Effect of recreational-fisheries management on fish biodiversity in gravel pit lakes, with contrasts to unmanaged lakes

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Impact of recreational-fisheries management on fish biodiversity in gravel pit lakes, with contrasts to unmanaged lakes

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Abstract

Gravel pit lakes are novel ecosystems that can be colonized by fish through natural or anthropogenic pathways. In central Europe, many of them are managed by recreational anglers and thus experience regular fish stocking. However, also unmanaged gravel pits may be affected by stocking, either through illegal fish introductions or, occasionally, by immigration from connected water bodies. We sampled 23 small (< 20 ha) gravel pit lakes (16 managed and 7 unmanaged) in north-western Germany using littoral electrofishing and multimesh gillnets. Our objective was to compare the fish biodiversity in gravel pit lakes in the presence or absence of recreational fisheries. Given the size of the sampled lakes, we expected species poor communities and elevated fish diversity in the managed systems due to regular stocking of game fish species. Our study lakes were primarily mesotrophic and did not differ in key abiotic and biotic environmental characteristics. Lakes of both management types hosted similar fish abundances and biomasses, but were substantially different in terms of fish community structure and species richness. Fish were present in all lakes, with a minimum of three species. Higher alpha diversity and lower beta diversity was discovered in managed gravel pit lakes compared to unmanaged lakes. Consequently, recreational-fisheries management fostered homogenization of fish communities, by stocking a similar set of fish species desired by anglers such as piscivorous fish and large bodied cyprinids. However, unmanaged gravel pit lakes were also affected by human-mediated colonization, presumably by illegal fish releases. Hardly any non-native species were detected, suggesting that recreational-fisheries management did not foster the spread of exotic species in our study region.

Key words: Fish conservation; novel ecosystems; non-native species; fish stocking; recreational fishing; fish community composition

1. Introduction

Freshwater ecosystems have been strongly altered by humans (Dodds *et al.*, 2013). While rivers in temperate regions have experienced substantial habitat loss and fragmentation (Vörösmarty *et al.*, 2010), lakes have mostly suffered from eutrophication, shoreline development, pollution and climate change (Brönmark & Hansson, 2002). Moreover, invasions by non-native species have become an important threat for freshwater ecosystems (Rahel, 2007). Today, freshwater biodiversity is declining at an alarming rate, with 37% of Europe's freshwater fish species categorized as threatened (Freyhof & Brooks, 2011). Habitat loss has been identified as the key stressor that impacts freshwater biodiversity (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010), but novel threats are on the rise (Reid *et al*., 2018).

Gravel pit lakes are lentic water bodies created through human mining of sand, clay, gravel and other natural resources. When properly managed, these novel aquatic ecosystems can counteract the freshwater biodiversity crisis by providing secondary habitats for a wide range of aquatic species (Dodson *et al*., 2000; De Meester *et al*., 2005; Santoul *et al*., 2009; Lemmens *et al*., 2013; Emmrich *et al*., 2014; Zhao *et al*., 2016; Biggs *et al*., 2017). Gravel pits are usually groundwater-fed and not necessarily connected to surrounding river systems (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard *et al.*, 2018); they thus display the interesting biogeographic feature of islands in a landscape (Olden *et al.*, 2010). This characteristic causes a slow natural colonisation and a potentially low species richness (Magnuson *et al.*, 1998), yet, gravel pit lakes as novel ecosystems are understudied relative to natural water bodies (Emmrich *et al*., 2014; Søndergaard *et al*., 2018).

Sand and gravel are extracted all over Europe in thousands of quarries and pits (e.g. over 23.000 quarries and pits in 2014 alone; UEPG, 2017). The resulting man-made lakes have thus become common landscape elements in industrialized countries (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard *et al.*, 2018). For example, in our study area of Lower Saxony, Germany, there are today more than 3,500 gravel pit lakes with an area larger than 1 ha, representing 95% of all similarly sized water bodies and covering 70 % of the total lentic water bodies in the region (Manfrin *et al*., unpublished data). Thus, gravel pits are the dominant lentic habitat in northwest Germany and accordingly, important for both biodiversity conservation and recreation (Emmrich *et al*., 2014).

Following well established species-area relationships, in northern Germany fish species richness in natural lakes is related to areal size, with more species occurring in larger natural lakes (Eckmann, 1995). Hence, comparably small gravel pit lakes are expected to naturally contain species-poor fish communities, and may due to their young age even lack fish populations (Schurig, 1972; Scheffer *et al*., 2006; Søndergaard *et al*., 2018; Werneke *et al*., 2018). There are natural pathways for the colonization of gravel pit lakes by fish, e.g., in river-fed gravel pits the immigration of fish with the inflow from the river is well documented (Molls & Neumann, 1994; Staas & Neumann, 1994; Borcherding *et al.*, 2002). However, the chances of fish to colonize isolated, recently formed water bodies is rather low (Scheffer *et al.*, 2006; Strona *et al.*, 2012). Natural colonization is then confined to rare events such as massive floods (Pont *et al.*, 1991; Olden *et al.*, 2010) or wind-based dispersal through hurricanes (Bajkov, 1949). Dispersal of eggs by waterfowl has, despite frequent claims, not been documented with certainty (Hirsch *et al.*, 2018). Accordingly, natural colonization of isolated gravel pit lakes is most probably a slow process resulting in species-poor local fish communities (i.e., low alpha diversity) and high between lake variation in the species pool (i.e., high beta diversity) within a region (Whittaker, 1972; Baselga, 2010).

Illegal releases from aquaria, garden ponds or bait buckets, or planned stocking within fisheries-management activities represent anthropogenic pathways that assist in colonization of human-made freshwater systems with fishes. In fact, human-assisted introductions today constitute the most common pathway of non-native fish dispersal globally (Gozlan *et al*., 2010; Olden *et al*., 2010; Patoka *et al*., 2017; Hirsch *et al*., 2018). It is thus likely that most gravel pits are more rapidly colonized with fishes through anthropogenic than through natural means.

In central Europe, the majority of gravel pit lakes are managed by recreational anglers organized in clubs and associations (Deadlow *et al*., 2011). Managers of angling clubs and other fisheries stakeholders regularly engage in fish stocking of native fishes in rivers and lakes (Cowx, 1994), including gravel pit ecosystems (Arlinghaus, 2006; Arlinghaus *et al*., 2015; Zhao *et al*., 2016; Søndergaard *et al*., 2018). However, not all newly created gravel pits are managed for and by recreational anglers. Although managed gravel pit lakes are far more numerous, in Germany, fishing rights of selected gravel pit lakes are sometimes not leased out to angling clubs and may instead be used by private people, enterprises or nature conservation organisations. These lakes may even be closed to recreational fisheries and be maintained for use by private people or for nature conservation purpose. In our study area of north-western Germany, the main discriminating factor of angler-managed and unmanaged gravel pit lakes is the presence of dedicated recreational-fisheries management in managed lakes, which includes regular fish stocking. While unmanaged gravel pit lakes may still receive illegal fish releases (Johnson *et al*., 2009), these lakes are not regularly stocked with a mix of species desired by recreational anglers and can thus be expected to represent more natural colonization pathways compared to managed lakes (Supporting information table 1).

Regular fish stocking in managed gravel pit lakes may increase alpha diversity (i.e., local species richness) but reduce beta diversity through the process of biotic homogenization (Radomski & Goeman, 1995; Rahel, 2000, 2002), particularly when fisheries managers stock a rather similar mix of angler-desired species (e.g., top predators, Eby *et al.*, 2006). A recent study of French gravel pit lakes indeed revealed that the fish community composition was strongly influenced by recreational angling as managed gravel pit lakes hosted more non-native species of high fisheries value, particularly top predators and common carp *Cyprinus carpio* L. compared to unmanaged gravel pit lakes (Zhao *et al.*, 2016). The objective of the present study was to compare the fish communities between managed and unmanaged gravel pit lakes in north-western Germany. We hypothesized that relative to unmanaged lakes recreational-fisheries management would lead to:

(1) an increase in local species richness, i.e. alpha diversity;

(2) an increase in the number of piscivorous and other highly desired game species;

(3) an increase in the number of non-native species, such as topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel 1846), that maybe introduced as prey species or inadvertedly through poorly sorted stocking material from pond aquaculture. Further, we hypothesized that the lakes managed by anglers would host more similar fish communities compared to the unmanaged lakes, and therefore that recreational-fisheries management would lead to:

(4) a decrease in beta diversity through biotic homogenisation.

2. Material and Methods

2.1 Study lakes and fish sampling

We surveyed the fish communities and a range of limnological lake descriptors in 23 gravel pit lakes located in the lowlands of Lower Saxony, north-western Germany in the Central Plain ecoregion (Fig. 1). A description of the basic differentiation of managed and unmanaged lake types can be found in Supporting Information table 1.

For each lake, two ages were determined; the onset and the end of gravel mining, as gravel pits started filling up with water and potentially became colonized by fish already before the end of mining. The depth was measured hydro-acoustically using a Simrad NSS evo2 with a Lowrance TotalScan transducer in parallel transects spaced about 30 m apart. These data were used to calculate depth contour maps using ordinary kriging in R (for further details see Supplementary of Monk & Arlinghaus, 2017). The contour maps were used to extract key morphometric variables of the lake (mean depth, maximum depth, shoreline length and area), including estimation of areas covered by different gillnet depth strata according to the CEN standard (2015) for the sampling of lake fish communities with multimesh gillnets (0 - 2.9 m, 3 - 5.9 m, 6 – 11.9 m, 12 – 19.9 m and 20 – 34.9 m). The morphometric data were also used for the calculation of the shoreline development factor (Osgood, 2005) and the share of the littoral zone (%; defined as area between 0 and 2.9 m depth).

Macrophyte coverage was visually estimated through diving using the Braun-Blanquet-scale and later transformed into percent coverage (Schaumburg et al., 2004). The perpendicular located transects varied between 4 and 20 depending on the lake size. In each transect, the macrophyte coverage of each macrophyte depth stratum (0 – 1 m, 1 – 2 m, 2 – 4 m and 4 – 6 m) was estimated. No macrophytes were found in areas deeper than 6 m. The average coverage per stratum was extrapolated to its respective total lake area drawn from the contour maps. Afterwards, the total macrophyte coverage for the lake was calculated using the extrapolated coverage from each stratum relative to its share of the total lake area.

The fish communities were sampled using day-time electrofishing in the littoral and multimesh gillnets in the benthic and profundal zones in autumn 2016 and 2017. During each fish sampling campaign, the lake's Secchi depth, conductivity and pHvalue were measured with a WTW Multi 350i sensor (WTW GmbH, Weilheim, Germany). In addition, at the deepest point of the lake an oxygen-depth-temperature profile was taken in steps of 50 cm also using the WTW Multi 350i sensor, and epilimnic water samples were taking for analysing total phosphorus concentrations (TP) and chlorophyll a (Chl a) as a measure of algal biomass. The TP was determined using the molybdenum blue method (ISO, 2004; Zwirnmann *et al*., 1999) and Chl a using high performance liquid chromatograph (Mantoura & Llewellyn, 1983; Wright *et al.*, 1991).

Littoral electrofishing was conducted from a boat by a two person crew using a FEG 8000 electrofishing device (8 kW; 150 - 300V / 300 - 600V; EFKO Fischfanggeräte GmbH Leutkirch) with one anodic hand net (40 cm diameter and mesh size 6 mm) and a copper cathode. Prior to sampling, the shoreline was divided in transects measuring between 50 and 160 m depending on local conditions. Shoreline habitats covered reeds, overhanging trees and branches, submersed and emersed macrophytes, unvegetated littoral zones with no or low terrestrial vegetation (in particular representing angling sites) and mixed habitats that were not dominated by one of these structures. Each transect was fished and enumerated separately. The number of transects per lake varied between 4 and 26, depending on the lake size. The length of all transects summed up to the whole lake shore except for the two largest lakes where in total only about two thirds of the shoreline were fished using random selection of transects. Littoral electrofishing was conducted in 16 managed and 4 unmanaged lakes from late August to early October 2016 when the water temperature was > 15°C. Multimesh gillnets were set for one night (approximately 12 hours) per lake following CEN (2015). An additional electrofishing sampling of the entire shoreline of the 16 managed and 4 unmanaged lakes was carried out from late August to mid-October in 2017. Additionally, in autumn 2017 three further unmanaged gravel pit lakes (for a total sample of 7 unmanaged lakes) were sampled by littoral electrofishing of the whole shoreline and multimesh gillnets following the same procedure as in 2016. Electrofishing data were standardized by meter shoreline fished for estimation of lake-wide catch per unit effort data as relative abundance index.

The multimesh gillnets differed slightly from the CEN standard (Appleberg, 2000; CEN, 2015) in a way that we included four additional mesh sizes with the attempt to also representatively capture large fishes up to 530 mm total length (Šmejkal *et al.*, 2015). The benthic gillnets had a length of 40 m, a height of 1.5 m and were composed of 16 mesh-size panels each being 2.5 m long, with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110 and 135 mm. For lakes < 20 ha the European gillnet sampling standard (CEN, 2015) considers a minimum of 8 or 16 gillnets, depending on whether the maximum depth is below or exceeds 12 m, respectively. As the largest gravel pit lake in our study (Meitzer See, 19.6 ha, 23.5 m depth) corresponds to the smallest lake in the CEN standard (20 ha), the gillnet sampling effort had to be adjusted to the smaller lakes to maintain a similar gillnet to total area ratio in all sampled lakes. This was achieved by applying the minimum number of 16 standard gillnets to the largest lake in our sample and calculating the quotient of the area of the 16 gillnets to total lake area as a measure of gillnet sampling pressure. Using this ratio, we calculated the appropriate gillnet numbers in smaller lakes to achieve the same sampling intensity in each lake, assuming that the fish encounter probability with a gillnet would scale with gillnet coverage.

The final number of gillnets set in each lake were distributed following a stratified sampling design by gillnet depth strata, where number of gillnets per stratum were set in proportion of the share of each depth stratum’s area to total lake surface area (CEN, 2015). Gravel pit lakes with an area larger than 10 ha or a maximum depth of ≥ 10 m were additionally sampled with pelagic multimesh gillnets to record open water species not captured otherwise (CEN, 2015). One pelagic multimesh gillnet was set in each of the following vertical depth strata: 0 - 1.5 m, 3 – 4.5 m, 6 – 7.5 m, 9 - 10.5 m and 12 – 13.5 m, but only if the depth strata contained >1 mg O_2 L^{-1}. We set benthic gillnets in anoxic conditions to confirm zero catches at oxygen levels below 1 mg O_2 L^{-1}. Note the pelagic gillnets were only used to complete the species inventory (presence-absence data) as recommended in the CEN standard (CEN, 2015), but not used for the fish abundance and biomass estimates in the benthic zone. Benthic biomasses and abundances were estimated as stratified means per area and night fished following CEN (2015).

Total length of all fish captured was measured to the nearest mm and weighted to the nearest g. In case of large fish catches, at least 10 fish per species and 2 cm length class were measured and weighted. Afterwards, fish were only measured for length and the weight was calculated with lake-specific length-weight regressions. Only in the rare case of catching several hundreds of young-of-the-year fish by electrofishing, a random subsample was measured for length and mass. Subsequently, all the other fish were pooled and weighted, then the number and length-frequency distribution of the whole sample was estimated using the length-frequency distribution of the subsample.

2.2 Fish community descriptors

For all calculations and analyses, data from 2016 and 2017 were pooled. This results in electrofishing data in 20 lakes from two years and in three lakes from only one year. Furthermore, data from one autumn sampling per lake with multimesh gillnets were analysed.

Species richness, number of piscivorous species, number of small-bodied non-game fish (after Emmrich *et al.*, 2014), number of threatened species (after the Red List of Lower Saxony, LAVES, 2011, the Red List of Germany, Freyhof, 2009, and the European Red List, Freyhof & Brooks, 2011), and number of non-native species in Germany (after Wiesner *et al.*, 2010 and Wolter & Röhr, 2010) were calculated to describe species inventory based presence-absence data, combining electrofishing (littoral zone) and multimesh gillnet data (benthic and pelagic). Perch *Perca fluviatilis* (L.) > 150 mm and eel *Anguilla anguilla* (L.) > 500 mm total length were assigned to the piscivorous fish guild, following Emmrich *et al.* (2014). Cyprinid hybrids were listed as fish caught in the gravel pit lakes (Table 1), but excluded from further analyses of species-specific patterns.

Species richness was used to compare alpha diversity between the management types. The number of piscivorous species was used as a fish community descriptor as anglers preferably catch predatory fishes and regularly stock these (Arlinghaus *et al.* 2015). We also assessed the number of small-bodied non-game fish species as many of these species are relevant in a conservation context. Also, many small-bodied species are pioneer colonizer of lakes, e.g. sunbleak *Leucaspius delineatus* (Heckel 1843; Kottelat & Freyhof, 2007). The number of threatened species was contrasted between the two management types to assess the potential impact of fisheries management on fish conservation objectives. Furthermore, the number of non-native species was compared among management types, as fish stocking is believed to promote the spread of exotic fishes, particularly in gravel pit lakes (Zhao *et al.*, 2016; Søndergaard *et al.*, 2018).

To assess the fish community composition, the mean lake-specific catch per unit effort (CPUE) was calculated as number per unit effort (NPUE) with individuals per shoreline length (N / 50 m) or gillnet area (N / 100 m²) and as biomass per unit effort (BPUE) with biomass per shoreline length (g / 50 m) or gillnet area (g / 100 m²). Note, only benthic gillnets were used for the gillnet CPUE calculation.

We compared all four species inventory metrics (piscivorous fish, small-bodied non-game fish, threatened fish, non-native fish) as well as the total and species-specific catch (abundance and biomass) among managed and unmanaged gravel pit lakes. We additionally calculated a further fish diversity index, the Shannon diversity combining presence-absence and species-specific abundance (Shannon, 1948), and compared the index between the two management types.

2.3 Statistical analysis

A principle component analysis (PCA) was conducted to visualize the distribution of the lakes in relation to the scaled and centred environmental variables. Afterwards, a redundancy analysis (RDA) was used to test for significant differences between the two management types in their scaled environmental variables. A Welch two sample t-test was conducted to test for mean fish community and diversity differences between the two management types when raw variables or $\log_{10}$-transformed variables were normally distributed and showed homogeneity of variances. In all other cases, a Wilcoxon rank sum test was performed. A conservative Bonferroni correction was used for all multiple pairwise comparisons.

Following Anderson *et al.* (2011), beta diversity of the fish communities in managed and unmanaged gravel pit lakes was visualized by non-metric multidimensional scaling (nMDS; Kruskal, 1964) using Bray-Curtis distances on species numbers and species-specific abundances and biomasses. A permutation test for homogeneity of multivariate dispersions (permutations: N = 9999) was performed to test for significant differences in the fish communities. To identify those species strongly contributing to the average dissimilarity between the two management types a similarity percentage analysis (SIMPER; permutations: N = 999; Clarke, 1993) was used. Finally, an average species accumulation curve (permutations: N = 100*;* Chiarucci *et al*., 2008; Colwell *et al*., 2012) was used to display the contribution of both management types to the regional overall fish biodiversity (gamma diversity) and to further visualize average local diversity (alpha diversity) and between management type variation in diversity (beta diversity). Differences between species accumulation curves of the both management types were tested against the species accumulation curve of all lakes pooled using Wilcoxon signed rank tests. All statistical analyses were conducted using R version 3.2.2 (R Core Team, 2016) and the package *vegan* (Oksanen *et al.*, 2018).

3. Results

3.1 Environmental variables in managed and unmanaged lakes

Managed gravel pit lakes varied between 1.0 and 19.5 ha in size with a shoreline length ranging from 417 to 2752 m. Unmanaged gravel pit lakes ranged from 2.1 to 10.6 ha in size and varied between 749 and 2091 m in shoreline length. The environmental variables differed among individual lakes, but were relatively similar among both management types, with the exception that the lake age was somewhat elevated in the managed lakes (Fig. 2). The PCA (Fig. 3) recovered two axes. The PC1 explained 31.6% of the variance and was mainly represented by morphometric variables: mean depth (loading = 0.44), maximum depth (loading = 0.44) and share of the littoral (loading = -0.42). The PC2 described 19% of the variance and was represented by morphometric variables and lake age: shoreline length (loading = -0.43), lake age end of mining (loading = 0.43) and lake area (loading = -0.36; Fig. 3).

The RDA revealed no differences in the environmental variables between the two management types (F = 1.022, p = 0.407).

3.2 Overview of fish diversity and community composition

In total, 117,303 fish were sampled, 108,237 individuals by electrofishing and 9,066 by gillnetting. The fish community in the 23 gravel pit lakes consisted of 23 fish species and one cyprinid-hybrid (Table 1). All lakes contained at least three fish species. *Perca fluviatilis* and roach *Rutilus rutilus* (L.) were found in all managed lakes, while they were present in less than a third of the unmanaged lakes. Piscivorous species such as pike *Esox lucius* L., *Anguilla anguilla* and pikeperch *Sander lucioperca* (L.) were also regularly found in managed, but only occasionally or not at all in unmanaged gravel pit lakes (Table 1). Littoral species, such as *Esox lucius*, *Anguilla anguilla* and tench *Tinca tinca* (L.), were mainly or even exclusively caught by electrofishing, while large individuals of less littoral-bound species such as *Perca fluviatilis* and *Rutilus rutilus* as well as *Sander lucioperca* were better detected by gillnetting.

Of the species pool of 23 species, *Anguilla anguilla*, *Sander lucioperca*, ruffe *Gymnocephalus cernua* (L.), white bream *Blicca bjoerkna* (L.), bitterling *Rhodeus amarus* (Bloch 1782), European whitefish *Coregonus lavaretus* (L.), spined loach *Cobitis taenia* L. and bleak *Alburnus alburnus* (L.) were only caught in managed gravel pits, while sunbleak *Leucaspius delineatus* (Heckel 1843), nine-spined stickleback *Pungitius pungitius* (L.), gudgeon *Gobio gobio* (L.), stone loach *Barbatula barbatula* (L.) and brown bullhead *Ameiurus nebulosus* (Lesueur 1819) only occurred in unmanaged gravel pits (Table 1). Note the non-native *Ameiurus nebulosus* was only detected as a single individual.

3.3 Contrasting the fish species diversity among managed and unmanaged lakes

On average, species richness (Wilcoxon rank sum test, $W = 111$, $p = 0.001$), number of piscivorous species (Wilcoxon rank sum test, $W = 111$, $p < 0.001$), and number of threatened species (Wilcoxon rank sum test, $W = 110$, $p < 0.001$) were significantly higher in managed gravel pit lakes compared to unmanaged lakes (Fig. 4). No significant differences between the two management types were found in the numbers of small-bodied non-game fish species (Wilcoxon rank sum test, $W = 37$, $p = 0.897$) and the number of non-native species (Wilcoxon rank sum test, $W = 43.5$, $p = 0.763$). The Shannon index revealed an overall greater diversity of littoral fishes in terms of abundance (NPUE; $p = 0.022$) in managed gravel pit lakes compared to those that were unmanaged (Table 2).

To investigate differences of the fish communities regarding beta diversity, nMDS biplots were constructed using presence-absence data (Fig. 5) and using abundance and biomass data (NPUE and BPUE) of each fishing gear separately (Fig. 6). Strong variation in the fish diversity and the fish community composition was visually striking between the unmanaged lakes (grey circles; Fig. 5 and 6). By contrast, the managed gravel pit lakes (black triangles) comprised a relatively small area in the nMDS biplots indicating a more similar fish diversity and fish community composition between individual managed lakes. Correspondingly, permutation tests revealed a significantly greater beta diversity for unmanaged gravel pit lakes compared to managed lakes using presence-absence data ($F = 88.401$, $p < 0.001$; Fig. 5), littoral species-specific fish abundance and biomass (NPUE: $F = 6.871$, $p = 0.017$; BPUE: $F = 12.856$, $p = 0.001$) and benthic species-specific fish abundance and biomass (NPUE: $F = 13.595$, $p = 0.001$; BPUE: $F = 10.106$, $p = 0.005$; Fig. 6).

The same pattern of larger beta diversity in unmanaged lakes was visually recovered by the steeper slope of the species accumulation curve in the unmanaged lakes compared to the managed lakes (Fig. 7), yet as before average local species richness was found to be larger in the managed compared to the unmanaged lakes (indicated by the greater intercept for managed lakes compared to unmanaged lakes in Fig. 7). Importantly, gamma diversity was significantly larger when combining the species pools present in the managed and the unmanaged lakes (comparing the combined species accumulation curve relative to each management type separately, managed lakes N = 16; V = 130, $p < 0.001$, unmanaged lakes N = 7; V = 28, $p = 0.016$, Fig. 7). Thus, regional species richness benefited from the distinct specific species pools present in both management types.

3.4 Contrasting species-specific fish abundance and biomass in managed and unmanaged lakes

No differences in total fish abundance (NPUE) and biomass (BPUE) were detected between the two management types, neither for electrofishing nor for multimesh gillnetting (Table 2). By contrast, greater abundances and biomasses (for both gear types) were found for piscivorous fish in managed gravel pit lakes compared to unmanaged lakes, however, after conservative Bonferroni correction differences were no longer significant. For species threatened in the study region of Lower Saxony (*Anguilla anguilla*, *Esox lucius*, European catfish *Silurus glanis* L., *Rhodeus amarus* and *Cobitis taenia*) higher littoral abundances ($p = 0.007$) and biomasses ($p = 0.015$) were detected in managed lakes compared to unmanaged lakes.

Two individuals of non-native *Pseudorasbora parva* were caught in one managed lake, while one specimen of *Pseudorasbora parva* was caught in an unmanaged lake, and one specimen of *Ameiurus nebulosus* was caught in another unmanaged lake. Thus, the presence and abundance/biomass of non-natives bordered detectability and accordingly did not differ among management types.

The SIMPER analysis revealed *Leucaspius delineatus*, *Perca fluviatilis*, rudd *Scardinius erythrophthalmus* (L.) and *Pungitius pungitius* contributing 74.8% to the differences between the two management types in the littoral fish community as assessed by electrofishing abundance data (NPUE; Table 3). As mentioned before, *Leucaspius delineatus* and *Pungitius pungitius* were not detected in managed gravel pit lakes, and they contributed significantly to the differences in the littoral fish community among management types (*Leucaspius delineatus*: p = 0.019, *Pungitius pungitius*: p = 0.009; Table 3). In terms of littoral fish biomass (BPUE), *Anguilla anguilla*, Prussian carp *Carassius gibelio* (Bloch 1782) and *Esox lucius* contributed most to the differences between the two management types, but due to high among lake variation in biomass for these species only littoral *Perca fluviatilis* biomass significantly differentiated among managed and unmanaged gravel pit lakes (p = 0.033), revealing significantly greater biomasses in managed lakes (Table 3).

When taking the multimesh gillnet data (NPUE and BPUE) as a metric of benthic fish community, *Perca fluviatilis* and *Rutilus rutilus* revealed the highest contribution to the difference in the fish community between the two management types, with significantly higher biomasses of *Perca fluviatilis* in managed gravel pit lakes (p = 0.020; Table 3). Furthermore, the benthic biomass of *Scardinius erythrophthalmus* differed significantly among management types, with a greater average biomass detected in unmanaged lakes (p = 0.031; Table 3). In terms of abundance (NPUE), *Leucaspius delineatus* was a significantly discriminatory species, who was found in multimesh gillnet catches only in unmanaged lakes (p = 0.013; Table 3).

4. Discussion

4.1 General findings

We compared the fish communities in angler-managed and unmanaged gravel pit lakes. The results supported three out of four of our hypotheses. In particular, species richness (H1) and the number of piscivorous species (H2) were significantly higher in managed gravel pit lakes. Furthermore, we found a larger number of threatened species and higher littoral abundances and biomasses of threatened fish in managed gravel pit lakes, while there were no differences in the number of small bodied non-game fish species among management types. Hence, as hypothesized, managed gravel pit lakes were found to contain a higher alpha diversity (local species richness). In contrast to our expectations (H3), the catches of non-native fish were low in both management types and not significantly greater in managed water bodies. The forth hypothesis of lower beta diversity in managed gravel pit lakes (H4) also received substantial support. The species-rich fish communities in managed lakes were more similar to each other than the species-poor fish communities in unmanaged lakes, suggesting biotic homogenization caused by recreational-fisheries management, particularly due to regular stocking.

4.2 Robustness of results to sampling bias

Both groups of gravel pits studied, whether managed by recreational fishing clubs or not, were similar in key environmental characteristics, such as morphology (e.g. lake area) and productivity – factors known in shaping lentic fish communities in the temperate regions (e.g. Persson *et al*., 1991; Jeppesen *et al*., 2000; Mehner *et al*., 2005). This underscores that the fish community differences we report were most likely a result of recreational-fisheries management and exploitation.

We used electrofishing and multimesh gillnetting to sample the fish community in the gravel pit lakes as adequately as possible because it is known that multiple fishing gears are needed to determine species richness and the habitat-specific abundance and biomass in lentic waters (Barthelmes & Doering, 1996; Diekmann *et al*., 2005; Jurajda *et al*., 2009; Scharf *et al*., 2009; Achleitner *et al*., 2012; Menezes *et al*., 2013; Mueller *et al*., 2017). Three unmanaged gravel pit lakes were only sampled once in 2017. This lower sampling effort in a subset of the unmanaged lakes might have underestimated rare species (Lyons, 1992; Angermeier & Smogor, 1995; Paller, 1995). However, when comparing mean species richness of managed and unmanaged lakes based on one fishing occasion in 2017 only, virtually identical results were obtained (results not shown). Thus, our conclusion of lower species richness in unmanaged lakes appeared to constitute a robust finding.

The benthic zone was sampled using multimesh gillnets following European standards (CEN, 2015). We adapted the gillnet numbers to lake size to harmonize fishing pressure across lakes. Following Šmejkal *et al.* (2015) we also supplemented the standard mesh sizes by a few larger mesh size panels to sample fish up to 530 mm total length more representatively. However, certain large-bodied species known to occur in Lower Saxonian gravel pit lakes (Schälicke *et al.*, 2012) and other angler-managed lakes in Germany (Borkmann, 2001), in particular large-bodied cyprinids such as *Cyprinus carpio*, might still be underrepresented in our sample. This finding most likely affected the abundance and biomass estimates by missing larger bodied individuals, yet this bias has unlikely affected the species inventory as we regularly captured *Cyprinus carpio* in all lakes where the local fisheries managers reported regular stocking of this species. Longer panels of large mesh sizes are needed to more representatively sample large-bodied individuals of *Cyprinus carpio* and top predators (e.g., *Esox lucius*, *Silurus glanis*, *Sander lucioperca*), yet such data would only reinforce our findings of a greater presence of angler-desired species and sizes in managed relative to unmanaged lakes. However, a possible underestimation of the total fish biomass in managed lakes cannot be ruled out and should thus be addressed in the future by using gillnets with longer panels of larger mesh sizes.

4.3 Species richness and presence of predators

Species richness and the number of piscivorous species were higher in gravel pit lakes managed for recreational fisheries, supporting our first two hypotheses. Agreeing with our results, a greater alpha diversity in lakes managed by and for recreational fisheries has previously been demonstrated for gravel pit lakes in southern France (Zhao *et al.*, 2016) and Minnesota lakes (Radomski & Goeman, 1995). Additionally, in managed gravel pit lakes we also detected a higher Shannon diversity of the littoral fish community in terms of abundance underlining the higher fish biodiversity present in managed lakes. Fisheries managers tend to introduce and stock preferentially high trophic level species (Eby et al., 2006; Arlinghaus et al., 2015) and large-bodied cyprinid fish such as *Cyprinus carpio* and *Tinca tinca* (Arlinghaus *et al*., 2015) to meet local angler demands (Arlinghaus & Mehner, 2004; Beardmore *et al*., 2011; Donaldson *et al*., 2011; Ensinger *et al*., 2016). Our data strongly support this management behaviour in angler-managed gravel pit lakes.

The high-demand species *Anguilla anguilla*, *Esox lucius* and *Perca fluviatilis* were found in all or almost all managed gravel pits. While *Esox lucius* and *Perca fluviatilis* become established and reproduce naturally after introduction, the abundance of *Anguilla anguilla* in the gravel pits we studied (who all lacked connections to nearby rivers) clearly indicates ongoing stocking. Correspondingly, no *Anguilla anguilla* and hardly any top predators, which are popular as game fishes, were found in unmanaged lakes. Accordingly, presence-absence of *Anguilla anguilla* was one of the major dissimilarities between the two management types following our SIMPER analyses (Supporting Information table 6). In gravel pit lakes managed for recreational fisheries, a higher relative frequency of *Anguilla anguilla* has previously been reported compared natural lakes predominantly managed for commercial fisheries (Emmrich *et al.*, 2014; Arlinghaus *et al.*, 2016), either indicating continuous stocking of eel into angler-managed gravel pit lakes or lower recapture rates relative to commercial fisheries. Given the poor conservation status of catadromous *Anguilla anguilla* (e.g. Bark *et al.*, 2007; Dekker, 2016), continuous stocking of this species into isolated lakes is problematic from a conservation perspective.

<u>4.4 Small-bodied non-game fish and threatened species</u>

Small-bodied *Rutilus rutilus*, *Alburnus alburnus* or *Perca fluviatilis* are considered forage fish for predators and are therefore regularly stocked in Germany (Arlinghaus et al., 2015). We found *Rutilus rutilus* and *Perca fluviatilis* in all managed gravel pits, but only in a few unmanaged ones. Both species are common and widespread in the Central Plain ecoregion and constitute key elements of reference fish communities in natural lakes (Mehner *et al.*, 2005; Emmrich *et al.*, 2014; Ritterbusch *et al.*, 2014). Already widespread species have, when becoming translocated to new water bodies, the highest fauna-homogenizing effects (Sommerwerk *et al*., 2017). Therefore, fisheries management fosters faunal homogenization by further establishing naturally widespread percid and cyprinid species.

Small-bodied non-game fish species were also found in both management types, but their occurrence strongly differed between management types. *Gymnocephalus cernua*, *Rhodeus amarus*, *Cobitis taenia* and *Alburnus alburnus* exclusively occurred in managed lakes, while *Leucaspius delineatus*, *Pungitius pungitius*, *Gobio gobio* and *Barbatula barbatula* were only caught in unmanaged lakes. *Leucaspius delineatus* and *Pungitius pungitius* strongly contributed to the average dissimilarity between the two management types. However, at the aggregate level, lakes of both management types hosted the same average number of small-bodied non-game fish species. On first sight, this rather surprising finding likely results from angling clubs regularly engaging in the release of non-game fishes for species conservation purposes. However, the release volumes of small-bodied species is small compared to the stocking density of game fishes (Arlinghaus *et al*., 2015), and the activity strongly varies by angling club type (Theis, 2016; Theis *et al.*, 2017). Angling-club specific releases of non-game species and other stochastic events related to establishment and natural colonization (Copp *et al.*, 2010) can collectively explain the large variation in the presence of small-bodied non-game species among lakes.

The studied lakes hosted a total number of five regionally threatened species, three of them exclusively in managed lakes indicating their potential for species conservation (Emmrich *et al.*, 2014). Note, however, that none of these regionally threatened freshwater species is listed in the national German Red List of freshwater fishes (Freyhof, 2009). Only *Anguilla anguilla* is globally threatened according to IUCN criteria (Freyhof & Brooks, 2011). Therefore, the conservation value of gravel pit lakes is confined to species that are regionally, yet not nationally, threatened.

4.5 Presence of non-native fish

The hypothesized support of non-native species introductions and accumulation of exotics by recreational-fisheries management as revealed for example in a French gravel pit study by Zhao *et al.* (2016) was not confirmed for gravel pit lakes in north-western Germany. It must be noted that several of the angler-desired fish species reported invasive for France (Zhao *et al*., 2016) are native to Germany, e.g. *Cyprinus carpio*, *Sander lucioperca* and *Silurus glanis*. In our study, only two individuals of non-native *Pseudorasbora parva* were found in one of 16 managed lakes, which were most likely unintendedly introduced through poorly sorted stocking of pond-reared *Cyprinus carpio* or poorly sorted stocking of wild-captured cyprinids (e.g. Copp *et al.*, 2005b; Wiesner *et al.*, 2010). In comparison, in two out of seven unmanaged lakes, one individual of either non-native *Pseudorasbora parva* or non-native *Ameiurus nebulosus*, were detected, showing that also unmanaged lakes receive non-natives. Illegal stocking from anglers interested in establishing desired species in a certain waterbody or releases of fish by owners of garden ponds or other private people, as indicated by a golden variety of *Scardinius erythrophthalmus* found in one unmanaged lake, have been reported vectors for fish dispersal around the globe (Copp *et al*., 2005a; Johnson *et al*., 2009; Hirsch *et al*., 2018). In fact, today, illegal release, often by non-angling stakeholders, rather than purposely planned fisheries management constitutes the most important pathway for the transfer of non-natives fishes across the world (Copp *et al.*, 2010). To conclude, in our study region proper recreational-fisheries management is not per se supportive for non-native species establishment, whilst not managing lakes for fisheries does not guarantee for their lack of establishment either.

4.6 Biotic homogenization caused by fisheries management

In agreement with our hypothesis, recreational-fisheries management collectively contributed to the homogenization of fish faunas, reducing beta diversity in fish communities compared to unmanaged lakes. Homogenization of fish communities as a result of anthropogenic influences has been repeatedly found across the world (Radomski & Goeman, 1995; Rahel, 2000; Villéger *et al.*, 2011). Gravel pit lakes in north-western Germany are no exception. In contrast to other studies, we can largely exclude non-fishing related impacts, because only the presence or absence of recreational-fisheries management discriminated among our study lakes. As natural lakes in Germany with similar key environmental characteristics (e.g., in relation to lake depth and productivity) were previously found to host rather similar (i.e., homogenous) fish communities (Diekmann *et al*., 2005; Mehner *et al*., 2005; Brucet *et al*., 2013; Ritterbusch *et al*., 2014), the results of our managed gravel pit lakes match the expectations of fish communities in natural lakes. One limitation to this statement is that also most of the natural lakes assessed by Diekmann *et al.* (2005), Mehner *et al.* (2005) and Emmrich *et al.* (2014) and used by Ritterbusch *et al.* (2014) to derive reference fish communities for lakes were managed for fisheries presently or in the past.

4.7 Conclusions and implications

Proper management of recreational fisheries does not necessarily lead to the development of artificial fish communities with many non-native fish species. Instead, we found recreational fisheries to foster local fish species diversity and the establishment of fish communities that are similar to those present in managed natural lakes of similar environmental characteristics in relation to size, depth and eutrophication (Emmrich *et al*., 2014; Ritterbusch *et al*., 2014). If newly created aquatic ecosystems would not be managed for fisheries, the establishment of a near-natural, species-rich fish community would likely take substantially longer. Such development would also be strongly influenced by stochastic events through natural and anthropogenic pathways that shape the specific local species pool in unmanaged lakes. Importantly, not managing gravel pit lakes for fisheries does not mean these systems remain fish free. Overall, the presence of both management types in a region increases the regional species pool (gamma diversity), because recreational-fisheries management in gravel pit fosters local species richness, at the cost of biotic homogenization.

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Contributions

SM: ideas, data generation, data analysis, manuscript preparation

ME: ideas, data generation, data analysis, manuscript editing

TK: data generation, manuscript editing, funding

CW: manuscript editing, funding

RN: data generation, data analysis, manuscript editing

NW: ideas, data generation, data analysis

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