European eel (*Anguilla anguilla* L.) was not considered a threatened species in this study because its occurrence in the (isolated) study lakes results from stocking. The number of alien species was also compared, which may be introduced through stocking and which are particularly successful in establishing populations in artificial ecosystems (reviewed in Strayer, 2010). For the detailed classification of the species into categories of predator, small-bodied non-game, threatened/near-threatened and alien species, see Table 1.

Data analysis

Abiotic lake characteristics and biotic fish community descriptors were compared among natural and gravel pit lakes using independent t-tests and chi-square tests for proportion data. If necessary, quantitative data were $\log_{10}$-transformed to meet assumptions of parametric test statistics. Categorical variables

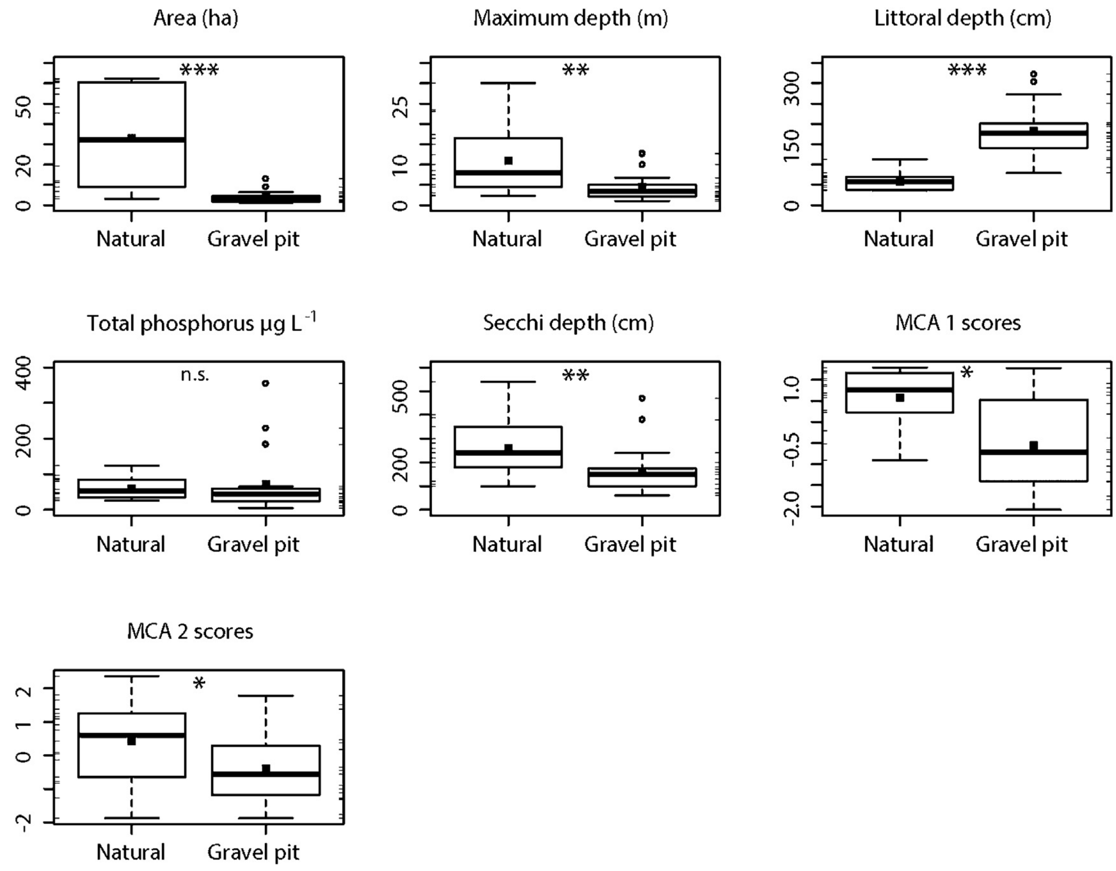

Fig. 2. Abiotic characteristics and measures of littoral complexity (MCA scores) of the natural and gravel pit lakes in northern Germany. Boxplots show 25–75th percentiles (box) with median (line), mean (black square) and outliers (circles). Whiskers represent the 95% range. Rugs on the vertical axes show the distribution of the lake variables. Significance level: * <0.05, ** <0.01, *** <0.001, n.s. = not significant.

Table 1
Relative frequency (%) and frequency of occurrence (% of 37 lakes) of fish species caught by electrofishing in the littoral zones of natural and gravel pit lakes.

Common name	Scientific name	Relative frequency	Frequency of occurrence
Perch[a]	*Perca fluviatilis*	28.3	97.3
Roach	*Rutilus rutilus*	24.5	89.2
Rudd	*Scardinius erythrophthalmus*	20.7	83.8
Bitterling[b]	*Rhodeus amarus*	6.4	13.5
Tench	*Tinca tinca*	4.1	75.7
White bream	*Blicca bjoerkna*	3.2	37.8
Sunbleak[b,c]	*Leucaspius delineatus*	3.2	18.9
Eel[a]	*Anguilla anguilla*	2.7	83.8
Bleak[b]	*Alburnus alburnus*	2.5	21.6
Pike[a]	*Esox lucius*	1.6	83.8
Common bream	*Abramis brama*	1.4	43.2
Crucian carp[c]	*Carassius carassius*	1.0	18.9
Spined loach[b]	*Cobitis taenia*	0.2	21.6
Cyprinid hybrid		0.1	18.9
Ruffe[b]	*Gymnocephalus cernuus*	0.1	16.2
Gudgeon[b]	*Gobio gobio*	<0.1	5.4
Carp	*Cyprinus carpio*	<0.1	16.2
Burbot[a]	*Lota lota*	<0.1	2.7
Three-spined stickleback[b]	*Gasterosteus aculeatus*	<0.1	2.7
Rainbow trout[d]	*Oncorhynchus mykiss*	<0.1	2.7
Weather loach[b,c]	*Misgurnus fossilis*	<0.1	2.7
Stone loach[b]	*Barbatula barbatula*	<0.1	2.7
Pikeperch[a]	*Sander lucioperca*	<0.1	5.4

[a] Piscivorous species (perch >15 cm total body length (TL) and eel >50 cm TL were classified piscivorous).
[b] Small-bodied non-game fish.
[c] Threatened/near-threatened species.
[d] Alien species.

describing the littoral complexity in the transects were converted into two synthetic continuous variables using multiple correspondence analysis (MCA) (Tenenhaus and Young, 1985). The first two MCA axes explained 45.4% of the variation in the categorical descriptors. The principal lake coordinates (scores) of the two axes (MCA1 and MCA2) were considered in subsequent analyses. The first axis (Eigenvalue = 0.26) discriminated lakes with littoral zones that were dominated by macrophytes (positive MCA1

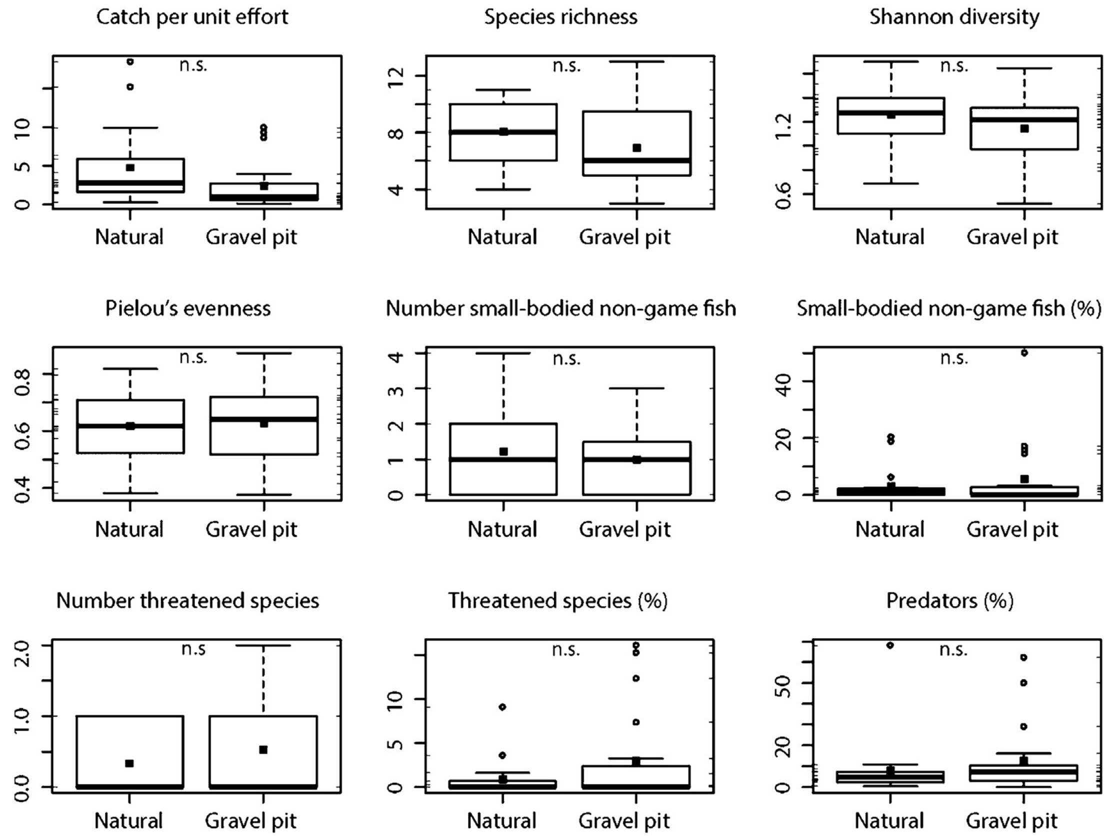

Fig. 3. Descriptors of littoral fish communities in the natural and gravel pit lakes in northern Germany. Boxplots show 25–75th percentiles (box) with median (line), mean (black square) and outliers (circles). Whiskers represent the 95% range. Rugs on the vertical axes show the distribution of the fish community descriptors. Significance level: * <0.05, ** <0.01, *** <0.001, n.s. = not significant.

scores) from lakes with strongly shaded littoral zones and less macrophyte coverage (negative MCA1 scores). The second axis (Eigenvalue = 0.19) discriminated lakes with higher amounts of submerged woody structures in the littoral zone (negative MCA2 scores) from lakes with less or no woody habitat structures (positive MCA2 scores).

None of the lakes appeared as an outlier (maximum average distance of 0.89 standard deviations away from the grand mean distance) such that littoral fish community data from the total lake set ($n = 37$) were analyzed. Constrained and unconstrained ordination techniques were selected to display multivariate patterns in the electrofishing CPUE data (site-species matrix). Non-metric multidimensional scaling (nMDS, Kruskal, 1964) was used to visualize compositional patterns of littoral fish communities in the natural and gravel pit lakes. Relationships among littoral fish community composition and abiotic lake descriptors and descriptors of littoral complexity (MCA scores) were examined and illustrated by analysis of principal coordinates (CAP, Anderson and Robinson, 2003; Anderson and Willis, 2003). In the CAP biplot, the importance of habitat characteristics is indicated by the length and direction of the vectors (arrows in Fig. 5). To identify species that contributed strongly to the multivariate pattern and potential differences in littoral fish community composition Pearson correlation of all species with the CAP axes were calculated. Only species with significant correlations of $|r| > 0.40$ ($P < 0.01$) were considered as important and displayed in the CAP plot (Fig. 5).

A one-way analysis of similarity (ANOSIM, $n = 999$ permutations, Clarke, 1993) was used to test for significant differences between littoral fish community composition in the natural and gravel pit lakes. Subsequent similarity percentage analysis (SIMPER, Clarke, 1993) identified species that contributed most to the between lake-type differences in case of significant ANOSIM test statistics.

Because the natural and gravel pit lakes differed significantly in some of the abiotic lake descriptors (Fig. 2), we additionally identified smaller lake subgroups sharing more homogeneous lake characteristics, which contained both natural and gravel pit lakes. This was done to exclude the possibility that any differences in fish community structure between the lake types were primarily caused by differences in lake morphometry and productivity. Lake subgroups were identified by hierarchical cluster analysis using Ward's algorithm (Ward, 1963) with average linkage grouping on $\log_{10}$-transformed lake descriptors. The Ward's algorithm joints clusters in a way to maximize the within clusters homogeneity. Three separate cluster analyses were conducted to classify the natural and gravel pit lakes according to lake depth (maximum and littoral depth), productivity (TP concentration and Secchi depth) and lake area. The lake clusters (subgroups) were also tested for differences in littoral fish community composition by calculating three separate two-way ANOSIMs (crossed design, $n = 999$ permutations) with lake classifications (related to depth, trophy and area) and lake type (natural, gravel pit) as factors.

Outlier analysis, ANOSIM, SIMPER and ordinations (nMDS, CAP) were calculated using Bray–Curtis distance on untransformed and non-standardized CPUE data. ANOSIM and SIMPER were calculated in Past (version 2.17, Hammer et al., 2001). Other statistical analyses were performed in the R environment (R Development Core Team 2012, version 2.14.2) using the packages 'vegan' (version 2.0-3, Oksanen et al., 2012) and 'ca' (version 0.53, Nenadić and Greenacre, 2007).

Results

Study lakes

The study lakes showed variation in abiotic characteristics, many of which strongly overlapped but differed significantly between the natural and gravel pit lakes (Fig. 2). We found the natural lakes to be on average larger ($t = -6.30$, $P < 0.001$) and characterized by larger maximum depths ($t = -3.29$, $P = 0.002$) compared to the gravel pit lakes. By contrast, the littoral depth was significantly deeper in the gravel pit lakes ($t = 9.86$, $P < 0.001$). Total phosphorus concentrations did not differ between lake types ($t = -0.90$, $P = 0.38$), yet the natural lakes were characterized by higher water transparencies ($t = -3.18$, $P = 0.003$). Littoral complexity also differed between lake types. Natural lakes were characterized by more macrophytes in the littoral zone ($t = -2.11$, $P = 0.04$), whereas in the gravel pit lakes more coarse woody habitat was detected ($t = 1.98$, $P = 0.05$). The overall littoral complexity (macrophytes and woody structures) was higher in the natural lakes (mean class: 2.1 natural lakes vs. 1.7 gravel pit lakes, $t = -6.4$, $P < 0.001$).

Littoral fish community structure

In total, 17,182 fishes representing 22 species from eight families and one cyprinid hybrid were caught by electrofishing in the littoral zones of the 37 lakes. Catches were numerically dominated by perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* L.) and rudd [*Scardinius erythrophthalmus* (L.)] (Table 1). Non-native fish were almost absent in the littoral zone of all lakes; only one rainbow trout [*Oncorhynchus mykiss* (WALBAUM)] was caught in a gravel pit lake. Lake-specific total CPUE differed substantially between lakes (0.11–18.47 fishes dip^{-1}) but was not significantly different between lake types ($t = 1.67$, $P = 0.10$; Fig. 3). Community diversity was also similar among lake types. Species richness (overall mean: $n = 7$; range: 3–13; $t = -1.44$, $P = 0.16$), the Shannon index ($t = 1.35$, $P = 0.18$) and Pielou's evenness ($t = -0.22$, $P = 0.83$) did not differ significantly between lakes types nor did the number and proportion of small-bodied non-game fishes ($t = 0.55$, $P = 0.59$; $\chi^2 = 79.20$, $P = 0.74$) and threatened or near-threatened ($t = -1.38$, $P = 0.18$; $\chi^2 = 39.6$, $P = 0.80$) species (Fig. 3). Similarly, the proportion of predatory species did not differ between the natural and gravel pit lakes ($\chi^2 = 306.27$, $P = 0.24$; Fig. 3).

Overall, littoral fish community composition was very similar among lake types as indicated by strongly overlapping confidence ellipses and closely associated centroids of the natural and gravel pit lakes in the nMDS biplot (Fig. 4). Similarly, an one-way ANOSIM revealed only weak taxonomic differences in littoral fish community composition between lake types (Global $R = 0.14$, $P = 0.004$). The small differences resulted from changes in the relative abundance of the three most dominant and frequently occurring eurytopic species rudd, roach and perch, which together accounted for 74.4% of the observed dissimilarity in the SIMPER analysis (Tables 1 and 2). These species were the only ones that were significantly correlated (Pearson's $|r| > 0.4$, $P < 0.01$) with the two CAP axes (Fig. 5). Larger lakes with high macrophyte abundances and higher water transparency (mainly natural lakes) were characterized by higher abundances of perch and rudd. By contrast, lakes with higher productivity and lower water transparency were associated with higher roach abundances (Fig. 5).

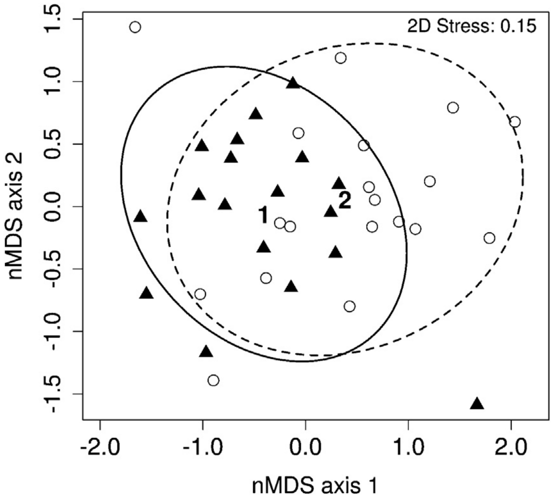

Fig. 4. Non-metric multidimensional scaling (nMDS) plot of littoral fish community catch-per-unit-effort data in natural (closed triangles) and gravel pit (open circles) lakes in northern Germany. Ellipses represent the 95% confidence intervals (solid line = natural lakes, dashed line = gravel pit lakes). Numbers indicate position of the group centroids (1 = natural lakes, 2 = gravel pit lakes).

The cluster analyses identified lake subgroups that were mainly separated by maximum depth, TP concentration and lake area and contained both natural and gravel pit lakes (Table 3). However, littoral fish community composition also did not differ significantly between these lake subsets and lake types (results of the two-factorial ANOSIM, Table 4).

Discussion

We tested whether lake origin, i.e. lakes that were either naturally formed by processes of glaciation and deglaciation or anthropogenically created through soil excavation, has an influence on the littoral fish community structure in small lakes in northern

Table 2

Results of the similarity percentages analysis of the differences of littoral fish catch per unit effort (CPUE) in natural and gravel pit lakes in northern Germany. Given are the species-specific average dissimilarity, the separate and cumulative contribution to the overall average dissimilarity (= 72.5), the mean relative abundance (CPUE) and overall relative frequency (% total) in the natural (NL) and gravel pit (GPL) lakes. Only species contributing more than 1% to the overall average dissimilarity are presented.

Species	Average dissimilarity	Contribution %		Mean abundance		% total	
		Separate	Cumulative	NL	GPL	NL	GPL
Rudd	19.3	26.6	26.6	1.2	0.3	26.7	16.4
Roach	17.4	24.1	50.7	0.9	0.8	19.7	27.9
Perch	16.9	23.4	74.1	1.6	0.6	33.7	24.5
White bream	5.7	7.9	82.0	0.3	<0.1	6.6	0.8
Bleak	2.2	3.0	85.0	0.3	<0.1	5.9	<0.1
Bitterling	2.0	2.7	87.7	<0.1	0.2	0.1	10.9
Tench	1.9	2.6	90.3	0.1	0.1	2.8	5.0
Eel	1.8	2.5	92.8	0.1	0.1	1.7	3.4
Pike	1.8	2.5	95.3	0.1	<0.1	1.5	1.7
Sunbleak	1.4	2.0	97.3	<0.1	0.2	<0.1	5.5
Common bream	1.1	1.5	98.8	<0.1	<0.1	0.5	1.9

Table 3
Lake classification according to the results of the cluster analysis for lake depth, trophy and size. Lake number and proportion of natural and gravel pit lakes within each cluster are given.

Lake depth	Maximum depth (m)	Littoral depth (m)	N lakes	% natural	% gravel pit
Cluster 1	<5	0.4–1.7	19	26.3	73.7
Cluster 2	5–9.99	0.6–2.7	7	71.4	28.6
Cluster 3	≥10	0.6–3.2	11	72.7	27.3
Lake trophy	Total phosphorus ($\mu g L^{-1}$)	Secchi depth (cm)			
Cluster 1	<80	90–540	28	42.9	57.1
Cluster 2	≥80	60–380	9	66.7	33.3
Lake size	Area (ha)				
Cluster 1	<10		21	19.0	81.0
Cluster 2	≥10		16	87.5	12.5

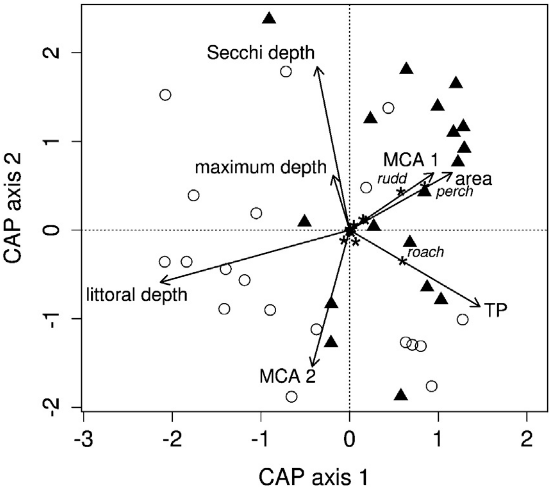

Fig. 5. Canonical analysis of principal coordinates (CAP) ordination of littoral fish community catch per-unit-effort data in natural (closed triangles) and gravel pit (open circles) lakes in northern Germany. Vectors indicate direction of maximum correlations of lake characteristics. MCA scores represent a measure of littoral complexity. Asterisks indicate species positions along the canonical axes. Only names of species are given that were significantly correlated with the CAP axes (Pearson's $|r| > 0.4$; $P < 0.01$).

Germany. Although our initial hypothesis in terms of structural and morphological differences in the littoral zone of natural and gravel pit lakes was supported, the two lake types were characterized by very similar fish communities. Hence, our hypothesis of dissimilar fish communities in natural and non-natural lake types with a greater fraction of alien and predatory fish and less threatened species to be found in gravel pit lakes was not supported. In fact, we found both lake types to be very similar in their littoral fish community structure. Hence, littoral fish communities of small natural lakes can be used as reference communities for the development of near-natural fish communities in non-natural lentic water bodies.

Although the gravel pit lakes were spatially separated from the natural lakes along a longitudinal gradient, geographical position was not an important predictor of fish community composition. Mehner et al. (2014) have demonstrated a spatial effect on fish community composition in large natural and hydrologically connected lakes even along small distances. Differences in community composition were primarily caused by an uneven distribution of small-sized littoral species. This effect was not observed in our small natural and gravel pit lakes. Overall species richness was lower in the small lakes we studied ($n = 22$) compared to the large lakes analyzed by Mehner et al. (2014) ($n = 31$ species) which is predictable following the species-area relationship of lake fishes (Barbour and Brown, 1974). Possibly, this overall reduced dissimilarity (i.e. lower species richness) of fish communities in small northern German lakes have weaken the geographical signal on fish community composition.

Table 4
Results of the two-factorial analysis of similarity (999 permutations, Bray–Curtis dissimilarity) of the lake subsets identified by the cluster analysis (Table 3) including *R*- and *P*-values.

Cluster variable	*R*-value factor 1: lake descriptor	*P*-value	*R*-value factor 2: natural/gravel pit	*P*-value
Lake depth	0.17	0.05	0.16	0.07
Lake trophy	0.08	0.24	0.07	0.16
Lake size	0.04	0.35	−0.04	0.58

Although time of sampling partly varied in our dataset, we assume that this has not severely influenced our results. All lakes were sampled within the growing season (end of May–early October) where most species have finished reproduction so that unusual high aggregations of certain species due to spawning activities in the littoral were unlikely. Although it is possible that young-of-the-year fish assemblages were sampled differently during summer and early autumn, it is unlikely this effect would have altered the conclusions and main findings of our study.

Although the two lake types in this study differed in many environmental features such as depth and structural complexity in the littoral zone, the fish community structure was very similar and was dominated by the same species that are also characteristic for larger central European lowland lakes, *viz.* perch, roach and rudd (Jeppesen et al., 2000; Mehner et al., 2005, 2007). Hence, the environmental differences were obviously not strong enough to lead to strikingly dissimilar fish communities. The littoral of the natural lakes was generally shallow and strongly structured caused by high macrophyte coverage. By contrast, the gravel pit lakes were characterized by slightly deeper, less structured littoral zones with less abundant macrophytes, but these systems offered more coarse woody habitat structures. We assume that the lake-wide differences in structural complexity of the littoral zone observed during late summer were not strong enough to form significantly different fish communities. Similarly, Lewin et al. (2014) reported that variables other than the habitat diversity in the littoral, such as trophic level, are responsible for the abundance of freshwater fish in shallow lakes in northeastern Germany. Although the natural lakes we studied were characterized by significantly higher maximum depths than the gravel pit lakes, water depth was still comparatively shallow to avoid that the littoral exerts large influence on the fish community (compare Lewin et al., 2014). Lewin et al. (2014) found that the importance of littoral structural variables was particularly pronounced for deep natural lakes. The importance of maximum water depth to structure lake fish communities increases when the pelagic lake habitat that was not investigated in this study is sampled as well (Diekmann et al., 2005).

Despite the differences in lake morphology, the more shallow gravel pit lakes shared also abiotic similarities with the natural lakes. In particular, they did not show characteristics typically seen in very young and deep gravel pit lakes. These often exhibit unique morphometric characteristics, which separates them from naturally formed lakes (Castro and Moore, 2000). In particular, relatively steep slopes and loose sandy substrate in young pit lakes prevent an establishment of widespread macrophyte stands (Duarte and Kalff, 1986), and many of these young systems are also nutrient poor (i.e., oligotrophic to slightly mesotrophic, [Schultze et al., 2010]). Although we also observed less macrophytes in the gravel pit lakes, they predominantly showed an advanced succession state with many of the gravel pit lakes being nutrient rich. Shallow lakes are typically characterized by high plankton biomass and large turbidity (Scheffer et al., 1993). The high productivity and stronger turbidity in the shallow gravel pit lakes might have favored a more littoral fish distribution (Jeppesen et al., 2006), which resulted in high littoral fish abundances that were not substantially differing from the fish abundance in clearer natural lakes. Although high turbidity suppresses macrophyte growth (Scheffer et al., 1993), littoral complexity in the gravel pit lakes was obviously high enough to support species-rich, diverse fish communities similar to those observed in natural lakes. It is possible that younger, deeper gravel pit lakes that are less structured than the system we studied might differ from the patterns reported here.

All gravel pit lakes in this study were managed by local angling clubs and angling was also allowed on the natural lakes. Unfortunately, detailed data of stocking and angling activities were not available for most of the lakes, so that the direct impact of stocking and angling on the fish community structure could not be analyzed. Freyhof (2002) and Freyhof and Brooks (2011) claimed that anglers are responsible for the introduction and transfer of non-native fish stocks, which are often extremely successful in establishing populations in non-natural or anthropogenically degraded ecosystems (Strayer 2010). However, we did not observe high abundances of non-native fishes in the littoral of the gravel pit lakes, either indicating such fish are rarely released by anglers in our study lakes or simply do not establish. An alternative explanation that we favor is also that the ecological conditions of a given ecosystem predetermine the fish community that can be supported locally given the regional species pool. Hence, artificial gravel pits will develop similar community structures than natural lakes after being given some succession time as long as the initial stocking does not introduce an unnatural mix of species. Our data suggest this was not the case or has been regulated ecologically such that the fish community structure of the gravel pit lakes was similar to natural fish communities. It is also important to realize that angling would alter the age and size distribution of fishes and may also reduce abundance (Lewin et al., 2006), but angling itself is has never been reported to lead to species extinctions. Hence, any differential fishing intensity in the lake types is unlikely to have exerted a strong effect on our findings.

Besides stocking, habitat enhancement is an increasingly popular management strategy of anglers to support local fish stocks (e.g., Arlinghaus and Mehner, 2005; Pedicillo et al., 2008). It is not known whether the angling clubs that managed the gravel pit lakes actively promote habitat diversity and structural complexity. However, coarse woody structures were more frequently observed in, from a genesis point of view, relatively young gravel pit lakes where the density of riparian coarse wood is typically low (Marbug et al., 2006). Presumably, the coarse woody structures were actively placed in the gravel pits to increase littoral complexity and to create new spawning areas and shelter for juvenile fishes (Sandström and Karås, 2002; Čech et al., 2012). Previously poorly structured habitats can thus be ecologically enhanced by creating new (artificial) structures (Bolding et al., 2004). It has been documented that woody structures can replace the function of natural habitat structures such as macrophytes (Lewin et al., 2004), which might explain why we did not find significant differences in fish density and community diversity and only weak differences in fish community composition between the natural and gravel pit lakes.

The impact of littoral complexity on fish community structure is likely to be strongly threshold-dependent. Studies in natural lakes in northern Germany did not reveal any strong relationship between shoreline development and fish community structure (Mehner et al., 2005; Emmrich et al., 2011; Lewin et al., 2014) whereas in some US lakes with much more modified shorelines fish community structure changed along a shoreline development gradient (Scheuerell and Schindler, 2004). Fish community structure in central European lowland lakes is mainly related to nutrient status and lake morphology and less affected by shoreline degradation (Mehner et al., 2005; Emmrich et al., 2011; Brucet et al., 2013; Lewin et al., 2014). Given the similar nutrient states of the natural and the gravel pit lakes we studied, possibly these similarities have overridden any structural effects and contributed to the homogeneity of the littoral fish community structure (Brucet et al., 2013). It has recently been demonstrated that the effects of littoral complexity and shoreline development on littoral fish abundance were stronger in deep than in shallow natural lakes (larger than 50 ha) likely due to the smaller proportion of the littoral relative to the total lake area in large lakes (Lewin et al., 2014). This might be a further reason why we did not observe strong differences in littoral fish abundance and community composition, because all our study lakes were relatively shallow and small, thus having a similar higher proportion of the littoral compared to total lake size.

Despite the general homogeneity of the fish communities, some minor differences were observed. In particular, higher mean abundances of perch and rudd were found in many of the natural lakes characterized by high water transparency and littoral zones strongly covered with macrophytes. By contrast, roach densities were higher in more productive and turbid (mostly gravel pit) lakes with steeper littorals and less macrophytes. The higher perch abundances observed in the natural lakes can be explained by differences in lake morphology and littoral complexity. Many of the natural lakes were larger and had a larger maximum depth than the gravel pit lakes. These are physical features that favor perch-dominated systems over roach-dominated systems (Haertel et al., 2002). Habitat complexity and turbidity affect the foraging success of perch and roach differently. Perch is a superior forager over roach in clearwater lakes with many macrophytes and hence high structural complexity whereas higher roach densities are typically observed in less structured more turbid lakes (Winfield, 1986; Diehl, 1988; Persson and Greenberg, 1990). Rudd as a typical littoral species is primarily associated with vegetated habitats (Kennedy and Fitzmaurice, 1974), which explains the higher abundances of rudd in the natural lakes.

In addition to these small between lake-type differences in fish community composition all other fish metrics did not differ significantly between the natural and gravel pit lakes. We did not observe systematically higher predator densities in the littoral of the gravel pit lakes, although predators such as pike and pikeperch [*Sander lucioperca* (L.)] are likely to have been stocked intensively by anglers (Eby et al., 2006). However, it has been shown that stocking of pike and pikeperch does not necessarily elevate stock sizes over natural limits due to strong intraspecific competition and cannibalism leading to self-regulation (Frankiewicz et al., 1999; Skov et al., 2003). This might also contribute to the finding that the species richness and abundance of small-bodied non-game fish did not differ between lake types because the predation pressure was not strong to cause declines or even extinctions of small-bodied fishes.

Surprisingly, only one non-native individual (rainbow trout) was detected in the littoral zones of the 37 lakes. Also, the abundances of popular stock-enhanced game fishes such as carp

(*Cyprinus carpio* L.) and pikeperch were absent (natural lakes) or occurred in very low densities only (gravel pit lakes). However, carp and pikeperch are predominantly found in lake offshore habitats (García-Berthou, 2001; Specziár et al., 2013) and hence have certainly not been representatively sampled with the electrofishing gear we used. In fact, random non-standardized sampling with multi-mesh gillnets (50–75 mm bar mesh size) in pelagic offshore habitats has identified carp in all sampled gravel pit lakes (Schälicke et al., 2012). Additionally, single individuals of non-native Asian carps including the silvercarp [*Hypophthalmichthys molitrix* (Valenciennes)], bighead carp [*Hypophthalmichthys nobilis* (*Richardson*)] and grass carp [*Ctenopharyngodon idella* (Valenciennes)] were caught in four gravel pit lakes indicating that pelagic habitats might host higher proportions of non-native species and popular game fishes (Schälicke et al., 2012). Species richness and abundance of threatened/near-threatened species was also similar in the natural and gravel pit lakes. For example, endangered species were found in more than 42% of the gravel pit lakes. Although abundances of threatened species were generally low (<3% on average) small non-natural water bodies can provide valuable habitat for endangered fish species when they are managed by angling clubs. Such low abundances of threatened species are also characteristic for fish communities in natural lakes that are typically dominated by perch and roach as shown here.

Conclusions

Patterns in littoral fish community structure of small northern German lowland lakes were found comparable to those typically occurring in larger central European lakes. Hence, natural fish communities from ecologically similar natural lakes can be used as targets for the management of gravel pit lakes despite their steeper littoral areas, higher turbidity and lower macrophyte abundances. Moreover, our study revealed that gravel pit lakes that are managed by angling clubs can serve as a refuge for fish biodiversity as long as their littoral zones are not strongly structurally degraded. Non-natural ecosystems can then provide valuable refuge habitats for hosting diverse, species-rich littoral fish communities including small-bodied non-game and endangered species to a degree that is comparable to natural lakes. The study is limited to relatively shallow gravel pit lakes. The situation might look differently in deeper oligotrophic and less structured non-natural water bodies of younger ages.

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