

Fish communities in gravel pit lakes: The impact of fisheries management and littoral structures

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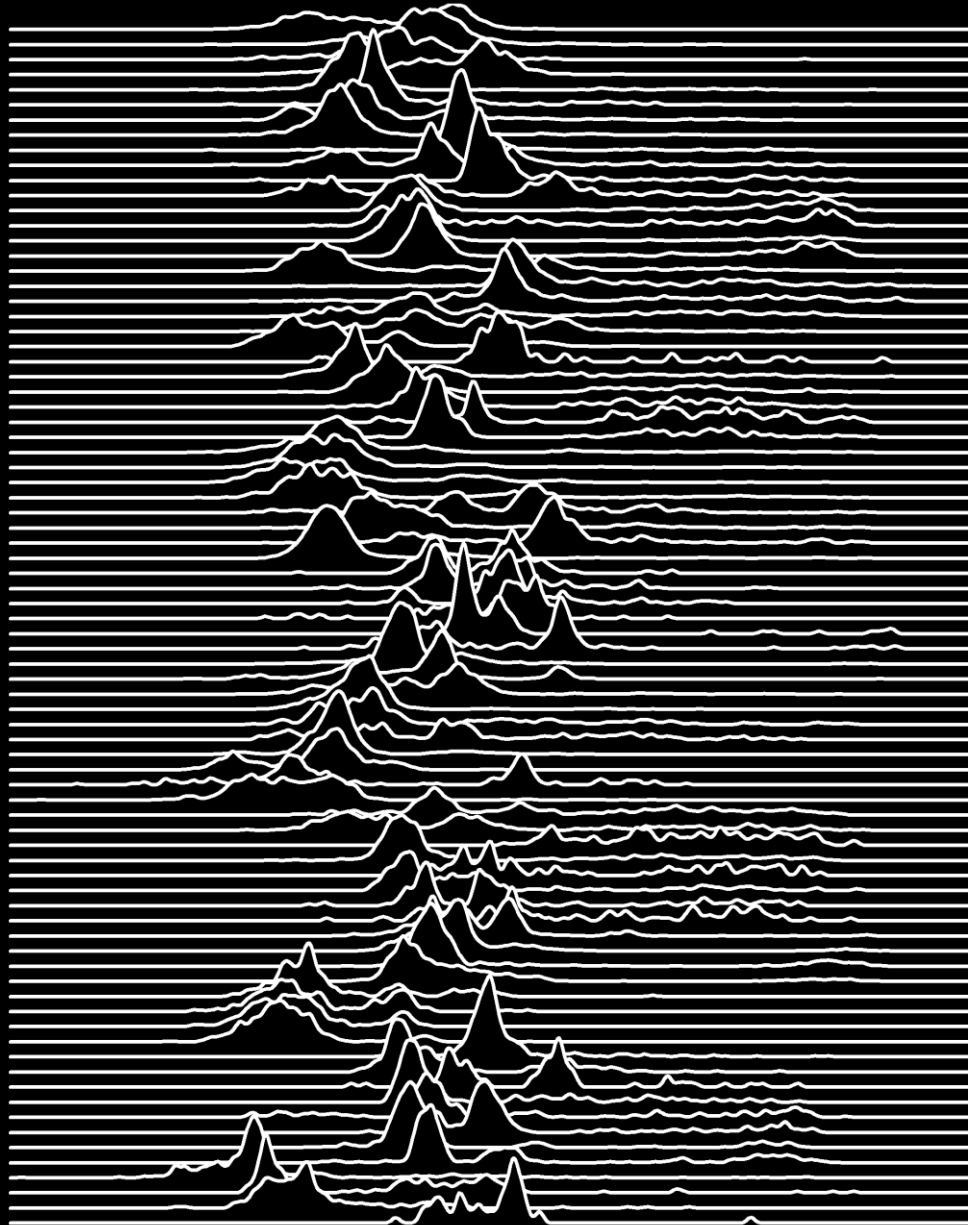
Fish communities in gravel pit lakes: The impact of fisheries management and littoral structures

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**Fish communities in gravel pit lakes:
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'Unknown pleasures' including length-frequency data of all fish caught for Paper IV of my thesis. Big thanks to Johannes Radinger for the great idea and the initial coding of my title picture.

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- Paper I: **Matern S.**, Emmrich E., Klefoth T., Wolter C., Nikolaus R., Wegener N., Arlinghaus R. (2019) Effect of recreational-fisheries management on fish biodiversity in gravel pit lakes, with contrasts to unmanaged lakes. *Journal of Fish Biology*, 94(6): 865-881. doi: 10.1111/jfb.13989
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Abstract

The fish species pool in Europe's natural lakes is mainly determined by natural colonization processes after the last ice age, while anthropogenic fish introductions further impact the fish species pool. Fish community composition in lakes is then driven by lakes' trophic state, lake morphology, habitat quality and quantity and biotic interactions. Besides natural lakes, young gravel pit lakes can represent the major water body type in formerly dry landscapes. These lakes originate from anthropogenic excavation processes and are mostly isolated with limited littoral zones. Although they are common, the mechanisms driving gravel pit lake fish communities are rather unknown.

In the first part of my thesis, I studied the effects of lake genesis and fisheries management on fish species richness and community composition in small lakes. I used fish communities in unmanaged natural lakes as reference and compared them to unmanaged gravel pit lakes as well as managed gravel pit and natural lakes. In the second part, I investigated the recruitment of littoral deadwood in gravel pit lakes and analysed the importance of deadwood and other littoral structures on littoral fish abundance in gravel pit lakes compared to the lake environmental variables such as nutrient level and lake morphology. I further analysed habitat-specific effects on species-specific littoral fish abundance and focussed explicitly on the effects of deadwood bundles implemented in the littoral zone.

I found fisheries management to increase the number of fish species in gravel pit and natural lakes, but not leading to different fish community compositions compared to unmanaged natural lakes. By contrast, unmanaged gravel pit lakes were characterized by a lack of typical lake fish species and a high variation in fish community composition among lakes (β -diversity). I detected littoral deadwood densities in gravel pit lakes to be mainly driven by lake age, riparian tree density in interaction with wind direction and littoral slope in angler-managed lakes, with lowest deadwood densities in shallow areas of angler-managed lakes. Furthermore, deadwood densities were lower in young gravel pit lakes compared to old natural lakes. I detected littoral structures, such as littoral deadwood, as important descriptors of the species-specific, littoral fish abundance in gravel pit lakes with generally positive effects of structure extension on fish abundance. Littoral habitat characteristics were mostly of similar, or even higher, importance for fish abundance compared to lake environmental

factors. The implemented deadwood bundles served as appropriate habitats for typical lake fish species in all seasons, especially in winter and attracted on average larger piscivorous fish species.

Overall, my findings suggest that fisheries management speeds up the colonization time of fishes in gravel pit lakes leading to species-rich fish communities. Fish community composition is then impacted by classical lake variables describing productivity as well as littoral habitats with species-specific littoral fish abundance being strongly driven by the quality and quantity of littoral structure. The generally low densities of littoral deadwood can be counteracted by implementing deadwood bundles, which serve as appropriate habitats for typical lake fish species, especially in winter.

Keywords: fish colonization, biodiversity, community composition, conservation, fish stocking, novel ecosystems, recreational fishing, fish distribution, habitat enhancement, littoral deadwood

Deutsche Zusammenfassung

Der Fischartenpool in europäischen Naturseen ist primär durch natürliche Besiedlungsprozesse nach der Eiszeit bestimmt, jedoch kann er durch menschliche Ansiedlungen von Fischarten erweitert werden. Die Zusammensetzung der Fischartengemeinschaft wird anschließend vom Nährstoffgehalt, der Seemorphologie, Qualität und Quantität der litoralen Lebensräume und biotischen Interaktionen getrieben. Im Gegensatz zu Naturseen entstehen Baggerseen durch den Abbau von Sand und Kies. Diese jungen und oftmals isolierten Gewässer mit steil abfallenden Ufern und geringen Litoralbereichen können in ehemals gewässerarmen Landschaften den dominierenden Gewässertyp darstellen. Über die Mechanismen, die ihre Fischgemeinschaft prägen ist jedoch wenig bekannt.

Im ersten Teil meiner Arbeit habe ich den Einfluss von Seeentstehung und fischereilicher Bewirtschaftung auf Artenreichtum und Zusammensetzung der Fischgemeinschaften in kleinen Seen untersucht. Dafür habe ich fischereilich ungenutzte Naturseen als Referenz herangezogen und deren Fischgemeinschaft mit der von unbewirtschafteten Baggerseen, sowie fischereilich genutzten Baggerseen und Naturseen verglichen. Im zweiten Teil meiner Arbeit habe ich die Mechanismen der Totholzrekrutierung in Baggerseen untersucht und die Wichtigkeit von Totholz und anderen Litoralstrukturen im Vergleich zu den klassischen Seenvariablen Nährstoffgehalt und Seemorphologie auf die Fischabundanz im Litoral analysiert. Des Weiteren habe ich die Habitat-spezifischen Effekte auf die artspezifische, litorale Fischabundanz und die Effekte von zusätzlich eingebrachten Totholzbündeln auf die Abundanz typischer Fischarten in Baggerseen analysiert.

Ich habe herausgefunden, dass fischereiliche Bewirtschaftung die Anzahl der Fischarten in Bagger- und Naturseen erhöht ohne die Zusammensetzung der Fischgemeinschaft im Vergleich zu fischereilich ungenutzten Naturseen signifikant zu verändern. Im Gegensatz dazu unterscheidet sich die Fischgemeinschaft in fischereilich ungenutzten Baggerseen durch das Fehlen von typischen Seefischarten und eine hohe Variabilität in der Zusammensetzung zwischen den Gewässern. Ich konnte zeigen, dass die litorale Totholzmenge in Baggerseen durch die Baumdicke am Ufer in Kombination mit der Windrichtung, durch fischereiliche

Bewirtschaftung in Interaktion mit der Uferneigung und das Alter der Gewässer getrieben wird und entsprechend in jungen Baggerseen niedriger ist als in alten Naturseen. Ich fand heraus, dass Litoralstrukturen, wie Totholz, wichtige Deskriptoren der art-spezifischen, litoralen Fischabundanz darstellen und die Fischabundanz grundsätzlich mit der Strukturmenge ansteigt. Eingebrachte Totholzbündel stellen wertvolle Lebensräume für typische Seefischarten dar, besonders für größere Individuen von typischen Raubfischarten und im Winter.

Zusammengefasst zeigen meine Ergebnisse, dass fischereiliche Bewirtschaftung die Ansiedlung von Fischen in Baggerseen beschleunigt und zu artenreichen Fischgemeinschaften führt. Die Zusammensetzung der Fischgemeinschaft ist anschließend sowohl durch die klassischen Seevariablen Nährstoffgehalt und Seemorphologie, wie auch die Litoralstruktur geprägt, wobei sowohl Qualität als auch Quantität der Litoralstruktur die art-spezifische Fischabundanz beeinflussen. Das Einbringen von Totholzstrukturen kann der geringen Häufigkeit von Totholz in Baggerseen entgegenwirken und stellt einen attraktiven Lebensraum für typische Seefischarten dar, speziell im Winter.

Schlagwörter: Fischbesiedlung, Biodiversität, Gemeinschaftszusammensetzung, Naturschutz, Fischbesatz, neue Ökosysteme, Angeln, Fischverteilung, Lebensraumaufwertung, litorales Totholz

1. Background

1.1 NATURAL LAKES AND THEIR FISH COMMUNITIES IN THE TEMPERATURE ZONE

Freshwater lakes cover > 3 % of the world's surface with an estimated number of $30.4 \cdot 10^7$ lakes (Downing *et al.*, 2006). In the northern Hemisphere the majority of freshwaters are located in formerly glaciated areas (Griffiths, 2006) as most lakes were formed by the melting glaciers (Dokulil, Hamm & Kohl, 2001). After their glacial genesis, lakes were often connected to other water bodies by the drainage of the melting ice shield allowing for fish colonization (Mandrak & Crossman, 1992; Bernatchez & Wilson, 1998; Griffiths, 2017). In northern Germany, the newly formed lakes were mainly colonized by fishes from the Ponto-Caspian area (Griffiths, 2006). Genetic methods revealed also glacial refugia in France and post glacial colonization processes from there to northern Germany (Nesbø *et al.*, 1999). Biogeographic barriers such as oceans and mountain ranges limit the potential for colonization events of freshwater fishes (Legendre & Legendre, 1984; Griffiths, 2006; Rahel, 2007). Fishes from the Iberian and Italian peninsulas were disconnected by mountain ranges and no natural fish colonization from there to central Europe has been detected yet (Griffiths, 2006).

The recent fish species pool in Germany contains 102 fish species (+ four species of lamprey) inhabiting lentic and lotic water bodies (Freyhof, 2009). The number of species that occur in lakes is lower and varies depending on the size of the lake, the availability of suitable habitats and the connectivity to rivers with even catadromous species such as the European eel (*Anguilla anguilla*) migrating into lakes (Eckmann, 1995; Tesch, 1999; Mehner *et al.*, 2005).

In the last century, north German lakes have been described by the dominant and - from a fisheries perspective - most valuable fish species. The descriptive fish species included eel, pike (*Esox lucius*), tench (*Tinca tinca*), pikeperch (*Sander lucioperca*), bream (*Abramis brama*), roach (*Rutilus rutilus*) and coregonids (as genus) (Bauch, 1955; Müller, 1987). The list of the most frequent fish species in German lakes is completed by perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*) (e.g. Emmrich *et al.*, 2014; Mehner *et al.*, 2005).

The first concepts of lake fish communities are inspired by the theory of island biogeography as isolated lakes display the features of aquatic islands in the terrestrial landscape (MacArthur

& Wilson, 1967; Browne, 1981). Filters have become a common element in community ecology and are often termed as 'environmental factor' or 'environmental driver' (Keddy & Laughlin, 2022). By using fish community data from multiple lakes in North America and Finland, Tonn *et al.* (1990) developed the first concept of fish community composition based on spatial and environmental filters.

1.2 ECOLOGICAL AND ANTHROPOGENIC FACTORS AFFECTING FISH COMMUNITIES IN LAKES

The fish species pool within each lake is affected by natural and anthropogenic colonization pathways (Figure 1). The fastest pathway for fishes to colonize a lake are permanent hydrological connections (Borcherding *et al.*, 2002; Kristensen *et al.*, 2020), however, they do not exist for isolated lakes by definition. Nevertheless, isolated lakes might have been connected to other water bodies temporarily after their glacial genesis, e.g. by the drainage of the melting ice shield (Mandrak & Crossman, 1992; Bernatchez & Wilson, 1998; Griffiths, 2017). Temporal hydrological connections as a result of flooding events can also lead to fish colonization events (Pont, Crivelli & Guillot, 1991; Olden *et al.*, 2010). Biotic vectors display a further colonization pathway. The transport of fish eggs by birds has long been postulated (Hirsch *et al.*, 2018) and recent studies demonstrated that fish eggs can be distributed by waterfowl (Silva *et al.*, 2019; Lovas-Kiss *et al.*, 2020) and potentially by flying invertebrates (Suetsugu & Togashi, 2020). Reports of fish rain initiated by hurricanes (Bajkov, 1949) are a further colonization mechanism, however, the chances for this pathway are relatively low, especially in central Europe where hurricanes are rare. Generally the chances for all colonization pathways rise with age and size of the lake (Hauffe *et al.*, 2020; Mehner & Brucet, 2022).

Anthropogenic fish colonization is a further dispersal mechanism, that has been recognized at least since Roman times 2,000 years ago (Hoffmann, 1995; Balon, 2004). Generally, two different forms can be distinguished: legal and illegal fish introductions. Fish stocking represents a legal form of anthropogenic fish introductions and is used as a popular measure in fisheries management (Cowx, 1994; Arlinghaus, Bork & Fladung, 2008; Arlinghaus *et al.*, 2022). It aims at establishing and promoting species of fisheries relevance, such as predatory and game fish species as well as common baitfish species (Eby *et al.*, 2006; Arlinghaus *et al.*, 2015; Cazelles *et al.*, 2019). Fish stocking can offset biogeographic distribution barriers (Rahel, 2002) and lead to the intentional (Hickley & Chare, 2004; Johnson, Arlinghaus & Martinez,

2009) or unintentional spread of non-native species (Gozlan, Pinder & Shelley, 2002; Zhao *et al.*, 2016). Fisheries management with regular stocking has indeed been identified as main driver for increased local species richness (α -diversity; Tammi *et al.*, 2003; Zhao *et al.*, 2016), but thereby homogenizing fish communities across regions and continents (β -diversity; Rahel, 2002; Olden, 2006; Villéger *et al.*, 2011; Cazelles *et al.*, 2019).

Illegal fish introductions are mainly conducted by private persons. Anglers, aquarists and garden pond owners release fish into regional water bodies either to establish a desired species or to dispose fishes (Cambray, 2003; Johnson *et al.*, 2009; Patoka *et al.*, 2017; Hirsch, N'Guyen & Burkhardt-Holm, 2021; Weir *et al.*, 2022). Especially in densely populated areas, illegal releases of ornamental and garden pond fishes have become a main vector for species introductions in urban waters (Copp, Wesley & Vilizzi, 2005; Copp, Vilizzi & Gozlan, 2010; Patoka *et al.*, 2017). These illegal introductions strongly participate to the spread of non-native fish species and to the homogenization of fish communities (Johnson *et al.*, 2009; Cazelles *et al.*, 2019; Hirsch *et al.*, 2021).

The fish community composition of a lake evolves from the local fish species pool and is shaped by abiotic and biotic conditions (Figure 1; Jackson, Peres-Neto & Olden, 2001). Trophic state and lake morphology represent the two main abiotic factors driving fish communities (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005). Trophic state of a lake is characterized by the amount of nutrients, mainly phosphorus (Schindler, 1977). The nutrient level affects fish communities in two ways. First, the availability of nutrients regulates the overall fish biomass of a lake (carrying capacity) via bottom-up control (Hanson & Leggett, 1982; Downing, Plante & Lalonde, 1990). Second, the amount of nutrients determines the species-specific domination of a lake. Fish communities shift along the productivity gradient from a domination of Salmoniformes (mainly coregonids) to Perciformes and finally Cypriniformes. Highest abundance of perch can be found in mesotrophic systems, while increasing nutrient levels first shift fish communities towards roach domination (eutrophic) and finally to bream dominated systems (polytrophic) (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005).

Morphological lake characteristics such as mean lake depth, lake size, shoreline length and shoreline development factor are known to shape lake fish communities and functional diversity (Eckmann, 1995; Diekmann *et al.*, 2005; Mehner *et al.*, 2005; Eros *et al.*, 2009; Brucet *et al.*, 2013). Especially mean lake depth is an important lake morphological descriptor as it

describes the availability of habitats. Deep lakes provide littoral, benthic and pelagic habitats, whereas shallow lakes can consist of only littoral habitats (LAWA, 2014). Mean lake depth further impacts the mixing regime and thus the suitability of habitats for fishes due to oxygen concentration as well as availability of nutrients (Mehner & Brucet, 2022). Accordingly, mean lake depth has been used to classify fish communities (e.g. in German lowland lakes; Ritterbusch *et al.*, 2014). The size of a lake is a further aspect of lake morphology that influences fish diversity. Larger lakes offer a higher diversity of habitats and are thus characterized by a higher fish species richness (Eckmann, 1995; Griffiths, 1997). Furthermore, larger lakes have higher colonization rates and lower probabilities of local species extinctions (Hauffe *et al.*, 2020; Mehner & Brucet, 2022). Finally, shoreline length and shoreline development factor (the relation of shoreline length to lake size; Hutchinson, 1957; Seekell, Cael & Byström, 2022) determine the quantity of littoral habitats and thus impact the abundance of littoral fish species and finally lake fish communities (Hampton *et al.*, 2011; Lewin *et al.*, 2014).

The littoral zone plays an outstanding role in lake ecosystems by connecting terrestrial and aquatic ecosystems (Schindler & Scheuerell, 2002; Winfield, 2004; Moss, 2008). Increasing littoral zones usually lead to diverse habitat characteristics (e.g. submerged macrophytes, emerged macrophytes and deadwood) and complexities, which benefit diverse littoral fish communities (Lewin, Okun & Mehner, 2004; Lewin *et al.*, 2014). Littoral structures are known to be crucial for the lifecycle of certain lentic fish species (e.g. pike; Casselman & Lewis, 1996; Nilsson *et al.*, 2014). Thus, changes in the shoreline habitat strongly affect species-specific abundance and community composition (Whitfield, 1986; Sass *et al.*, 2006b, 2012; Helmus & Sass, 2008; Ziegler, Gregory-Eaves & Solomon, 2017). Nevertheless, the importance of littoral structures compared to lake-level variables such as trophic state or lake morphology is low in natural lakes in northern Germany (Lewin *et al.*, 2014).

The main biotic factors that structure fish communities and food chains are predation and competition. Predation impacts fish communities as a top-down force and can lead to strong abundance declines in prey species (He & Kitchell, 1990). Often depending on environmental conditions, the presence of predatory fish species (e.g. perch and pike) can even lead to the extinction of some native and typically small fish species in lakes (Englund *et al.*, 2009; Henriksson *et al.*, 2016). Hence, predation impacts fish species richness and community composition of lake fishes (He & Kitchell, 1990; Chapleau, Findlay & Szenasy, 1997). However,

the effect of predation on the abundance and biomass of fish species that can coexist with the predatory species is rather low (Mehner, 2010; Mehner *et al.*, 2016; Kokkonen *et al.*, 2019). Competition mainly occurs for food and habitat and can be observed between individuals of different species (interspecific competition) and between individuals within a species (intraspecific competition). The effects of competition on fish communities are rather low (MacDougall *et al.*, 2018), however, most studies focused on competitive interactions between two (or more) species. Perch and roach are among the most frequent and most abundant fish species in lentic waters of north and central Europe and both species strongly shape fish community composition (Tammi *et al.*, 2003; Mehner *et al.*, 2005; Emmrich *et al.*, 2014). Their interaction via competition and also predation has been studied intensively and it is strongly impacted by environmental gradients such as nutrient-level (Persson *et al.*, 1991; Olin *et al.*, 2002) and quality and quantity of littoral structures (Eklöv & Persson, 1995; Persson & Eklöv, 1995). Hence, biotic interactions between fishes are controlled by environmental conditions (Cordero & Jackson, 2021).

1.3 GRAVEL PIT LAKES: ORIGIN, EXTENSION AND KEY LIMNOLOGICAL CHARACTERISTICS

Humans are strongly shaping the landscape including the creation of various forms of standing water bodies, such as gravel pit lakes, ponds, mining lakes and reservoirs. The industrial excavation of sand and gravel started in the middle of the 20th century and the resulting gravel pit lakes are therefore on average less than 100 years old (Zhao *et al.*, 2016; Søndergaard *et al.*, 2018; Seelen *et al.*, 2021b). Gravel pit lakes have become common landscape elements in industrialised countries (Bartmann *et al.*, 1990; Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Nikolaus *et al.*, 2020) with sizes mostly below 10 ha (Völkl, 2010; Søndergaard *et al.*, 2018; Nikolaus *et al.*, 2020; Seelen *et al.*, 2021b).

By contrast, ponds can be either natural or man-made, but are usually smaller and shallower with a median size of 1.5 ha (Richardson *et al.*, 2022). Similar to natural lakes, natural ponds and kettle holes in the German lowlands are remnants from the ice age (Håkanson, 2012), while man-made ponds were often created for fish farming (Lemmens *et al.*, 2013). When no longer used, these ponds become naturalized and effectively serve as artificially created shallow lake ecosystems (De Meester *et al.*, 2005; Lemmens *et al.*, 2013, 2015).

Mining lakes are pit lakes that result from mining, e.g. lignite mining (Schultze, Boehrer & Geller, 2013; Soni, Mishra & Singh, 2014; Blanchette & Lund, 2016). In central Germany about

140 mining lakes exist with lake sizes up to 2,000 ha and the maximum lake depth can even exceed 80 m (Schultze, Pokrandt & Hille, 2010).

Artificially created standing waters in river systems are called reservoirs. They are either constructed to control and manage the water of a river basins, e.g. for drinking water, or they result from the creation of a hydropower plant (Egré & Milewski, 2002; Jorgensen *et al.*, 2013). Gravel pit lakes display the probably most abundant type of artificially created water bodies, with over 26,000 active quarries and pits existing all over Europe (UEPG, 2020). In 1990, the number of gravel pit lakes in Germany was estimated to be around 20,000 (Bartmann *et al.*, 1990) and our study area of Lower Saxony, Germany, is characterized by > 3,500 potentially artificial lakes with an area larger than 1 ha (Nikolaus *et al.*, 2020). Most of these lakes originate from the excavation of sand and gravel, representing 59 % of the area of all lentic water bodies in the region (Nikolaus *et al.*, 2020). Their small size of generally less than 50 ha excludes nearly all gravel pit lakes from regular monitoring required by the Water Framework Directive (EU, 2000). Nevertheless, the highly abundant and small gravel pit lakes constitute important habitats for biodiversity (Santoul *et al.*, 2009; Damnjanović *et al.*, 2019; Nikolaus *et al.*, 2021; Seelen *et al.*, 2021b; Müllerová, Řehouňková & Prach, 2022) and display popular sites for various forms of recreation (Meyerhoff, Klefoth & Arlinghaus, 2019; Schafft *et al.*, 2021; Seelen *et al.*, 2021a; Kaemingk *et al.*, 2022).

The genesis of gravel pit lakes leads to some of their typical features. Gravel pit lakes are often located close to large rivers as the flood plains host large amounts of sand and gravel (Mollema & Antonellini, 2016), but most gravel pit lakes are not connected to the river system or other water bodies (Seelen *et al.*, 2021b). During the excavation process the gravel pits fill up with nutrient-poor groundwater and become gravel pit lakes with the features of aquatic islands (Mollema & Antonellini, 2016). The generally mesotrophic conditions are a further characteristic of gravel pit lakes, which distinguishes them from natural lakes in the same area with usually elevated nutrient levels (Søndergaard *et al.*, 2018; Vucic *et al.*, 2019; Seelen *et al.*, 2021b).

The intense excavation of mineral resources leads to a high lake depth compared to the relatively small size of gravel pit lakes (Søndergaard *et al.*, 2018; Vucic *et al.*, 2019). Accordingly, most gravel pit lakes can be characterized as deep dimictic lakes (Søndergaard *et al.*, 2018; Seelen *et al.*, 2021b). Steep slopes and a reduced littoral zone compared to natural lakes are further features of gravel pit lakes, that can be referred to their intense exploitation

(Gee, 1978; Emmrich *et al.*, 2014). The steep slopes and the reduced littoral zone display a rather suboptimal habitat for macrophytes (Duarte & Kalff, 1986). However, the species pool of macrophytes in European gravel pit lakes comprises several hundred different species (Søndergaard *et al.*, 2018; Nikolaus *et al.*, 2021; Seelen *et al.*, 2021b; Müllerová *et al.*, 2022). Deadwood is a further abundant and important littoral structure in natural lakes (Sass, 2009; Czarnecka, 2016). The amount of littoral deadwood in natural lakes depends on riparian tree density, wind exposure and human land-use (Christensen *et al.*, 1996; Marburg, Turner & Kratz, 2006). Riparian trees that fall into the water create highly diverse underwater habitats (Bozek, 2001; Newbrey *et al.*, 2005) and can remain there for several centuries (Guyette & Cole, 1999). By contrast, gravel pit lakes are very young water bodies and might thus lack valuable deadwood structures as a result of the short accumulation time, but studies on deadwood recruitment and densities are missing.

1.4 FISH COMMUNITIES IN GRAVEL PIT LAKES

Little is known about fish communities in gravel pit lakes. Most gravel pit lakes lack hydrological connections to other water bodies, which serve as the fastest mechanism for natural fish colonization (Borcherding *et al.*, 2002; Kristensen *et al.*, 2020). Hence, in the beginning gravel pit lakes are free of fish (Søndergaard *et al.*, 2018; Werneke *et al.*, 2018). All other natural colonization events are limited to either extreme weather conditions, such as floodings (Pont *et al.*, 1991; Olden *et al.*, 2010) or hurricanes (Bajkov, 1949), or to random dispersal by other animals, such as the transport of fish eggs by birds (Silva *et al.*, 2019; Lovas-Kiss *et al.*, 2020) or invertebrates (Suetsugu & Togashi, 2020). Similar to natural lakes, illegal fish introductions by humans display a further colonization pathway (Copp *et al.*, 2010; Patoka *et al.*, 2017; Hirsch *et al.*, 2021). Importantly, the chances of all colonization events rise with lake age (Barbour & Brown, 1974; Mehner & Brucet, 2022).

Most gravel pit lakes in central Europe are managed by recreational anglers (Deadlow, Beard & Arlinghaus, 2011; Umweltbundesamt, 2021) and a study from southern France revealed recreational-fisheries management as an important factor for fish colonization leading to an elevated species richness in gravel pit lakes, including various non-native warmwater species (Zhao *et al.*, 2016). Water temperature is an important descriptor for species distribution and impacts the establishment of native and non-native species (Trochine *et al.*, 2018; Anas & Mandrak, 2021). The gravel pit lakes in northern Germany are approximately 1,000 km north

of the gravel pit lakes studied by Zhao *et al.* (2016). The different climatic conditions between both regions might affect the impact of fisheries management. However, a study on gravel pit lakes with and without recreational-fisheries management to reveal the effect of fisheries management on fish diversity and the resulting fish community composition is lacking for northern Germany.

Emmrich *et al.* (2014) already investigated the littoral fish community composition by electrofishing in managed gravel pit lakes in northern Germany and compared it to littoral fish communities of managed natural lakes. Fish communities were species-rich and did not differ between both lake types (Emmrich *et al.*, 2014). However, the benthic fish community was not considered in this study. All habitats (littoral, benthic and pelagic zone) need to be sampled to appropriately explore fish species richness and diversity of a lake (Achleitner, Gassner & Luger, 2012; Mehner & Brucet, 2022). Furthermore, all lakes were managed for fisheries, which can impact fish diversity and community composition (e.g. Zhao *et al.*, 2016). Information on the fish community composition of small, unmanaged natural lakes in northern Germany are scarce, but they can serve as important reference for fish communities in gravel pit lakes. Comparative analyses between gravel pit- and natural lakes, both with and without fisheries management are needed to reveal the effects of fisheries management and lake genesis (gravel pit lake / natural lake) on fish communities in small lakes.

The fish community composition in gravel pit lakes is, similar to natural lakes, further impacted by the nutrient level and lake morphology (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005; Zhao *et al.*, 2016) as well as biotic interactions (Tonn & Magnuson, 1982; He & Kitchell, 1990). The littoral zone is also of major importance for various fish species (Winfield, 2004), as they use it for purposes such as spawning, refuge and feeding (e. g. Brosse & Lek, 2000; Hölker *et al.*, 2002; Lewin, Okun & Mehner, 2004; Winfield, 2004). The effects of the littoral zone and its structures on lake fish abundance and dispersal have been studied intensively in natural lakes and the effects were rather low compared to lake morphology and trophic state (Lewin *et al.*, 2004, 2014). Gravel pit lakes are characterized by limited littoral zones, which might lead to an increased importance of the littoral zone and its structures for fish communities similar to some cases in natural lakes with limited littoral zones (Gasith, 1991; Hampton *et al.*, 2011). The availability of littoral habitats in gravel pit lakes has already been detected to be an important predictor of perch growth (Höhne *et al.*, 2020). However,

the importance of the littoral zone for the abundance of typical fish species in gravel pit lakes has not been evaluated yet.

The most important littoral habitats for fishes in lakes encompass submerged macrophytes, emerged macrophytes (mainly reeds) and deadwood (Okun, Lewin & Mehner, 2005; Lewin *et al.*, 2014; Czarnecka, 2016). Reed and deadwood habitats have been found to strongly affect littoral fish abundance, with generally higher abundance compared to unstructured habitats (Lewin *et al.*, 2004; Okun & Mehner, 2005). Submerged macrophytes also represent highly relevant littoral structures (e.g. for pike and tench) (Casselman & Lewis, 1996; Lewin *et al.*, 2014) and the coverage of submerged macrophytes has further been detected to impact littoral reliance of perch in gravel pit lakes (Trudeau, 2018). Importantly, too dense structures might also limit the foraging success (Savino & Stein, 1982; Diehl, 1988) and, therefore, non-linear relationships with intermediate peaks of species-specific fish abundance can be expected along the coverage gradient of littoral structures and especially submerged macrophytes. However, the effects of littoral structures along a gradient on fish abundance in gravel pit lakes have not been analysed yet.

Littoral deadwood displays an outstanding role as fish habitat in lentic waters by impacting fish abundance, behaviour and diet (Lewin *et al.*, 2004, 2014; Sass *et al.*, 2006a; Ahrenstorff, Sass & Helmus, 2009). However, littoral deadwood is often removed as a result of anthropogenic shoreline development (Christensen *et al.*, 1996; Marburg *et al.*, 2006). The effects of deadwood removal can impact fish growth, feeding behaviour and abundance (Sass *et al.*, 2006b; Helmus & Sass, 2008). By contrast, a before-after control-impact study with multiple lakes did not detect significant changes in fish abundance after deadwood removal (Smokorowski *et al.*, 2020). The introduction of deadwood also impacts lake fish species e.g. by leading to a greater home range and a change in diet, while impacts on abundance have not been detected (Sass *et al.*, 2012; Smith *et al.*, 2021). The detailed mechanisms of deadwood in the littoral zone have not been fully understood yet and further studies are needed (Sass *et al.*, 2019), e. g. to reveal the effect of littoral deadwood additions on fish abundance and spatio-temporal distribution.

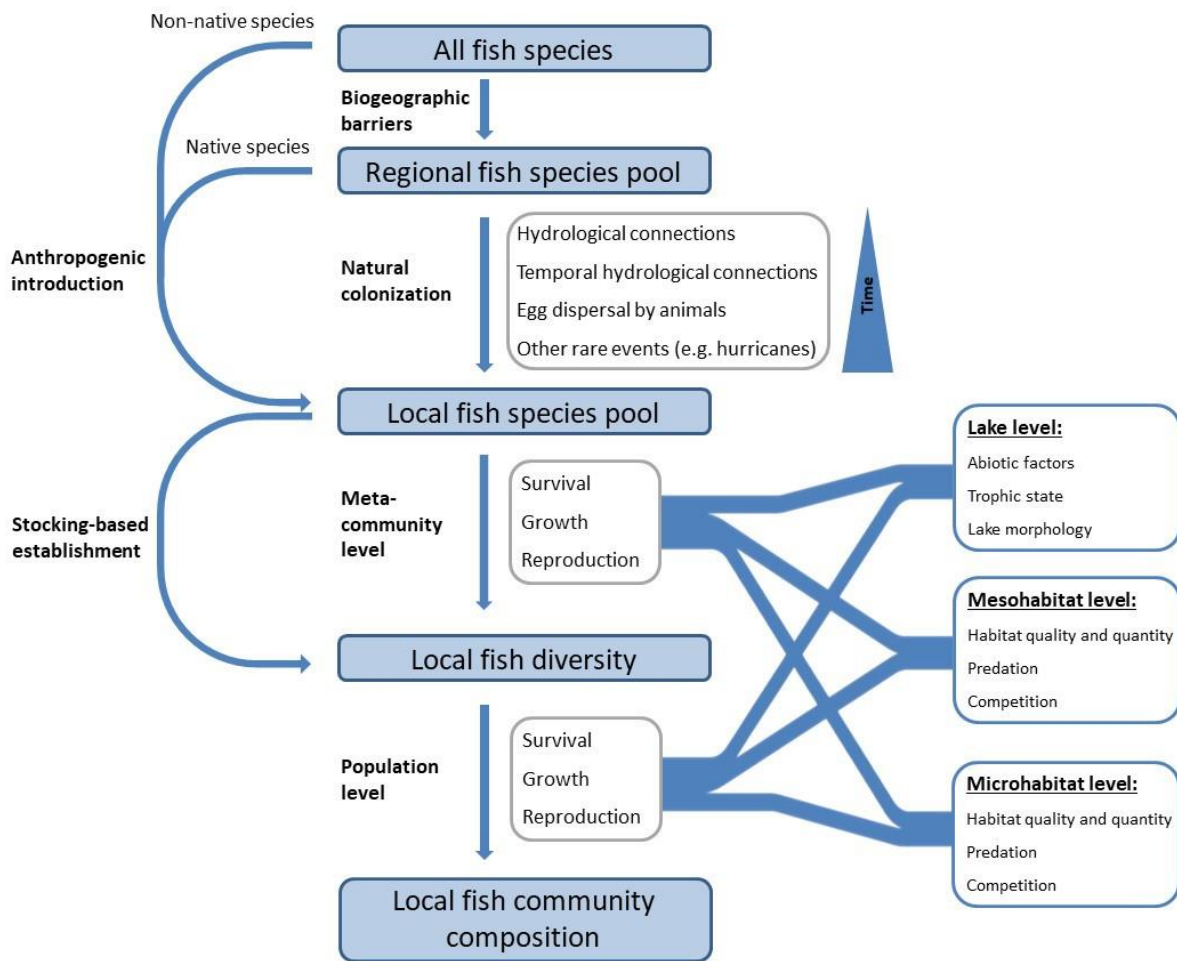


Figure 1: Mechanisms determining fish diversity and community composition in lakes. Blue vertical arrows display natural filters that determine local fish community composition. Legal and illegal stocking activities can offset these natural filters (curved arrows).

2. Objectives and Structure of the Dissertation

The aim of my dissertation was to deepen the understanding of mechanisms impacting fish diversity, species-specific abundance and the resulting community compositions in gravel pit lakes.

In the first part of my dissertation, I investigated on the effects of fisheries management (managed / unmanaged) and lake genesis (gravel pit lake / natural lake) on lake fish diversity and community composition in small lakes (**Paper I and II**; Figure 2). In the second part of my thesis, I focussed on the littoral characteristics of gravel pit lakes. I investigated the factors driving littoral deadwood accumulation (**Paper III**), the effects of littoral structures on littoral fish abundance (**Paper IV**) and the impact of supplemented deadwood structures on littoral fish abundance and distribution throughout the year (**Paper V**; Figure 2).

I hypothesized that,

- I. fisheries management leads to an increase in species richness (α -diversity), specifically of desired and piscivorous fish species as well as invasive fish species, while it reduces β -diversity compared to unmanaged gravel pit lakes (**Paper I**).
- II. fisheries management impacts fish communities in gravel pit and natural lakes leading to species rich but similar composed fish communities as common in unmanaged natural lakes (reference lakes), while unmanaged gravel pit lakes have a high β -diversity due to the slow and stochastic colonization processes (**Paper II**).
- III. the density of littoral deadwood in gravel pit lakes is driven by riparian tree abundance in combination with wind exposure, recreational-fisheries management in combination with water depth and lake age. I further hypothesized, that deadwood densities are lower in young gravel pit lakes compared to old natural lakes (**Paper III**).
- IV. the importance of littoral- and lake variables driving fish abundance differs between species and size classes. I further hypothesized, that complex, littoral habitats and shallow water zones positively affect the abundance of small fish, while effects of

littoral structure on large individuals are more species-specific with non-linear effects, especially for piscivorous species (**Paper IV**).

- V. supplemented deadwood bundles display an appropriate habitat for various typical lake fish species and that the usage of these structures is increased during the day and in winter (**Paper V**).

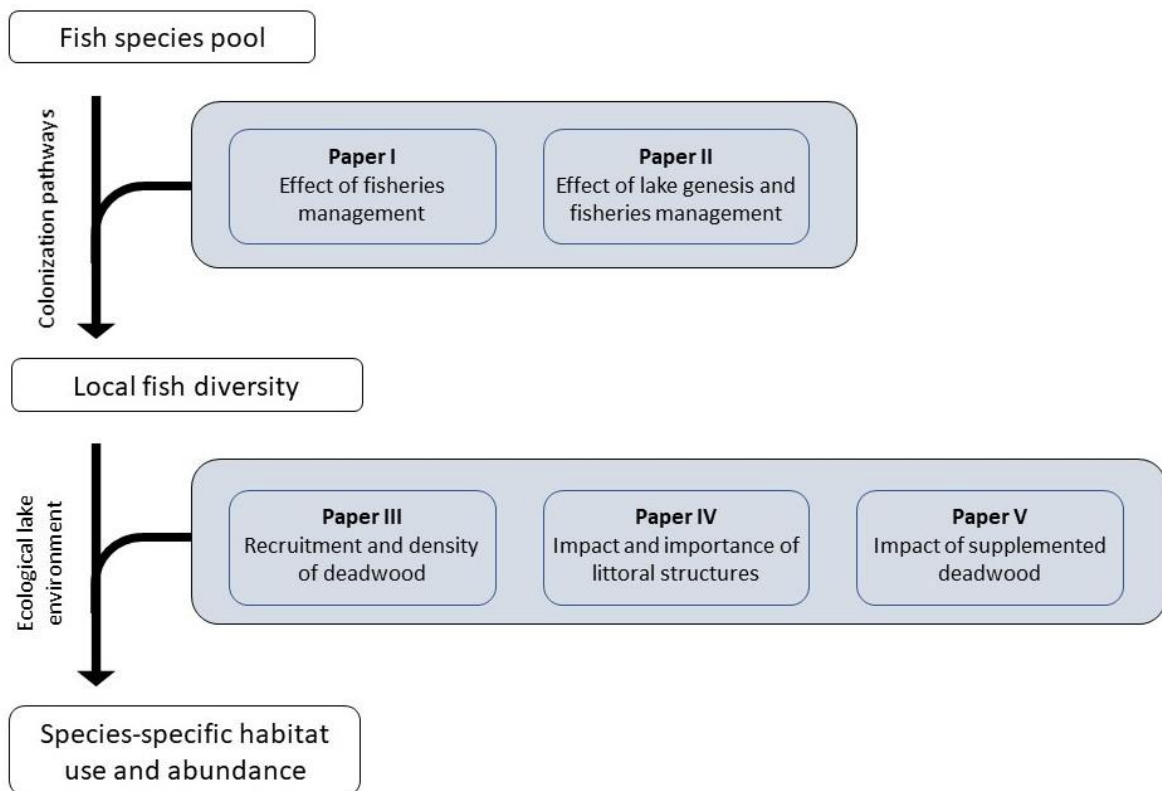


Figure 2: Schematic overview of the studies conducted in this dissertation. Paper I and II investigate the effects of fisheries management and lake genesis on fish communities in lentic water bodies. Paper III tackles the recruitment and density of deadwood in gravel pit lakes. Paper IV analyses the effects and importance of littoral structures on species-specific habitat use and abundance in gravel pit lakes, while Paper V focusses on the effects of supplemented deadwood bundles on species-specific habitat use and abundance.

3. Methodological Overview

3.1 STUDY SITES

In this thesis, I used data sampled in 67 small lakes. Fish communities and environmental variables were sampled in 50 gravel pit lakes ($n_{\text{managed}} = 37$ and $n_{\text{unmanaged}} = 13$) and 16 natural lakes ($n_{\text{managed}} = 10$ and $n_{\text{unmanaged}} = 6$). All fish community data were analysed in **Paper II**, while the research questions of **Papers I, IV and V** were investigated on a subset of the gravel pit lakes. For **Paper III** a subset of the above-mentioned gravel pit lakes plus a further unmanaged gravel pit lake were analysed, where fish data could not be sampled.

All gravel pit lakes were located in north-western Germany with 48 gravel pit lakes being located in the federal state of Lower Saxony and one gravel pit lake in North Rhine-Westphalia and one gravel pit lake in Mecklenburg-Western Pomerania (Figure 3). Due to the low number of natural lakes in this area, the sampling of ecologically similar natural lakes was conducted in the federal state of Brandenburg, which is located at the same latitude in north-eastern Germany at a distance of about 400 km.

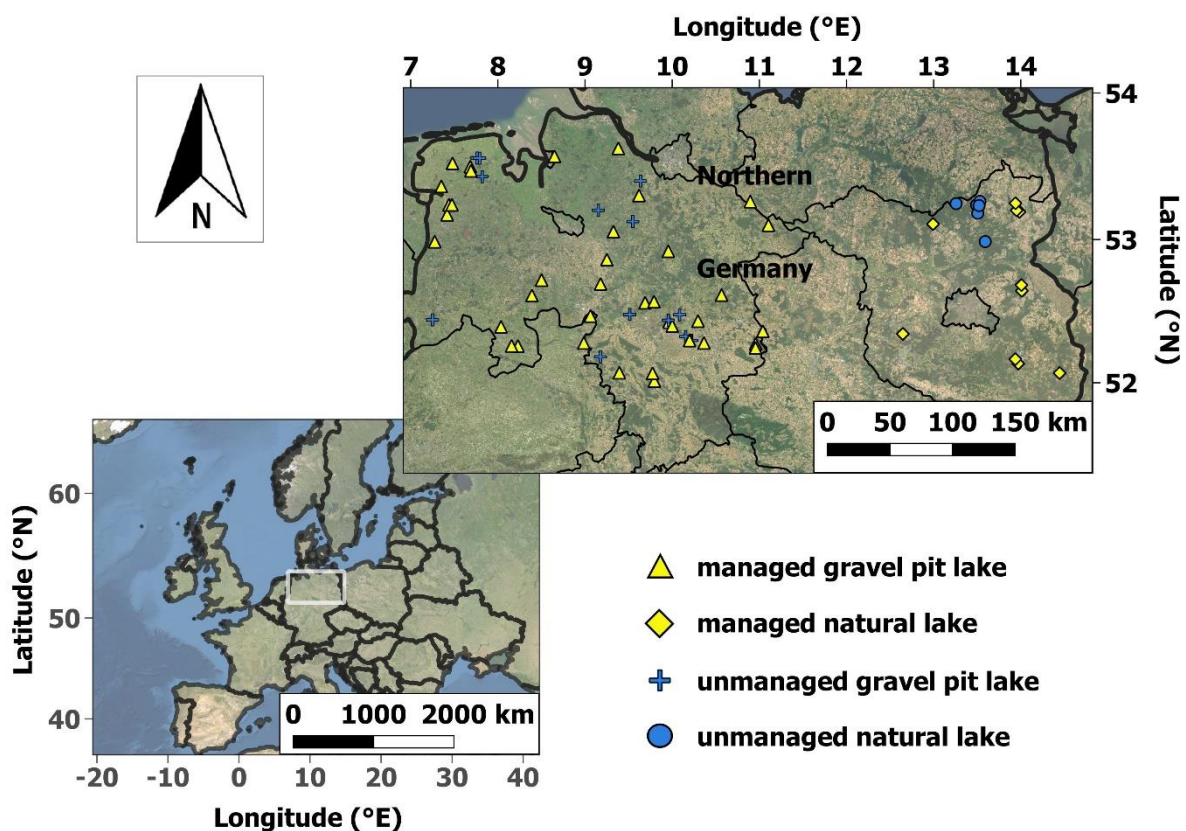


Figure 3: Map of all sampled gravel pit lakes and natural lakes in northern Germany.

3.2 SAMPLING FISH IN LAKES

Littoral electrofishing and multimesh gillnetting represent the two standard methods to sample fish communities in lentic waters (Diekmann *et al.*, 2005; Achleitner *et al.*, 2012; Mueller *et al.*, 2017). In **Paper I and II**, I used both methods to investigate the effect of fisheries management and lake genesis on fish diversity and community composition. In **Paper IV and V**, the effects of littoral structures on littoral fish abundance were investigated by using only electrofishing data.

3.2.1 Littoral Electrofishing

I conducted electrofishing from a boat using a FEG 8000 electrofishing device (8kW; 150 – 300V / 300 – 600V; EFKO Fischfang GmbH; www.efko-gmbh.de) with a 4 m copper cathode and a netted anode ring (4 m long, mesh size = 6 mm, ring diameter = 0.45 m; **Paper I**). The dataset for **Paper II** was extended by data collected from the Angler Association of Lower Saxony (AVN) and the Institute of Inland Fisheries (IfB) with different electrofishing devices. To ensure comparability between the datasets, I only included data sampled by electrofishing devices with similar power.

Generally, two major sampling designs for scientific purposes can be distinguished: continuous (or transect-based) electrofishing (**Paper I, II and IV**) and point abundance electrofishing (**Paper V**).

3.2.1.1 Continuous electrofishing

Transects parallel to the shoreline were defined prior to sampling with varying lengths between 30 m and 300 m depending on the local conditions. In most sampling lakes, the entire shoreline was fished to ensure good quality of the data. The littoral zone of each transect was fished by immersing the anode every 3 - 4 m and netting all stunned fishes. Catches were noted separately for every transect. All fishing events using continuous electrofishing were conducted in autumn (late August – late October) and during daytime (**Paper I, II and IV**).

For analysis, I calculated the catch per unit effort (CPUE) as either individuals or biomass per 50 m fished shoreline. For **Paper IV**, I analysed the data on transect level and for the analysis of **Paper I and II**, I summarized the data on lake level.

3.2.1.2 Point abundance electrofishing

Point abundance electrofishing allows for sampling specific littoral microhabitats (Copp, 2010). For **Paper V**, the active anode was immersed for 10 seconds at each sampling point and

all stunned fish were netted. The catches and the specific littoral habitat characteristics were noted at each sampling point. Point abundance electrofishing was conducted at all four seasons during day- and night-time.

For the analysis, the catch per unit effort (CPUE) was calculated as individuals per fishing point.

3.2.2 Multimesh gillnetting

We used benthic multimesh gillnets as recommended by the European Standard protocol for sampling lake fish communities (CEN, 2015). Additional pelagic gillnets were used in gravel pit lakes > 10 ha or deeper than 10 m to properly sample fish species richness in **Paper I** as recommended for larger lakes (CEN, 2015). The pelagic gillnets were set only in oxygenated depth strata (0 – 1.5 m; 3 – 4.5 m; 6 – 7.5 m; 9 – 10.5 m and 12 – 13.5 m). All gillnets were set before sunset and lifted after sunrise to cover activity peaks of all fishes (Prchalová *et al.*, 2010). Standard multimesh gillnets measure 30 m in length with 12 different panels (Table 1). Each panel measures 2.5 m in length and 1.5 m in height and the mesh-sizes follow a geometric series ranging from 5 mm to 55 mm knot to knot (CEN, 2015). However, this method often underrepresents individuals < 100 mm and > 400 mm (Olin, Malinen & Ruuhijärvi, 2009; Prchalová *et al.*, 2009; CEN, 2015). To counteract the bias towards larger individuals, we attached four additional panels with a panel length of 2.5 m and larger mesh-sizes (see Table 1 for details) to the 30 m multimesh gillnets, in order to sample larger individuals (**Paper I**).

The dataset for **Paper II** contained data sampled for different projects with benthic multimesh gillnets in four slightly different specifications. However, data were transferred to a comparable dataset with CPUE data calculated as individuals per 100 m².

Table 1: Mesh size distribution (knot to knot) and thread diameter in 30 m multimesh benthic gillnets after CEN (2015) and in modified 40 m multimesh benthic gillnets.

30m multimesh gillnets after CEN (2015)			Modified 40m multimesh gillnets		
Mesh no.	Mesh size (mm)	Thread diameter (mm)	Mesh no.	Mesh size (mm)	Thread diameter (mm)
1	43	0.2	1	43	0.2
2	19.5	0.15	2	19.5	0.15
3	6.25	0.1	3	6.25	0.1
4	10	0.12	4	10	0.12
5	55	0.25	5	55	0.25
6	8	0.1	6	8	0.1
7	12.5	0.12	7	12.5	0.12

8	24	0.17	8	24	0.17
9	15.5	0.15	9	15.5	0.15
10	5	0.1	10	5	0.1
11	35	0.2	11	35	0.2
12	29	0.17	12	29	0.17
			13	90	0.25
			14	110	4x0.14
			15	135	6x0.20
			16	70	0.25

3.2.2.1 Sampling design after the European standard protocol

The European standard protocol for sampling lake fish communities recommends eight multimesh gillnet nights for lakes < 20 ha with a maximum depth of < 12 m (Table 2). Lakes < 20 ha with a maximum depth ≥ 12 m should be sampled by 16 multimesh gillnet nights.

Table 2: Number of recommended multimesh gillnet nights and their distribution according to depth strata in lakes < 20 ha after CEN (2015).

Depth stratum (m)	Maximum depth (m)				
	< 6	6 - 11.9	12 - 19.9	20 - 34.9	35 - 49.9
< 3	4	3	4	4	3
3 - 5.9	4	3	4	3	3
6 - 11.9		2	4	3	3
12 - 19.9			4	3	3
20 - 34.9				3	2
35 - 49.9					2
Total number of gillnet-nights	8	8	16	16	16

3.2.2.2 Adjusted sampling design for gravel pit lakes

The investigated gravel pit lakes in this thesis substantially varied in size (between one and 21 ha) and I, therefore, adjusted the CEN sampling design by standardizing the number of benthic multimesh gillnets to the lake size. I calculated the number of gillnets per lake as follows:

$$\text{Number of gillnets} = \frac{\text{lake area} * 0.005}{\text{gillnet length} * \text{gillnet height}} \quad (1)$$

with lake area in m² and gillnet length and gillnet height in m. The value 0.005 represents the quotient of gillnet area to lake area in the largest gravel pit lake (20 ha) in the dataset of **Paper I**, which was used as reference for the calculation. Importantly, a reduced sampling effort with benthic gillnets leads to similar results regarding fish community composition and species-specific CPUE (Blabolil *et al.*, 2021). The number of gillnets were proportionally distributed in each lake with respect to the different depth strata as recommended in European Standard protocol and set over night (CEN, 2015).

For later analysis, overall and species-specific CPUEs were calculated for each gillnet as either individuals or biomass per 100 m² multimesh gillnet. Lake-specific CPUEs were then calculated with respect to sampling effort in each depth stratum.

3.3 LITTORAL DEADWOOD

3.3.1 Littoral deadwood sampling

We sampled deadwood in the littoral zone of 26 gravel pit lakes (**Paper III**). We used a transect-based sampling design with a riparian plot measuring 10 x 10 m and a littoral zone plot with a width of 6 m and a length depending on the local water depth. However, due to sampling time constraints the width of the littoral plot was reduced to 2 m in six gravel pit lakes.

In the riparian plot, we classified all trees according to their height (small: < 3 m; medium: 3 – 10 m; tall: > 10 m). In the littoral plot, we assessed all deadwood structures. We defined three criteria for the classification of all deadwood structures: 1) length ≥ 50 cm; 2) diameter ≥ 5 cm and 3) complexity ≥ 2. Complexity was determined according to the maximum number of branch orders (1 = main trunk / 1st order branch; 2 = 2nd order branch; 3 = 3rd order branch; 4 = 4th order branch and 5 = 5th order branch; following Newbrey *et al.*, (2005)). Each deadwood structure that fulfilled at least two of the three criteria was classified as 'large' and measured in detail (length, diameter, complexity and percentage of submersion). All other deadwood structures were classified as 'small'.

3.3.2 Littoral deadwood implementation

We implemented deadwood bundles in eight gravel pit lakes in Lower Saxony between December 2017 and March 2018. The number of deadwood bundles varied by lake as we aimed to manipulate 20 % of each lake's shoreline. In total, we implemented 800 deadwood bundles with 30 bundles in the smallest lake and 190 bundles in the largest lake. The bundles

consisted of branches from deciduous trees, mainly European hornbeam (*Carpinus betulus*), birch (*Betula spp.*) and alder (*Alnus glutinosa*), which were machine pressed and bundled with hemp ropes. The branches varied in diameter between 0.5 and 21 cm. The resulting bundles measured 3 m in length with a diameter of 0.8 m and an individual weight of approximately 300 kg.

At each lake the deadwood bundles were unloaded and transported to predefined locations by boats with the help of the local angling club (Figure 4). Jute bags filled with sand and gravel were used to drown the deadwood bundles and keep them in place. Shortly after the implementation, the deadwood bundles were often covered with algae (Figure 5). With ongoing decomposition of the hemp ropes, the morphology of bundles changed and created more diverse habitats.



Figure 4: Process of the deadwood implementation: A) Arrival of deadwood bundles at the gravel pit lake; B) Heavy gear was used to place the deadwood bundles in the lake; C) the swimming deadwood bundles were distributed by angling club members from boats; D) jute bags filled with sand and gravel were used to drown the deadwood bundles in the predefined locations (Pictures: Thomas Klefoth; Anglerverband Niedersachsen e.V.).

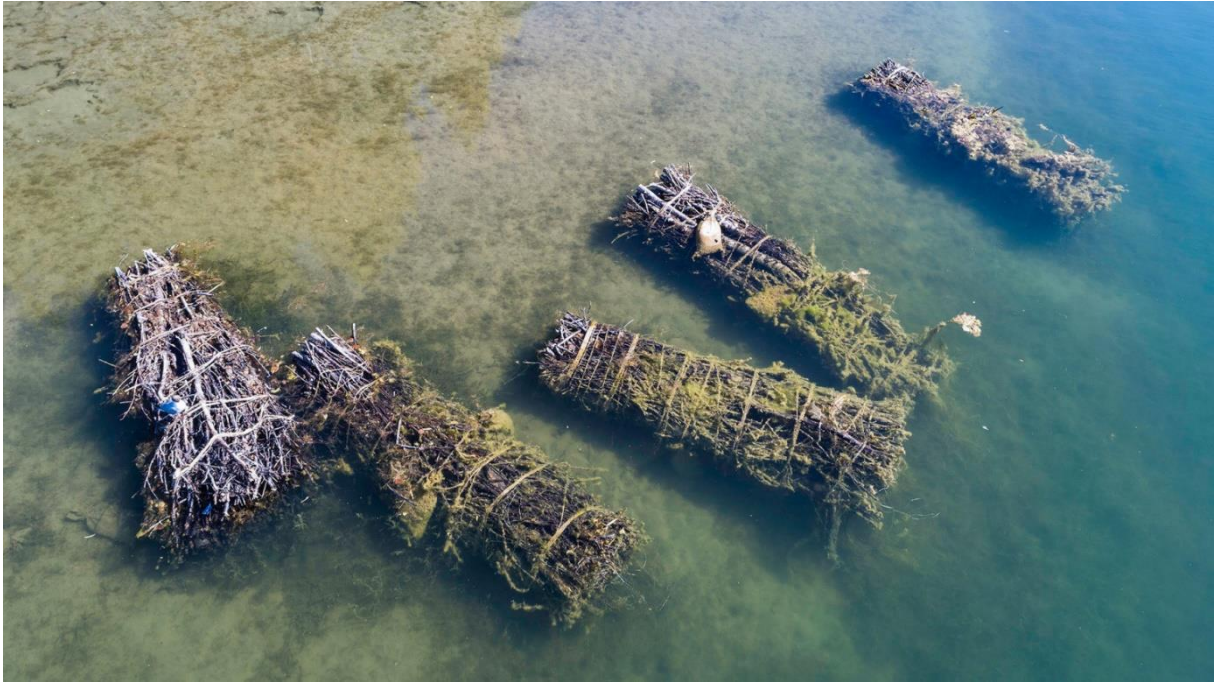


Figure 5: Deadwood bundles a few months after their introduction in the littoral zone of a gravel pit lake in Lower Saxony (Picture: Florian Möllers; Anglervverband Niedersachsen e.V.).

3.4 ENVIRONMENTAL ASSESSMENT

3.4.1 Lake-level variables

Lake size and shoreline length were measured using QGIS (QGIS Development Team, 2019). Shoreline development factor (SDF) was calculated after Hutchinson (1957) for **Paper I, IV and V** and after Seekell, Cael & Byström (2022) for **Paper II** as an index of shoreline complexity and extension. Contour maps were created from echo sounder data to extract mean lake depth, maximum lake depth and shares of the different depth strata (0 – 2.9 m; 3 – 5.9 m; 6 – 11.9 m; 12 – 19.9 m and 20 – 34.9 m) from each lake according to the depth strata used in the European Standard protocol (CEN, 2015).

Trophic and hydrochemical variables were sampled at each fishing event. Secchi depth, pH-value and conductivity were measured from a boat above the deepest point of the lake, while oxygen concentration and temperature were measured throughout the water column in steps of 50 cm. Water samples for total phosphorus and Chlorophyll a analysis were taken at the water surface above the deepest point of the lake and later analysed in the lab.

We aimed at reconstructing two ages for each gravel pit lake, the onset and the end of excavation, as the gravel pits started filling up with groundwater and colonization with fish was already possible before the end of excavation. The natural lakes sampled in **Paper II** were

of glacial genesis and accordingly information on lake age were condensed into a variable called 'lake genesis' with two levels (gravel pit lakes < 100 years; natural lakes ~ 10,000 years). All lakes were categorized as either managed for fisheries or not. Fisheries management encompassed regular fish stocking including initial fish stocking with desired species in the gravel pit lakes (Arlinghaus *et al.*, 2015; Zhao *et al.*, 2016; Cucherousset *et al.*, 2021); recreational angling including harvest regulation (e.g. minimum-length and daily bag limits) (Arlinghaus *et al.*, 2016) and habitat management (e.g. creating angling sites or deadwood supplementation for fish) (Arlinghaus & Mehner, 2005; Sass, 2009). By contrast, the unmanaged gravel pit lakes were either owned by private persons or nature conservation agencies and did not receive initial fish stocking. The unmanaged natural lakes were under nature protection since 1990 and did not receive any fish stocking or habitat management since then. Recreational fishing was prohibited at all unmanaged lakes.

3.4.2 Habitat variables

We visually estimated macrophyte coverage using a transect-based approach following the Braun-Blanquet scale (Schaumburg *et al.*, 2004) and then extrapolated macrophyte coverage for the total lake area including depth strata from the contour maps to compare macrophyte coverage between managed and unmanaged gravel pit lakes (**Paper I**).

For **Paper IV**, I noted the extensions of the all littoral structures (in %) within each electrofishing transect and later transformed the detailed information into one of the following five categories: reeds, submerged macrophytes, wood, deadwood and open littoral. Furthermore, I noted the average fished depth of each transect as categorical variable (very shallow: < 0.5 m; shallow: 0.5 – 1.0 m and deep: 1.0 – 2.0 m). For **Paper V**, the shoreline structure at each electrofishing point was noted as categorical variable to specifically investigate the effect of supplemented deadwood bundles. The subsequent analysis focussed on the main occurring littoral structures: supplemented deadwood bundles, emerged macrophytes and open littoral.

3.5 STATISTICS

3.5.1 Analysis of the effects of fisheries management and lake genesis on the fish community composition

I compared lake-level environmental variables between managed and unmanaged gravel pit lakes using pairwise comparison (**Paper I**), followed by a redundancy analyses (RDA) to

evaluate the effects of environmental variables, fisheries management and lake genesis on fish community composition (**Paper I and II**). I displayed the fish community compositions using non-metric multidimensional scaling (nMDS; Kruskal, 1964) and thereby allowing for comparison to other relevant studies (e.g. Emmrich et al., 2014). I used permutation tests to test for significant differences in fish community composition regarding lake genesis and the presence or absence of fisheries management. I conducted additional similarity percentage analyses (SIMPER) to reveal species-specific contribution to the overall differences between lake types (Clarke, 1993).

3.5.2 Analysis of deadwood recruitment and density

I used a stepwise Variance Inflation Factor (VIF) section to reduce collinearity among variables and ran linear mixed models with lake as random effect to analyse the most important predictors of small and large deadwood in gravel pit lakes (**Paper III**). I further compared the deadwood densities in the gravel pit lakes with deadwood data from natural lakes in northern Wisconsin and Upper Michigan, USA extracted from Christensen *et al.* (1996) and natural lakes in Ontario, Canada extracted from Pearce, Mallory & Smokorowski (2022). To achieve comparable data sets, I integrated only deadwood structures from the gravel pit lakes with similar bole diameter dimensions as used in the two North American studies.

3.5.3 Analysis of the effects and importance of littoral habitat structures on littoral fish abundance

For **Paper IV**, I visualized lake environmental variables using a principle component analysis (PCA) and I used PC scores from the first axis for the subsequent analysis. The first PC axis displayed information about nutrient level and lake morphology and, therefore, represented lake productivity. Afterwards, I ran boosted regression trees (BRT) to analyse the importance of lake environmental variables and littoral habitat variables on fish abundance by integrating electrofishing data from 20 gravel pit lakes fished for four continuous years (2016 – 2019). I conducted BRTs for small (≤ 100 mm) and large (> 100 mm) individuals of perch, roach, rudd, tench, small (≤ 300 mm) and large (> 300 mm) eel and small (≤ 200 mm), medium (201 – 400 mm) and large (> 400 mm) pike. I utilized BRTs instead of linear models as BRTs are superior in detecting of non-linear relationships of environmental variables on species-specific fish abundance (Elith, Leathwick & Hastie, 2008).

In **Paper V**, we applied generalized linear mixed models (GLMM) with negative binominal (NB) distribution and lake as random effect to analyse the effects of littoral structures and

especially supplemented deadwood bundles on species-specific littoral fish abundance on diurnal and annual scale. In line with **Paper IV**, we focussed on the most abundant species in the littoral zones of gravel pit lakes, namely perch, roach, rudd, tench, pike and eel.

4. Key Findings and Discussion

In my thesis, I found lake genesis and fisheries management to impact fish species richness and community composition, with an increased number of fish species in lakes managed for fisheries and highly variable fish community compositions in unmanaged gravel pit lakes compared to unmanaged natural lakes (**Paper I and II**). I further observed low littoral deadwood densities in gravel pit lakes, mainly driven by lake age, riparian tree density in interaction with wind direction and fisheries management in interaction with littoral slope (**Paper III**). I detected a high importance of the littoral zone and its structures on the species-specific abundance of typical fish species in gravel pit lakes with partly non-linear effects (**Paper IV**) and supplemented deadwood bundles displayed an appropriate habitat for various fish species in gravel pit lakes and were intensively used in winter (**Paper V**).

In the following, I will present and discuss my key findings in further detail and integrate them in the existing body of literature. I will start with the natural and anthropogenic colonization processes of fishes in lentic waters (Figure 1) and explain how lake genesis and fisheries management affects the fish species pool in lakes and thus the diversity patterns of fish communities in gravel pit lakes. Afterwards, I will present my findings on how lake environment (abiotic factors), biotic interactions and littoral habitats in gravel pit lakes affect fish species in their survival, abundance and distribution leading to the final fish community composition.

4.1 NATURAL COLONIZATION

I found lake genesis to strongly affect the local fish species pool, with roach, tench, rudd and pike being typical fish species of natural unmanaged lakes (**Paper II**). By contrast the occurring fish species in unmanaged gravel pit lakes varied strongly with no species occurring in more than 50 % of the lakes (**Paper I and II**).

Natural lakes in the north German lowlands were formed during the last ice age that ended roughly 10,000 years ago (Håkanson, 2012). Refugia for fishes to survive the last ice age in northern Europe were rare and natural lakes were free of fish after their genesis (Andersen & Borns Jr., 1994). With the melting of the ice shield, the remaining lakes became hydrologically linked, allowing a fast colonization by fish (Mandrak & Crossman, 1992; Bernatchez & Wilson, 1998; Griffiths, 2017). Fishes colonized the newly formed lakes of northern Germany mainly

from the Ponto-Caspian area (Griffiths, 2006), but also from France (Nesbø *et al.*, 1999). Biogeographic barriers such as oceans and mountain ranges limit the potential for colonization events of freshwater fishes (Legendre & Legendre, 1984; Griffiths, 2006; Rahel, 2007). Fishes from the Iberian and Italian peninsulas were disconnected by mountain ranges and no natural fish colonization from there to central Europe has been detected yet (Griffiths, 2006).

Gravel pit lakes in the same region and in other European areas are relatively young with a lake age of less than 100 years (**Paper I and II**; Zhao *et al.*, 2016; Søndergaard *et al.*, 2018; Seelen *et al.*, 2021a). The probability of colonization events rises with lake age (Barbour & Brown, 1974; Peel *et al.*, 2019; Mehner & Brucet, 2022) and is, thus, relatively low in gravel pit lakes compared to natural lakes. However, all investigated gravel pit lakes were colonized by fishes (**Paper II**).

Still today permanent hydrological connection display the fastest colonization pathway for fishes (Borcherding *et al.*, 2002; Kristensen *et al.*, 2020). However, all lakes investigated in this thesis are isolated, but hydrological connections might have existed for the natural lakes within the last 10,000 years since their genesis.

Flooding events provide a temporally limited connection between water bodies and can also lead to colonization events (Pont *et al.*, 1991; Olden *et al.*, 2010). Gravel pit lakes are often located in the floodplain area of large rivers (Mollema & Antonellini, 2016) and, thus, chances for fish colonisations during a flooding event are relatively high. The transport of fish eggs by birds displays a further colonization mechanism for fishes, that has been postulated for a long time (Hirsch *et al.*, 2018) with limited evidence (Riehl, 1991). Indeed, recent studies demonstrated that fish eggs can be distributed by waterfowl (Silva *et al.*, 2019; Lovas-Kiss *et al.*, 2020) and by flying invertebrates (Suetsugu & Togashi, 2020). Reports of fish rain initiated by hurricanes (Bajkov, 1949) are a further pathway for fish colonizations, however, the chances for this pathway are very low, especially in Europe.

In **Paper II**, I investigated the fish species pool of unmanaged natural lakes and unmanaged gravel pit lakes. I detected fishes in all lakes (including all unmanaged gravel pit lakes), but with severe differences in species richness and community composition. However, I did not specifically investigate the odds as well as temporal and spatial aspect for all colonization mechanisms, which remain further unknown (see section 'further research needs' for detailed discussion). Nevertheless, I can conclude that fishes can colonize isolated gravel pit lakes via natural colonization pathways within several years or decades, while anthropogenic

colonization pathways further affect the fish species pool in gravel pit lakes, even in unmanaged ones.

4.2 ANTHROPOGENIC COLONIZATION

In **Paper I and II**, I showed that natural and gravel pit lakes managed for fisheries and subjected to regular fish stocking are characterized by an increased fish species richness, compared to unmanaged lakes. Fish communities of managed lakes were comprised of the typical species occurring also in unmanaged natural lakes such as roach, tench and pike, plus fish species of fisheries interest such as eel and common carp (*Cyprinus carpio*) (**Paper I and II**). I also found signs of illegal fish releases (e.g. eel and golden phenotypes of rudd) in unmanaged gravel pit lakes (**Paper I and II**).

Human-induced fish colonization has been widespread at least since the medieval times (Hoffmann, 1995; Balon, 2004) and we distinguish two pathways, legal fish introductions and illegal fish introductions.

Fish stocking represents a legal form of anthropogenic fish colonization and is the most popular measure in fisheries management (Arlinghaus *et al.*, 2008, 2015, 2022). The purposes are manifold and Cowx (1994) defined four categories of stocking strategies: stocking for mitigation, stocking for enhancement, stocking for restoration and creation of new fisheries. Stocking for mitigation and stocking for enhancement require by definition an already existing fish stock in the water body. Stocking for enhancement is often conducted on an annual basis (e.g. in gravel pit lakes) with huge numbers and biomasses of various fish species (i.e. 77 million fishes with a total biomass of 3.7 t in Germany in 2010 and 90 million fishes with a total biomass of 2 t in France in 2013) (Arlinghaus *et al.*, 2015; Theis *et al.*, 2017; Cucherousset *et al.*, 2021). However, fish stocking to increase species-specific abundance with successfully recruiting species has often been proven to fail (Anwand, 1995; Knösche, 1995; Li *et al.*, 1996; Hühn *et al.*, 2014) and basically fulfils similar characteristics as biomanipulation, which has also been proven to fail in long term (Bernes *et al.*, 2015). Stocking for restoration aims at the recolonization of a species (e.g. restocking of salmon populations) while stocking for the creation of a new fisheries displays a pathway for fish species to colonize new water bodies (Cowx, 1994; Baer *et al.*, 2007; Arlinghaus *et al.*, 2015). Especially predatory species are popular targets for recreational anglers and often stocked in central Europe to create a new fisheries (Arlinghaus *et al.*, 2015; Cucherousset *et al.*, 2021). The introduction of new fish

species increase fish species richness and the number of predatory species in lakes and further impact fish community composition (Tammi *et al.*, 2003; Zhao *et al.*, 2016; Skeate *et al.*, 2021). Importantly, at least in Germany fish stocking is limited to native species by law (compare Baer *et al.*, 2007; Lewin, Bischoff & Mehner, 2010; Arlinghaus *et al.*, 2017). However, all described forms of legal stocking face several challenges and threats to local biodiversity. Fish stocking can offset natural biogeographic barriers and lead to the unintentional spread of non-native species as well as the coordinated distribution of native fish species thereby fostering biotic homogenisation (Rahel, 2000, 2002, 2007; Villéger *et al.*, 2011; Sommerwerk *et al.*, 2017). Illegal introductions can occur in different forms. The intentional spread of non-native fish species is generally not allowed (Baer *et al.*, 2007; Lewin *et al.*, 2010). Furthermore, individual persons can introduce native and non-native fish species in nearby water bodies to either establish a desired species or to dispose fishes (Cambray, 2003; Johnson *et al.*, 2009; Hirsch *et al.*, 2021; Weir *et al.*, 2022). Individual persons conducting these illegal introductions mainly comprise anglers, aquarist or garden pond owners (Cambray, 2003; Johnson *et al.*, 2009; Hirsch *et al.*, 2021; Weir *et al.*, 2022). Illegal fish introductions can contribute to the spread of fish species and especially in densely populated areas, illegal releases of ornamental and garden pond fishes have become a main vector for species introductions in urban waters (Copp *et al.*, 2005, 2010; Patoka *et al.*, 2017). Furthermore, illegal introductions contribute to the homogenisation of fish communities (Cazelles *et al.*, 2019; Hirsch *et al.*, 2021).

4.3 DIVERSITY PATTERN OF FISH COMMUNITIES

All investigated lakes in my studies were colonized by fishes and I found higher species richness (α -diversity) and an elevated number of predatory species in lakes with fisheries management compared to unmanaged lakes (**Paper I and II**).

In gravel pit lakes subjected to fishing rights (as it is common in Germany; Arlinghaus *et al.*, 2017), fish stocking is regularly conducted to introduce a fishable stock of various species (Cowx, 1994; Arlinghaus *et al.*, 2015). Predatory fish species are popular targets of anglers (Eby *et al.*, 2006; Donaldson *et al.*, 2011) and thus regularly stocked in German lakes (Arlinghaus *et al.*, 2015). Furthermore, various cyprinid species, such as larger-bodied tench and common carp, but also baitfish species, such as roach or rudd, and small-bodied non-game fish species are stocked in European gravel pit lakes (Arlinghaus *et al.*, 2015; Cucherousset *et al.*, 2021). My findings are in line with other studies, that detected an increased species richness and

number of predatory species in natural lakes and gravel pit lakes as a result of introductory fish stocking with native species under fisheries management (Tammi *et al.*, 2003; Zhao *et al.*, 2016; Skeate *et al.*, 2021). Furthermore, the elevated species richness in managed gravel pit lakes is also driven by the repeated and often annual stocking of fish species without in-lake recruitment such as eel and common carp (Arlinghaus *et al.*, 2015; Zhao *et al.*, 2016).

Fisheries management and stocking is often associated with the spread of non-native fish species (Rahel, 2002; Hickley & Chare, 2004). The overall number of non-native species in my studies was low with only single individuals of rainbow trout (*Oncorhynchus mykiss*), brown bullhead (*Ameiurus nebulosus*) and topmouth gudgeon (*Pseudorasbora parva*) and the number of invasive species did not differ between managed and unmanaged lakes (**Paper I and II**).

Non-native species in Europe can be divided into two groups: species from European catchments that were translocated among them and exotic species from outside the western Palearctic (Sommerwerk *et al.*, 2017; Trochine *et al.*, 2018). Common carp is naturally found in eastern and central Europe, but introduced in parts of western Europe (Kottelat & Freyhof, 2007; Maceda-Veiga *et al.*, 2010; Skeate *et al.*, 2021). Common carp is a popular fish among recreational anglers in Europe and regularly stocked (Arlinghaus *et al.*, 2015; Cucherousset *et al.*, 2021). In England and France, common carp is classified as non-native and common carp stocking has been found to negatively affect diversity of lake fish communities (Zhao *et al.*, 2016; Skeate *et al.*, 2021). By contrast, common carp is classified as native in Germany (Hoffmann, 1995; Freyhof, 2009) and regular stocking is in agreement with fisheries management (Baer *et al.*, 2007). Hence, different classifications of fishes that are native in parts of Europe can lead to strong differences in the evaluations of fisheries management actions.

Zhao *et al.* (2016) also detected non-native warmwater species from outside of Europe (e.g. largemouth bass (*Micropterus salmonids*) or Mosquitofish (*Gambusia affinis*)) in angler-managed gravel pit lakes in southern France. Largemouth bass and Mosquitofish have become frequently distributed over southern Europe (Kottelat & Freyhof, 2007; Vidal *et al.*, 2010), but I did not detect them during my studies (**Paper I, II, IV and V**). For both species only limited detections have been reported in German waters (Kottelat & Freyhof, 2007; Wolter & Röhr, 2010) and their threat to biodiversity in Germany is considered as rather low (Nehring *et al.*, 2010; Wiesner *et al.*, 2010).

The lowlands of northern Germany are located around 1,000 km north of southern France and strongly differ in environmental conditions such as temperature. Indeed, temperature has been detected as a major driver for the establishment of non-native fish species (Trochine *et al.*, 2018; Anas & Mandrak, 2021) and might explain the different findings between Zhao *et al.* (2016) and my studies (**Paper I and II**). Accordingly, the impact of fisheries management differs by geographical region, with higher chances of non-native warmwater species establishment in southern Europe compared to northern and central Europe.

I detected only single individuals of non-native fish species, which encompassed rainbow trout, brown bullhead and topmouth gudgeon (**Paper I and II**). Brown bullhead and topmouth gudgeon are usually unintentionally released in new water bodies through poorly sorted fish stocking (Kinzelbach, 1995; Waterstraat, 2002). Rainbow trout is the only non-native species of fisheries importance that is intentionally released (Arlinghaus *et al.*, 2015; Cucherousset *et al.*, 2021). Stocked rainbow trout normally remain in the water body for only a short period of time due to predation and rapid recapture by anglers (Baker & Sammons, 2021). As a result, Daupagne *et al.* (2021) found negligible impacts of trout stocking on lake fish communities. The low number of non-native species over all managed lakes suggests, that stocking actions of fisheries managers in the study area were predominately in line with regional fisheries law, while stocking of maladapted fish species, which might be errored out over time by predation and competition with native fish species, cannot fully be excluded. Importantly, I found topmouth gudgeon in one unmanaged gravel pit lake and the only individual of brown bullhead in my whole dataset in another unmanaged gravel pit lakes (**Paper I and II**). Accordingly, non-native species also colonize unmanaged lakes, most likely via illegal human assistance (Copp *et al.*, 2005; Patoka *et al.*, 2017; Hirsch *et al.*, 2021).

I found the small-bodied non-game fish species bitterling (*Rhodeus amarus*), three-spined stickleback (*Gasterosteus aculeatus*) and bleak (*Alburnus alburnus*) exclusively in managed gravel pit lakes, while stone loach (*Barbatula barbatula*) and ninespine stickleback (*Pungitius pungitius*) were only found in unmanaged gravel pit lakes (**Paper I and II**). The number of small-bodied non-game fish species did not differ between managed and unmanaged gravel pit lakes (**Paper I**). Apart from stocking desired game fish species, angling clubs also engage in stocking prey fish species and small-bodied non-game fish species for conservation purpose (Arlinghaus *et al.*, 2015). However, the release volume of small-bodied non-game fish is rather small (Arlinghaus *et al.*, 2015) and strongly depends on the focus of the individual fishing clubs

(Theis *et al.*, 2017). Furthermore, rare and highly stochastic events of natural colonization (e.g. egg dispersal via birds (Silva *et al.*, 2019; Lovas-Kiss *et al.*, 2020)) and illegal fish releases (Copp *et al.*, 2010; Hirsch *et al.*, 2021) might benefit the dispersal of small-bodied non-game fish in unmanaged gravel pit lakes. Sunbleak (*Leucaspis delineates*) and ninespine stickleback are also known as pioneer species and water bodies without predation pressure by typical piscivorous species such as perch and pike further benefit the successful establishment of these species (Englund *et al.*, 2009). Accordingly, colonisation events of ninespine stickleback in managed gravel pit lakes might have happened as well, but chances of successful establishment are rather low due to the high predation pressure by regularly occurring predatory species.

I detected five regionally threatened fish species in gravel pit lakes, namely pike, eel, European catfish (*Silurus glanis*), bitterling and spined loach (*Cobitis taenia*) (**Paper I**). By extending the data set, I could also detect threatened crucian carp (*Carassius carassius*) in a further gravel pit lake (**Paper II**). The number of threatened fish species was significantly higher in managed gravel pit lakes compared to unmanaged gravel pit lakes (**Paper I**). This significant difference was mainly driven by pike and eel, which are considered as threatened species in Lower Saxony (LAVES - Landesamt für Verbraucherschutz und Lebensmittelsicherheit, 2011). Both species are desired game fish species for anglers and thus regularly stocked (Arlinghaus *et al.*, 2015; Cucherousset *et al.*, 2021). However, eels are considered as globally threatened according to IUCN criteria (Freyhof & Brooks, 2011) and should - from a conservation point of view - not be stocked in isolated water bodies to allow migration and natural reproduction. Pike are only considered as threatened in Lower Saxony (LAVES - Landesamt für Verbraucherschutz und Lebensmittelsicherheit, 2011), but they are not listed on the German Red List of freshwater fishes (Freyhof, 2009). Accordingly, the higher number of threatened species in managed lakes should be interpreted carefully, especially in the case of catadromous eel which need water bodies with migration possibilities to the sea to fulfil their lifecycle (Dekker, 2016). However, crucian carp is also considered as nationally threatened (Freyhof, 2009) and in line with my findings, crucian carp and other threatened fish species such as bitterling have also been detected in other gravel pit lakes in Lower Saxony and throughout Europe (Emmrich *et al.*, 2014; Søndergaard *et al.*, 2018; Lyach, 2022). Both species require habitats with dense aquatic vegetation (Pettersson & Brönmark, 1993; Kottelat & Freyhof, 2007) and rather shallow gravel pit lakes with abundant macrophyte extensions can

display habitats for their conservation. Generally, the environmental features of the gravel pit lake have to match the species-specific demands to function as appropriate conservation habitat.

I detected β -diversity of fish community composition to be significantly lower in gravel pit lakes managed for recreational fisheries compared to unmanaged gravel pit lakes (**Paper I**). Fish communities in managed gravel pit lakes were composed of typical and native lake fish species, while no fish species occurred in at least half of the unmanaged gravel pit lakes (**Paper I**). In **Paper II**, I related these findings to natural lakes with and without fisheries management and detected that β -diversity of fish communities in managed gravel pit lakes did not differ from those in managed and unmanaged natural lakes, while β -diversity of fish communities in unmanaged gravel pit lakes was still significantly higher resulting from the regular absence of typical lake fish species (e.g. tench, pike and roach) and the presence of atypical fish species (e.g. ninespine stickleback and stone loach).

The homogenization of fish communities as a result of anthropogenic activities such as fish stocking has regularly been reported (Rahel, 2002; Villéger *et al.*, 2011; Cazelles *et al.*, 2019). My findings show, that gravel pit lakes are no exception. However, fish communities in unmanaged natural lakes did not differ from managed lakes leading to the assumption that quite similar fish communities will establish over time as a result from colonization and extinction events, environmental conditions of the lakes and biotic processes within the ecosystem. Accordingly, fisheries management acts as colonization booster in managed gravel pit lakes, while the high spatial β -diversity of fish communities in unmanaged gravel pit lakes displayed their highly stochastic and variable succession status with fish based on random natural colonization events as well as illegal introductions (**Paper I and II**). Importantly, a lake's carrying capacity is driven by nutrient level (Hanson & Leggett, 1982; Downing *et al.*, 1990) and, thus, I found no difference in fish biomass (BPUE) between managed and unmanaged gravel pit lakes at similar nutrient level (**Paper I**; Figure 6; Table 3).

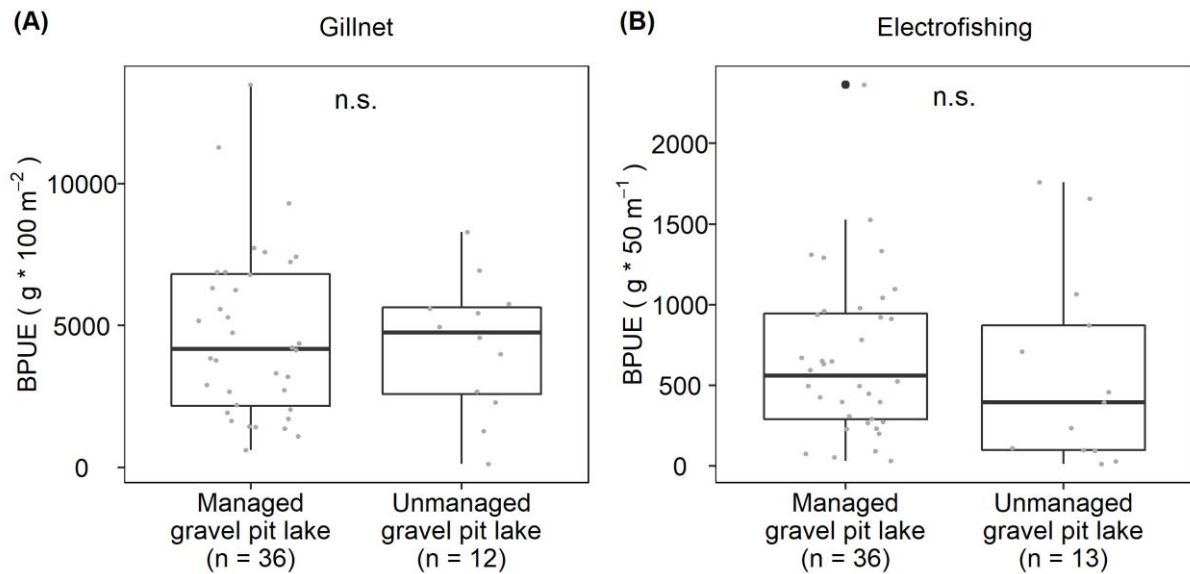


Figure 6: Comparison of catch (as biomass) per unit effort (BPUE) in managed and unmanaged gravel pit lakes using multimesh gillnetting (A) and electrofishing (B). The box of each boxplot displays the 25th to the 75th percent quartile with the vertical line as median. The length of the whiskers is limited to 1.5 x inter-quartile range and large black dots indicate outliers. Grey dots represent the lake-specific raw data.

Table 3: Results from Wilcoxon test comparing BPUE values between managed and unmanaged gravel pit lakes.

	Sampling method	W	p-value
Managed gravel pit lake vs. Unmanaged gravel pit lake	Gillnet	218	0.972
Managed gravel pit lake vs. Unmanaged gravel pit lake	Electrofishing	276	0.352

4.4 LAKE ENVIRONMENT

The abiotic conditions of a lake determine the suitability as fish habitat and impact species-specific abundance. First, I will present and discuss my findings on oxygen-levels and water temperatures (including lake mixing regime) and pH value, which determine the general suitability as fish habitat as well as species-specific survival after colonization / introduction. Afterwards, I will focus on the important environmental variables trophic state (nutrient level) and lake morphology and their effect on fish abundance and community composition.

I detected 46 out of 50 gravel pit lakes to be stratified at the fishing events in autumn with unoxygenated water below the thermocline (**Paper I and II**). Only four rather shallow gravel

pit lakes were characterized by a completely mixed water column with all lake habitats being available for fish. The surface temperature at the fishing events extended the recommended 15 °C (CEN, 2015) in all but three gravel pit lakes with a minimum surface temperature of 12.8 °C. The highest surface water temperature, that I detected during an additional young fish survey (not further mentioned in this thesis) was 30.3 °C at the gravel pit lake 'Lohmoor' in July 2018.

Oxygen-rich water is the basis for a high diversity of aquatic plants and animals. Only a few fish species of the temperate zone are adapted to very low oxygen conditions such as crucian carp (Pettersson & Brönmark, 1993; Olsén & Bonow, 2022). The oxygen saturation of water depends on its temperature, which varies over the seasons in lentic water bodies of the temperate zones (Schwoerbel & Brendelberger, 2013). A similar seasonal variation of water temperature and oxygen-level as observed in natural lakes has already been described for German gravel pit lakes (Blöchl, 2004; Braune, 2004). Oxygen-level, temperature and pH value in lakes are also affected by a lake's mixing regime (Schwoerbel & Brendelberger, 2013; Mehner & Brucet, 2022). The mixing regime determines the availability of lake habitats (littoral, benthic and pelagic zone) and thereby the suitability for certain fish species (e.g. smelt, burbot and coregonid species) (Ritterbusch *et al.*, 2014). The gravel pit lakes in my studies comprised, compared to natural lakes, rather small and mostly stratified water bodies as it is typical for gravel pit lakes (Søndergaard *et al.*, 2018; Vucic *et al.*, 2019; Nikolaus *et al.*, 2020; Seelen *et al.*, 2021b). The lake characteristics of deep lakes and polymictic lakes as described by Ritterbusch *et al.* (2014) were only rarely found in gravel pit lakes. Hence, the investigated lakes offered suitable conditions as fish habitat in terms of oxygen-level and temperature for fish species typically found in small and stratified lakes (**Paper II**).

The pH values in the investigated gravel pit lakes varied between 6.8 and 10.1 and were elevated in managed gravel pit lakes compared to managed natural lakes ($p = 0.056$; **Paper II**). Importantly, I could not detect an impact of pH value on fish community composition (**Paper II**).

The pH value is usually slightly higher in gravel pit lakes compared to natural lakes (Søndergaard *et al.*, 2018; Vucic *et al.*, 2019; Seelen *et al.*, 2021b), which is mostly caused by the wash out of carbonates during the excavation process (Mollema & Antonellini, 2016). The pH value provides important information, if the water body offers suitable conditions for fishes with species-specific effects (E.I.F.A.C., 1969). Low pH levels have been found as

important discriminants of fish species richness in lakes (Somers & Harvey, 1984; Matuszek & Beggs, 1988; Magnuson *et al.*, 1998) with typical fish species (i.e. Cypriniformes) missing at pH values below 6.2 (Rahel & Magnuson, 1983). Accordingly fish community compositions of lakes with very low or very high pH values significantly differ from those in lakes with a neutral pH values (Rahel & Magnuson, 1983; Magnuson *et al.*, 1998). Extreme pH values are regularly found in pit lakes from lignite mining (Schultze *et al.*, 2010), but in my thesis I focussed on pit lakes from sand and gravel excavation which usually offer pH conditions between 7.2 and 10.4 (Mollema & Antonellini, 2016). Accordingly, pH values in the investigated lakes were suitable for fish species typically found in small lakes, but did not impact fish community composition (**Paper I and II**; Emmrich *et al.*, 2014; Søndergaard *et al.*, 2018).

The investigated gravel pit lakes were on average mesotrophic (**Papers I – V**). Total phosphorus (TP) concentrations in natural lakes were slightly higher than in gravel pit lakes and significant differences in TP were only detected between managed gravel pit lakes and managed natural lakes (**Paper II**).

Young gravel pit lakes are generally fed by nutrient-poor groundwater explaining their often mesotrophic conditions (Mollema & Antonellini, 2016). The concept of lake aging describes the accumulation process of organic material in lakes leading to increased nutrient levels over time (Callisto, Molozzi & Barbosa, 2014) and thus the trophic state of relatively old natural lakes from glacial genesis is expected to be elevated compared to relatively young gravel pit lakes. My findings are in line with other relevant studies from the Northern Hemisphere, that also detected increased nutrient levels in natural lakes compared to gravel pit lakes (Emmrich *et al.*, 2014; Søndergaard *et al.*, 2018; Vucic *et al.*, 2019).

I further found trophic state as important drivers for fish community composition and littoral fish abundance (**Papers II and IV**).

Lakes' trophic state shapes fish communities in two ways. First, the amount of nutrients determines the fish biomass of a lake, i.e. the carrying capacity (Hanson & Leggett, 1982; Downing *et al.*, 1990). Second, species-specific domination of the fish community changes along the trophic gradient. In oligotrophic lakes, European lake fish communities are dominated by salmonid species (mainly coregonids). Increasing nutrient levels lead to a domination of perch (mesotrophic systems), then of roach (eutrophic systems) and finally a domination of bream (polytrophic systems) (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005). Zhao *et al.* (2016) also found an impact of trophic state on fish

communities in gravel pit lakes, but did not investigate species-specific effects. In **Paper II**, I detected roach abundance to increase at elevated total phosphorus concentrations, while perch abundance was highest at mesotrophic conditions (Figure 7 and Figure 8), thereby demonstrating similar effects of trophic state on fish communities in gravel pit lakes as already observed for natural lakes (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005). Hence, I found perch as the most abundant fish species in the mesotrophic gravel pit lakes (**Paper I, II, IV and V**).

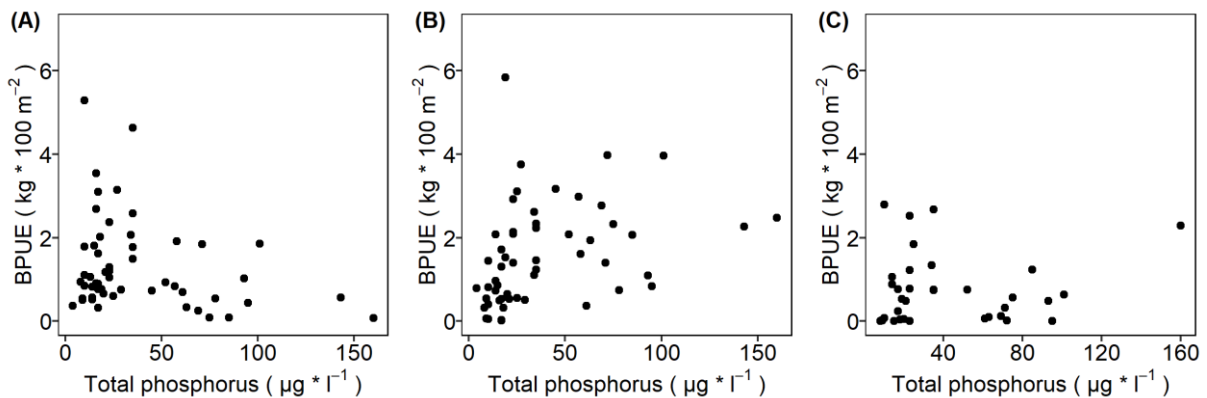


Figure 7: Catches as biomass per unit effort (BPUE) for (A) perch, (B) roach and (C) bream from multimesh gillnetting in 65 small lakes. Lakes without species-specific catches were removed.

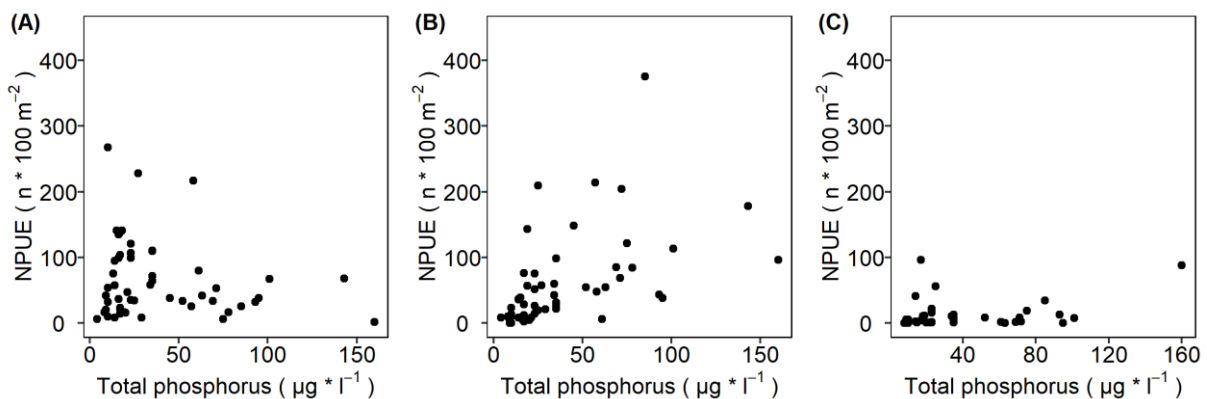


Figure 8: Catches as numbers per unit effort (NPUE) for (A) perch, (B) roach and (C) bream from multimesh gillnetting in 65 small lakes. Lakes without gillnet catches were removed.

The investigated gravel pit lakes were 8.0 ± 6.2 ha (mean \pm SD; range: 0.7 - 21.1 ha) with a mean depth of 4.1 ± 2.9 m (mean \pm SD; range: 0.5 - 13.0 m). Using a redundancy analyses (RDA), I found no effects of lake morphological variables on fish community composition in **Paper I and II**. However, in **Paper IV** the morphological variables ‘mean lake depth’ and ‘share of shallow areas’ were loading on the same PCA axis as the trophic variables ‘total phosphorus

concentration', 'chlorophyll a concentration' and 'Secchi depth'. Therefore, I integrated them as a combined variable called 'lake productivity' and found littoral fish abundance (especially of Cypriniformes species) to increase with lake productivity. Morphological lake characteristics such as mean lake depth, lake size, shoreline length and shoreline development factor are known to shape lake fish communities (Eckmann, 1995; Post D., Pace M. & Hairston N., 2000; Mehner *et al.*, 2005; Brucet *et al.*, 2013). Lake size has repeatedly been found to impact species richness via the availability of habitats (Matuszek & Beggs, 1988; Eckmann, 1995). Mean lake depth strongly impacts the mixing regime and thus the suitability of the lake for species such as smelt, burbot and coregonid species (Diekmann *et al.*, 2005; Ritterbusch *et al.*, 2014). Accordingly, morphological characteristics have already been used to classify fish communities (e.g. in German lowland lakes; Ritterbusch *et al.*, 2014). The investigated gravel pit lakes in my studies were rather small, but matched the typical morphological characteristics of gravel pit lakes in Europe (Zhao *et al.*, 2016; Søndergaard *et al.*, 2018; Seelen *et al.*, 2021b). The small gradients of the morphological characteristics limited their detrimental power on the fish community composition (**Paper II**), but I found lake productivity (including morphological characteristics) to impact littoral fish abundance (**Paper IV**) and Höhne *et al.* (2020) detected the shoreline development factor to impact perch growth in gravel pit lakes. Hence, lake morphology influences fishes even in small gravel pit lakes, but effect sizes are rather small due to limited morphological gradients.

4.5 BIOTIC INTERACTIONS

Biotic interactions impact community composition as important filters (Jackson *et al.*, 2001; Keddy & Laughlin, 2022; Mehner & Brucet, 2022). The number of species in each lake determine the number of biotic interactions (i.e. competition and predation) in each lake, while lake environmental factors (abiotic conditions, nutrient level, lake morphology and quality and quantity of littoral habitats) control the degree of competition and predation and thus co-occurrence patterns (Cordero & Jackson, 2021). The top-down effect of predation on abundance, biomass and size spectra of lower trophic cascades, and thereby finally on fish communities, is considered rather low compared to lake environmental factors (Mehner, 2010; Mehner *et al.*, 2016; Kokkonen *et al.*, 2019). Long-term data from a large Estonian lake (Lake Võrtsjärv) confirmed that the food web is driven by bottom-up processes (Bhele *et al.*, 2022). However, the introduction of a new predator (e.g. pike) has led to strong abundance

declines of certain prey fish species in a small lake (He & Kitchell, 1990) and several species extinctions have been found as a result of predator introduction by using data from 821 Swedish lakes (Henriksson *et al.*, 2016). The comparison of fish species richness and community composition also revealed significant impacts of the presence or absence of predatory species (Chapleau *et al.*, 1997). I found ninespine stickleback only in lakes without the predatory species pike and perch (**Paper I and II**). Ninespine sticklebacks are sensitive to predation and the introduction of predatory species (pike, perch or both) can lead to their extinction in lake ecosystems (Englund *et al.*, 2009; Henriksson *et al.*, 2016; Kristensen *et al.*, 2020). Even though my findings are just of correlative nature, they are in line with recent literature and serve as further examples of the structuring effect of predation on species presence or absence. Accordingly, top-down effects impact fish communities with an increased predation pressure on some species, that might lead in some cases even to species-specific extinctions. Importantly, the effects of predation on fish communities are mediated by abiotic factors (Cordero & Jackson, 2021) and Tonn & Magnuson (1982) found fish communities to be impacted by predation in interaction with oxygen concentrations in winter and Englund *et al.* (2009) found the presence of crucian carp in lakes to be depended on predation and lake depth. Importantly, total lake fish abundance and biomass are predominantly determined via bottom-up effects (Hanson & Leggett, 1982; Downing *et al.*, 1990; Bartrons *et al.*, 2020).

Competition is a further biotic interaction, that mainly occurs for food and habitat and can be observed between individuals of different species (interspecific competition) and between individuals within a species (intraspecific competition). Interspecific competition has been studied intensively on individual level and population level, however, studies on the effects of competition on fish communities are rare (compare Mehner & Brucet, 2021). The most important study was conducted by MacDougall *et al.* (2018), who found limited evidence for competition as a displacement factor of certain fish species independent of environmental conditions.

Perch and roach are among the most frequent and most abundant fish species in lentic waters of north and central Europe and both species shape their fish community compositions (Tammi *et al.*, 2003; Mehner *et al.*, 2005; Emmrich *et al.*, 2014). The interactions between both species have been studied intensively with perch being dominant in oligo- and mesotrophic conditions, while roach are dominant at elevated nutrient levels (e.g. eutrophic

conditions) (Persson *et al.*, 1991; Jeppesen *et al.*, 2000). Habitat structures also impact their competitive situation with perch dominating in structured habitats and roach in rather unstructured habitats (Eklöv & Persson, 1995; Persson & Eklöv, 1995). In line with the literature, I found perch to be dominant in oligo- and mesotrophic conditions, while roach were more abundant in gravel pit lakes with eutrophic conditions or even higher nutrient levels (**Paper I, II, IV**; Figure 7 and Figure 8). Furthermore, I found perch to be more dependent on littoral structures than roach with highest perch abundance in submerged macrophytes and deadwood structures (**Paper IV and V**). Accordingly, the environmental-mediated abundance pattern of perch and roach in my studies match findings from other important studies, but the exact effects of competition between these two and other fish species on the resulting fish community composition have not been studied in detail in my thesis.

Fish stocking as a measure of fisheries management can further impact predation and competition in lentic waters. Apart from the introduction of a new predator (discussed above), stocking for enhancement aims to increase the fish abundance. However, the effect of stocking for enhancement into a successfully reproducing population has been proven to fail (Li *et al.*, 1996; Hühn *et al.*, 2014) as the carrying capacity limits the overall fish biomass that can coexist within a water body (Hanson & Leggett, 1982). By introducing further individuals of a certain fish species via stocking, competition within this species and also to other species with a certain niche overlap for food and habitat should increase. Furthermore, predation pressure on prey species should also increase and thereby, stocking for enhancement fulfils similar characteristics as biomanipulation, which has also been proven to fail in long term (Bernes *et al.*, 2015). Hence, enhancement stocking affects biotic interaction in lake ecosystems only on a short-term scale, while the introduction of a new species that establishes in the new environment impacts predation and competition in the long term and thus fish community composition (He & Kitchell, 1990).

4.6 LITTORAL HABITATS

In **Paper IV**, I estimated the extension of littoral structures in gravel pit lakes and found open littoral as the most frequent littoral structure (35.1 % ± 20.3 %), followed by wood (24.2 % ± 15.7 %), reeds (22.9 % ± 20.5 %), submerged macrophytes (13.2 % ± 12.1 %) and deadwood (4.5 % ± 4.0 %; **Paper IV**). In **Paper III**, I investigated the factors driving deadwood recruitment in gravel pit lakes and my results revealed that the abundance of tall riparian trees especially

when exposed to wind and lake age were important drivers for littoral deadwood densities in the investigated lakes. I further detected recreational-fisheries management to affect littoral deadwood densities in interaction with littoral slope resulting in lowest deadwood densities in shallow zones of angler-managed gravel pit lakes. Overall the amounts of littoral deadwood were lower in gravel pit lakes compared to natural lakes in North America.

The littoral zone and its structures display a highly valuable habitat, that connects aquatic and terrestrial ecosystems (Naiman & Décamps, 1997; Schindler & Scheuerell, 2002; Pusey & Arthington, 2003). The littoral zone of small lakes is mostly structured by trees, deadwood, reed belts or submerged macrophytes (Völkl, 2010; Schwoerbel & Brendelberger, 2013). By contrast, the largest share of the littoral zone in the investigated gravel pit lakes was unstructured with open, mostly soft bottom or sandy substrates such as angling sites or sandy beaches (**Paper IV**). In relatively young gravel pit lakes the succession is still in progress (Müllerová *et al.*, 2022), which might explain the large shares of unvegetated littoral areas. Furthermore, the typical morphology of gravel pit lakes with steep slopes and relatively high maximum depths limits the spread of submerged and emerged macrophytes and thus their abundance (Duarte & Kalff, 1986; Søndergaard *et al.*, 2018; Vucic *et al.*, 2019). Submerged macrophyte densities vary throughout the year with density peaks in summer (Barko, Hardin & Matthews, 1982). The habitat estimation in **Paper IV** was conducted in autumn and might, thus, slightly underestimate the maximum submerged macrophyte density in the investigated gravel pit lakes. However, the rather low densities of submerged macrophytes are in line with the extrapolation of summer macrophyte density in gravel pit lakes from **Paper I** and other relevant literature (Emmrich *et al.*, 2014; Vucic *et al.*, 2019).

Littoral deadwood is a further important habitat structure in lake ecosystems and it is available throughout the whole year (Sass, 2009; Czarnecka, 2016). I detected the abundance of riparian trees in interaction with wind direction and lake age as important drivers of littoral deadwood densities (**Paper III**).

Riparian trees and their branches are the key source for littoral deadwood (Sass, 2009) and, thus, riparian tree abundance has already been identified as a main driver for littoral deadwood densities in natural lakes (Jennings *et al.*, 2003; Marburg *et al.*, 2006). The investigated gravel pit lakes were relatively young with a lake age ranging between seven and 55 years (**Paper III**) and due to the ongoing succession (Müllerová *et al.*, 2022; Nikolaus *et al.*, 2022), riparian tree abundance has not reached its maximum yet. By contrast, natural lakes

originate from the last ice age with an age of more than 10,000 years (Mandrak & Crossman, 1992) and a fully developed riparian vegetation (Sass *et al.*, 2019). Hence, old natural lakes have already reached an equilibrium of deadwood accumulation and decomposition with accumulation rates ranging from 0.5 to 1.9 logs km⁻¹ year⁻¹ (Marburg *et al.*, 2009) and retention times of up to several centuries (Guyette & Cole, 1999). This equilibrium has not been reached in young gravel pit lakes yet, explaining the significantly lower deadwood densities compared to natural lakes (**Paper III**). Furthermore, the increasing deadwood accumulation rates as a result of the ongoing succession and the long retention times of littoral deadwood (Guyette & Cole, 1999; Marburg *et al.*, 2009) explain the positive effect of lake age on deadwood densities in gravel pit lakes.

I further found littoral deadwood density to be significantly affected by fisheries management in interaction with littoral slope. Deadwood densities increased in angler-managed gravel pit lakes with increasing littoral slope, while no effect was detected in unmanaged gravel pit lakes (**Paper III**).

Anthropogenic activities can impact littoral deadwood densities and shoreline development has been found to negatively impact littoral deadwood densities in North American lakes (Christensen *et al.*, 1996; Jennings *et al.*, 2003; Marburg *et al.*, 2006). In Germany, angling clubs buy or lease the gravel pit lakes including fishing rights and regularly meet for shoreline clean-up activities, which might include the removal of woody structures to maintain angling sites. Furthermore, individual anglers might remove easily accessible deadwood structures in shallow areas to prevent entanglement with fishing gear. In line with my findings, Mallory *et al.* (2000) also detected increased deadwood densities in deeper areas and anthropogenic impacts on deadwood density and distribution. Hence, anthropogenic activities such as recreational fishing can negatively impact deadwood densities even in gravel pit lakes with relatively low deadwood densities.

In **Paper IV**, I analysed the effects and importance of littoral habitats on the littoral fish abundance. The species and size-class specific analyses revealed in all cases a lake variable, mostly productivity, as most important variable for littoral fish abundance. However, by adding up the importance of all lake variables and all littoral variables, I found a mostly similar or even slightly higher importance of littoral habitat characteristics compared to lake environmental variables (**Paper IV**).

Lewin et al. (2014) used a similar methodological approach and found lake-level variables to be more important than littoral variables for species-specific abundance in German natural lakes, which is in contrast to my findings. Fish communities in natural lakes are generally driven by the lake variables nutrient level and lake morphology (Persson *et al.*, 1991; Jeppesen *et al.*, 2000; Mehner *et al.*, 2005) with elevated nutrient levels in natural lakes compared to gravel pit lakes (**Paper II**; Emmrich *et al.*, 2014; Søndergaard *et al.*, 2018; Vucic *et al.*, 2019). Furthermore, natural- and gravel pit lakes differ in morphological characteristics with steeper slopes and reduced littoral zones in gravel pit lakes (Gee, 1978; Emmrich *et al.*, 2014), which negatively impacts the distribution of submerged macrophytes and reeds (Duarte & Kalff, 1986). The amount of littoral deadwood structures is also lower in gravel pit lakes compared to natural lakes (**Paper III**). Generally, littoral structures serve as refuge, foraging and spawning habitat for fishes (Pusey & Arthington, 2003; Winfield, 2004) and thereby impact species-specific abundance and community composition (Whitfield, 1986; Sass *et al.*, 2006a; Helmus & Sass, 2008). Limited availability of these crucial nearshore habitats leads to their disproportionately importance (Hampton *et al.*, 2011). Accordingly, the structural deficits of gravel pit lakes with reduced littoral zones and low amounts of littoral structures might explain their increased importance in gravel pit lakes compared to natural lakes studied by Lewin et al. (2014).

I found species and size-class specific effects of littoral structures on fish abundance (**Paper IV and V**), with partly non-linear and threshold effects (**Paper IV**). Submerged macrophytes were the most important habitat structure for small pike with abundance peaking at intermediate coverage (**Paper IV**). Small and large perch also intensively used submerged macrophytes (relative importance: 9.2 % and 14.8 % respectively) and perch abundance increased with macrophyte coverage (**Paper IV**). I further detected submerged macrophytes as most important littoral structure for large tench (relative importance: 24.2 %) and second most important littoral variable for small rudd (relative importance: 12.8 %; **Paper IV**). In both cases fish abundance increased with increasing amounts of submerged macrophytes.

Submerged macrophytes display an important habitat in lentic ecosystems that often inhabit high fish abundance and species richness (Randall *et al.*, 1996; Winfield, 2004; Lewin *et al.*, 2014). Perch is the most abundant fish species in mesotrophic gravel pit lakes (**Paper I and II**; Emmrich *et al.*, 2014) and intensively uses the littoral zone including submerged macrophytes (Rossier, Castella & Lachavanne, 1996; Hargeby *et al.*, 2005; Lewin *et al.*, 2014). Perch are

superior to roach in using littoral structure (Eklöv & Persson, 1995; Persson & Eklöv, 1995), however, too dense structures limit their foraging efficiency (Mattila, 1992; Eklöv, 1997). Similar to perch, phytophilic pike often use submerged macrophytes as forage habitat, but their foraging efficiency is also reduced at high macrophyte coverage (Savino & Stein, 1989; Eklöv, 1997). Accordingly, predatory pike and perch benefit from intermediate macrophyte coverage, while small individuals use densely structured macrophyte patches as shelter habitats to avoid predation (Grimm, 1989; Casselman & Lewis, 1996; Randall *et al.*, 1996). Tench and rudd are further phytophilic fish species of the littoral zone, that prefer eutrophic conditions (Eklöv & Hamrin, 1989; Perrow, Jowitt & Johnson, 1996; Lewin *et al.*, 2014). In line with Lewin *et al.* (2014), I found especially tench to rely on submerged macrophytes, while rudd prefer emerged macrophytes over submerged macrophytes. Overall, the investigated gravel pit lakes were mesotrophic with low amounts of submerged macrophytes, which might have caused the generally low catches of tench. Hence, gravel pit lakes with mesotrophic conditions and low abundance of submerged macrophytes display rather suboptimal habitats for tench.

I found reeds as the most important habitat structure for pike, and medium-sized and large pike reacted positively to reed habitats with strong abundance increases at a threshold of at least 50 % reed habitat (**Paper IV and V**). I further detected reeds as important habitat for small roach (relative importance: 15.7 %), large rudd (relative importance: 27.5 %) and large eel (relative importance: 10.3 %; **Paper IV**). Abundance of large rudd and large eel increased in a linear pattern with increasing shares of reeds on the shoreline, while highest abundance of small roach was detected in transects with at least 90 % reeds (**Paper IV**). Seasonal fishing also revealed a strong preference of pike, eel and rudd for reed habitats with usually highest abundance compared to other littoral habitats throughout all seasons (**Paper V**). The results from fishing at night showed higher abundance of perch in reed habitats compared to daytime fishing, while abundance of rudd and roach decreased in reed habitats at night (**Paper V**).

Similar to submerged macrophytes, reed stands are attractive habitats for the phytophilic species pike, tench and rudd (Eklöv & Hamrin, 1989; Perrow *et al.*, 1996; Lewin *et al.*, 2014). Small pike depend on highly structured habitats such as submerged macrophytes, but with increasing size predation risk decreases and pike prefer less structured habitats such as reed stands (Chapman & Mackay, 1984; Rosell & MacOscar, 2002; Kobler *et al.*, 2008, 2009).

Rudd are typically described as phytophilic fish species (Eklöv & Hamrin, 1989), that select for reed stands as preferred habitat to avoid predation (Bean & Winfield, 1995; Lewin *et al.*, 2014). My findings add further evidence to that as I found higher rudd abundance in reed habitats compared to other habitats (**Paper IV and V**). Apart from rudd, also young roach and perch use reed stands as shelter and feeding habitat during the day (Okun & Mehner, 2002, 2005; Okun *et al.*, 2005). At night small individuals of perch, roach and rudd leave their safe habitats and perform diurnal horizontal migrations to more profitable open habitats for feeding (Bohl, 1980; Lewin *et al.*, 2004; Gliwicz, Slon & Szynekarczyk, 2006). This pattern was also visible in the gravel pit lakes, but effects were not significant (**Paper V**). However, in the case of perch, catches increased in all habitats at night (**Paper V**) rather reflecting increased catchability of perch at night (Alabaster, 1978; Paragamian, 1989).

Large individuals of benthic eel usually select for littoral structures that create appropriate habitats at the bottom of the littoral zone such as riprap or deadwood structures (Glova, Jellyman & Bonnett, 2010; Lewin *et al.*, 2014). However, shoreline structures of gravel pit lakes are often characterized by open littoral and woody structures that reach into the water column, but do not touch the bottom, while riprap and deadwood structures are scarce (**Paper III and IV**). My results revealed that reed stands are highly important habitats for large eel with increasing eel abundance at increasing shares of reeds. Importantly, eel abundance in isolated gravel pit lakes depends completely on stocking, which impacts their overall abundance (Emmrich *et al.*, 2014; Simon & Dörner, 2014). Hence, appropriate environmental conditions including reed stands and deadwood structures are needed in gravel pit lakes to make eel stocking reasonable from a fisheries perspective (Anwand, 1982), while eel stocking in isolated water bodies should generally be abandoned from a conservation perspective (Freyhof & Brooks, 2011; Dekker, 2016).

I found open littoral as an important variable for small perch (relative importance: 19.0 %) and small rudd (relative importance: 24.3 %) as well as small and large eel (relative importance: 13.1 % and 14.4 %, respectively; **Paper IV**). Abundance of small rudd and large eel decreased with increasing shares of open littoral, while abundance of small perch and small eel did not show a clear pattern in relation to the share of open littoral (**Paper IV**). Microhabitat-specific fishing revealed open littoral as suitable habitat for perch in gravel pit lakes and night time fishing revealed highest perch abundance in open habitats at night throughout all seasons (**Paper V**).

In line with Lewin *et al.* (2014), I detected reed stands as important habitats for rudd (**Paper IV and V**), however, open littoral was the most important habitat for small rudd (**Paper IV**). Importantly, the definition of open littoral in my studies defines this variable as the inverse measurement of structured habitats and the abundance of small rudd decreased with increasing amounts of open littoral. This points to a preference of generally structured habitats by small rudd, but not to a specific preference of reed habitats as found for large rudd (**Paper IV**). Studies on eel species in rivers also found an increased importance of littoral cover for individuals larger 300 mm, while smaller eel preferably selected for diverse sediments as shelter habitats (Jellyman *et al.*, 2002; Glova *et al.*, 2010). Hence and in line with literature, my findings indicate a general dependence of small rudd and large eel on structured habitats, but not on a specific habitat type, while small eel also find suitable habitats in open littoral with diverse sediments.

Perch also rely on the littoral zone during their ontogeny (Amundsen *et al.*, 2003) and intensively use the littoral zone from spring to autumn with a preference for structured habitats in winter (Fischer & Eckmann, 1997; Lewin *et al.*, 2004, 2014). However, high macrophyte coverage increases the reliance on benthic food sources and reduces perch growth (Persson & Eklöv, 1995; Trudeau, 2018), while the availability of various littoral habitats generally benefits perch growth in gravel pit lakes (Höhne *et al.*, 2020). The increased perch catches at night reflect the increased efficiency towards resting individuals at night, especially in unstructured habitats as previously reported (Alabaster, 1978; Pierce *et al.*, 2001; Ross *et al.*, 2016). However, this finding was not observed across all species and especially large perch are known to migrate to the littoral zone after dawn (Jacobsen *et al.*, 2015; Nakayama *et al.*, 2018) and thereby also explaining the high catches of perch at night.

Deadwood structures were an important habitat for medium and large pike (relative importance: 12.0 % and 8.0 %, respectively) as well as large perch (relative importance: 14.9 %; **Paper IV**). In all cases highest abundance was detected at a threshold of 40 % deadwood within a transect (**Paper IV**). The abundant wood structures (e.g. overhanging trees) were important for small and large roach (relative importance: 17.6 % and 7.6 %, respectively) and roach abundance increased with increasing shares of wood (**Paper IV**). The implemented deadwood bundles offered a suitable habitat for all investigated fish species (eel, perch, pike, roach, rudd and tench) with generally higher abundance than in open littoral and larger sizes of eel, perch and pike compared to unstructured habitats (**Paper V**). For tench highest

abundance was detected in implemented deadwood bundles in autumn, while pike and perch abundance in littoral deadwood peaked in winter (**Paper V**).

Deadwood structures have repeatedly been found as important fish habitat in lentic waters (Newbrey *et al.*, 2005; Sass, 2009; Czarnecka, 2016). With increasing size pike are less reliant on dense vegetation cover (Chapman & Mackay, 1984; Kobler *et al.*, 2008, 2009) and prefer less densely structured habitats such as reeds and deadwood habitats (Casselman & Lewis, 1996; Eklöv, 1997). Littoral deadwood has also repeatedly been found as suitable habitat for perch (Lewin *et al.*, 2004, 2014). Especially in winter when macrophyte densities are strongly reduced, structure-oriented species constantly use the suitable cover conditions and prey availability in habitats dominated by deadwood structures (Skov & Berg, 1999) explaining the increased usage of deadwood structures by pike and perch in winter, while predation risk for prey fish species increases (Diana & Mackay, 1979; Lemmens, De Meester & Declerck, 2016). Roach use littoral structures as shelter as well as shoaling behaviour to avoid predation (Christensen & Persson, 1993; Eklöv & Persson, 1996). In complex habitats, however, roach are inferior to other fish species (e.g. perch) in competing for prey (Eklöv & Persson, 1995; Persson & Eklöv, 1995) and, therefore, prefer open water habitats with higher prey abundance (Jacobsen & Berg, 1998). My findings show, that large roach selected for woody habitats which were often characterized by overhanging trees that ranged into the water column, but did not cover the complete water column (**Paper IV**). By selecting for these habitats roach might use the advantages of both habitats, shelter from the overhanging trees and high plankton abundances as food source from open water habitats (Lewin *et al.*, 2004).

The presence of deadwood in aquatic systems increases the complexity of the littoral zone and creates important habitats for various fish species (e.g. Newbrey *et al.*, 2005; Smokorowski & Pratt, 2007), thereby positively affecting their abundance (**Paper IV and V**; Lewin *et al.*, 2004, 2014). The anthropogenic removal of these important deadwood structures has been found to lead to reduced abundance and growth rates of typical lake fish species (Sass *et al.*, 2006b; Helmus & Sass, 2008). Furthermore, climate change leads to stronger water level alteration (Woolway, Sharma & John, 2022), which then reduces the amount of available deadwood habitats in the littoral zone (Gaeta, Sass & Carpenter, 2014). As a result from a drought-driven lake level decline, Gaeta *et al.* (2014) also detected reduced abundance and growth rate of typical lake fish species. By contrast, Smokorowski *et al.* (2020) could not detect a significant reduction in abundance or biomass of typical lake fish species by reducing the

deadwood density by 50 % in natural lakes using a robust before-after-control-impact design. Importantly, Smokorowski *et al.* (2020) mentioned that the treatment lakes were still characterized by high deadwood densities after deadwood removal as well as high availability of alternative habitat structures such as macrophytes and rocks.

The anthropogenic increase in littoral deadwood densities to support fish populations and fisheries is becoming more and more popular (Sass *et al.*, 2017, 2019, 2022). My results show, that supplemented deadwood structures are a suitable habitat for several lake fish species and especially the popular game fish species pike and perch use the new structures intensively in winter, when availability of alternative habitats (e.g. submerged macrophytes) is lowest (**Paper V**). Smith *et al.* (2021) further detected, that added trees in the littoral zone positively impacted home range of predatory sport fish species in North American lakes. However, a first whole lake experiment in a BACI design did not detect an increase in overall fish abundance as a result of deadwood supplementation (Sass *et al.*, 2012). Importantly, the effect of (positive and negative) changes in deadwood density on fish abundance and biomass is impacted by various factors, such as lake morphology, nutrient level and the availability of alternative habitat structures (Smokorowski *et al.*, 2020; Sass *et al.*, 2022).

5. Synthesis: Driving factors of fish communities in gravel pit lakes and typical fish species composition

The fish species pool in small and isolated lakes is impacted through natural and anthropogenic colonisation pathways (**Paper I and II**; Figure 1). I demonstrated that the chances of natural colonisation events depend on lake genesis, which functions as proxy for lake age (**Paper II**). I used unmanaged and old natural lakes as reference lakes and their fish communities were composed of typical lake fish species such as roach, rudd, tench and pike (**Paper II**). By contrast, fish communities in unmanaged and newly created gravel pit lakes were highly variable with no fish species occurring in 50 % of the lakes (**Paper I and II**).

I further demonstrated that fisheries management enhances fish species richness and the number of predatory species in gravel pit lakes and natural lakes via fish stocking, while the spread of non-native species was not promoted by fisheries-management measures (**Paper I and II**). Importantly, even unmanaged gravel pit lakes received anthropogenic fish colonization through private and illegal fish releases (**Paper I**). The resulting fish community composition in gravel pit- and natural lakes managed for fisheries did not differ compared to unmanaged natural lakes (reference lakes), while fish communities in unmanaged gravel pit lakes were characterized by a high β -diversity (**Paper I and II**). Hence, without initial fish stocking, the fish communities of newly created gravel pit lakes are shaped by natural and illegal human-mediated colonization events. Both processes, are rather slow and highly stochastic and lead to fish communities that strongly differ from those in unmanaged natural lakes, without hosting fewer fish biomass (**Paper I and II** and Figure 6).

After introduction into a new water body, independent of colonization mechanism, fishes that find suitable conditions can survive and establish new populations. I demonstrated species-specific abundance and fish community composition of gravel pit lakes to be mainly determined by lake productivity and the availability of littoral habitat structures (**Paper II and IV**), while biotic interactions are less important (see discussion above). Lake productivity (mostly total phosphorus concentration) was the most important abiotic factor governing fish abundance and community composition in the investigated gravel pit lakes (**Paper II and IV**), but all littoral habitat characteristics combined partially even better explained species- and size-class-specific fish abundance in the littoral zone of gravel pit lakes (**Paper IV**).

Generally, the littoral zones of gravel pit lakes were characterized by high shares of unstructured open littoral and reed habitats, while the amounts of deadwood were low (**Paper IV**), especially in comparison to natural lakes (**Paper III**). I demonstrated that littoral deadwood densities increase with lake age and with increased riparian tree abundance especially on the shore with wind from land. Furthermore, I showed littoral deadwood densities to decrease in shallow waters of angler-managed gravel pit lakes (**Paper III**).

The impact of quality and quantity of littoral habitats on fish abundance in gravel pit lakes was species- and size-class-specific (**Paper IV**). Reeds displayed an important habitat in the littoral zone of gravel pit lakes, especially for rudd, roach, pike and eel (**Paper IV and V**). Generally, fish abundance increased with productivity and increasing amounts of littoral structures often following non-linear patterns. Abundance of perch and pike peaked at intermediate submerged macrophyte densities of approximately 70 %, while highest abundance in deadwood habitats was reached at approximately 40 % deadwood habitats (**Paper IV**). Furthermore, implemented deadwood bundles provided a suitable habitat for typical lake fish species, which were intensively used in winter (**Paper V**).

Consequently, fish diversity and community composition in gravel pit lakes are shaped by two major forces. First, fish colonization processes determine the local fish species pool present in gravel pit lakes. Second, abiotic and biotic factors affect survival, growth and reproduction of the species from the local fish species pool with lake productivity and habitat quality and quantity being most important and thereby shaping species-specific establishment and abundance and finally fish community composition.

6. Management implications

All lakes in my studies were colonized by fishes either through natural or anthropogenic pathways, but fish community composition was significantly different in unmanaged gravel pit lakes. My results suggest that fisheries- and aquatic ecosystem managers should use fish communities in ecologically similar natural lakes as benchmark for planning initial stocking practices in newly created gravel pit lakes. This practice leads to an establishment of a species-rich and naturally composed fish community. Typical lake fish species may be regionally listed as (critically) endangered (e.g. crucian carp in Lower Saxony; LAVES, 2011) and initial stocking of such species in gravel pit lakes with suitable environmental characteristics can be a valuable contribution to species conservation (Lyach, 2022). I only detected single individuals of non-native fish species over all lakes, but incautious fish stocking of poorly sorted fish can contribute the spread of invasive species (Kinzelbach, 1995; Waterstraat, 2002; Gozlan *et al.*, 2010). and even the translocation of native species over large distances can lead to faunal homogenisation (Sommerwerk *et al.*, 2017). Accordingly, fish stocking should always be conducted carefully by stocking healthy individuals from regional populations of native species (Lewin, Arlinghaus & Mehner, 2006; Baer *et al.*, 2007).

In addition to that, my results add further empirical evidence for the importance of diversely structured littoral zones with size-class and species-specific effects of the different littoral structures. I, thus, recommend fisheries managers to consider habitat enhancement as management tool in structure-poor gravel pit lakes. Widening the bottleneck of habitat limitation by creating suitable habitats for typical lake fish species represents a promising approach to promote fish abundance in gravel pit lakes.

7. Further research needs

My thesis revealed some knowledge gaps that should be addressed to gain a further understanding about lake fish communities, specifically the quantification of the odds of natural fish colonization pathways and the effect of littoral habitat enhancement on lake fish abundance.

The colonization mechanisms of fish into isolated water bodies have not been fully investigated yet, especially the dispersal of fish eggs by waterfowls as natural colonization pathways has long been speculated, but with very little evidence (Riehl, 1991; Hirsch *et al.*, 2018). In recent years two publications demonstrated the survival of fish eggs via the gut passage of birds (Silva *et al.*, 2019; Lovas-Kiss *et al.*, 2020). Flying insects can act as a further distributor of fish eggs (Suetsugu & Togashi, 2020). The chances of these colonization events are considered as rather low, but have never been quantified. Furthermore, fish egg dispersal by birds might be species-specific for birds and fish, with factors such as spawning depth of the fishes and stickiness of the eggs impacting fish species-specific suitability for dispersal, while species-specific feeding habits of waterfowl might also be important. In addition to that, birds might not only feed on fish eggs with a few fish eggs surviving the passage through the digestive tract, but birds might also disperse fish eggs within their feathers. Further research is needed to completely uncover the bird mediated colonization of fish eggs and quantify the chances of these events.

Maximum lake fish abundance (carrying capacity) is mainly driven by nutrient level and lake morphology (Hanson & Leggett, 1982; Downing *et al.*, 1990; Mehner & Brucet, 2022). In my thesis, I demonstrated that littoral habitats in structure-poor gravel pit lakes are mostly of similar or even higher importance for littoral fish abundance than lake productivity (**Paper IV**). Furthermore, fish abundance in newly created deadwood habitats was higher than in unstructured open littoral (**Paper V**). Based on these results, habitat enhancement through deadwood supplementation, might increase the carrying capacity of degraded lakes. The removal of littoral deadwood has already been found to lead to decreases in abundance of typical lake fish species (Sass *et al.*, 2006b; Helmus & Sass, 2008), while overall fish abundance not necessarily declines (Smokorowski *et al.*, 2020). By contrast, deadwood additions in lentic water bodies are rare (Sass *et al.*, 2019), with first studies showing no increase in fish abundance in previously well-structured natural lakes (Sass *et al.*, 2012). Gravel pit lakes are

characterized by large shares of unstructured open littoral and low amounts of littoral deadwood (**Paper III and IV**) and thus deadwood additions might be promising approach to increase fish abundance (Smokorowski *et al.*, 2020; Sass *et al.*, 2022).

Limited littoral zones with steep slopes display a further feature of gravel pit lakes (Gee, 1978; Emmrich *et al.*, 2014), which leads to a low abundance of submerged macrophytes (**Paper I and IV**, Emmrich *et al.*, 2014; Vucic *et al.*, 2019). Shallow and vegetated littoral zones are crucial young fish habitats (Winfield, 2004) and the creation of additional shallow water zones in gravel pit lakes might also increase the carrying capacity of fish and further serve as important habitat for other biological taxa such as submerged macrophytes. Accordingly, future whole-ecosystem manipulations are needed to shed further light on the question, whether habitat enhancement via deadwood supplementation and/or the creation of shallow water zones in structure-poor gravel pit lakes can increase overall lake carrying capacity (Carpenter, 1998; Sass *et al.*, 2022).

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Declaration of authorship

I hereby declare that this PhD thesis has been written only by the undersigned and that no sources other than those indicated have been used. This thesis has not been submitted for a doctor's degree at any other institution. I am aware of the underlying doctorate regulations of the faculty this thesis is submitted to, i.e., Faculty of Life Sciences of the Humboldt-University at Berlin.

Hiermit erkläre ich, die Dissertation selbständig und ohne unerlaubte Hilfe angefertigt zu haben. Ich habe die Arbeit an keiner anderen Institution zur Erlangung des Doktorgrades eingereicht. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin.

Berlin, den 18.10.2022

Sven Matern

Appendices



Paper I

Matern S., Emmrich E., Klefoth T., Wolter C., Nikolaus R., Wegener N., Arlinghaus R. (2019)

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

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Effect 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 electro-fishing 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 α -diversity and lower β -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.

KEYWORDS

community composition, conservation, non-native species, novel ecosystems, recreational fishing, stocking

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 categorised as threatened (Freyhof & Brooks, 2011). Habitat loss has been identified as the key stressor that affects 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 (Biggs *et al.*, 2017; De Meester *et al.*, 2005; Dodson *et al.*, 2000; Emmrich *et al.*, 2014; Lemmens *et al.*, 2013; Santoul *et al.*, 2009; Zhao *et al.*, 2016). Gravel pits are usually groundwater-fed and not necessarily connected to surrounding river systems (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard *et al.*, 2018); thus, they 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 become common landscape elements in industrialised countries (Blanchette & Lund, 2016; Mollema & Antonellini, 2016; Søndergaard *et al.*, 2018). For example, in our study area of Lower Saxony, Germany, there are > 3500 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.*, 2018, unpublished data). Thus, gravel pits are the dominant lentic habitat in north-west 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, owing to their young age, may even lack fish populations (Scheffer *et al.*, 2006; Schurig, 1972; Søndergaard *et al.*, 2018; Werneke *et al.*, 2018). There are natural pathways for the colonisation 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 (Borcherding *et al.*, 2002; Molls & Neumann, 1994; Staas & Neumann, 1994). However, the chances of fish to colonise isolated, recently formed water bodies is rather low (Scheffer *et al.*, 2006; Strona *et al.*, 2012). Natural colonisation is then confined to rare events such as massive floods (Olden *et al.*, 2010; Pont *et al.*, 1991) 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 colonisation of isolated gravel pit lakes is most probably a slow process resulting in species-poor local fish communities (*i.e.*, low α -diversity) and high between lake variation in

the species pool (*i.e.*, high β -diversity) within a region (Baselga, 2010; Whittaker, 1972).

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

In central Europe, the majority of gravel pit lakes are managed by recreational anglers organised 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; Søndergaard *et al.*, 2018; Zhao *et al.*, 2016). 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 individuals, enterprises or nature conservation organisations. These lakes may even be closed to recreational fisheries and be maintained for private use 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 colonisation pathways compared with managed lakes (Supporting Information Table S1).

Regular fish stocking in managed gravel pit lakes may increase α -diversity (*i.e.*, local species richness) but reduce β -diversity through the process of biotic homogenisation (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). In a study of French gravel pit lakes Zhao *et al.* (2016) found 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. 1758 compared with unmanaged gravel pit lakes. The objective of the present study was to compare the fish communities between managed and unmanaged gravel pit lakes in north-western Germany. We hypothesised that relative to unmanaged lakes recreational-fisheries management would lead to: (1) an increase in local species richness, *i.e.*, α -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 inadvertently through poorly sorted stocking material from pond

aquaculture. Furthermore, we hypothesised that the lakes managed by anglers would host more similar fish communities compared with the unmanaged lakes and therefore that recreational-fisheries management would lead to: (4) a decrease in β -diversity through biotic homogenisation.

2 | MATERIALS AND METHODS

Our fish sampling complied with fisheries law in Lower Saxony and included permission for electrofishing (# 34.4-65434-IV).

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 (Figure 1). A description of the basic differentiation of managed and unmanaged lake types can be found in Supporting Information Table S1.

For each lake, two ages were determined; the onset and the end of gravel excavation, as gravel pits started filling up with water and potentially became colonised by fish already before the end of excavation. The depth was measured hydro-acoustically using a Simrad NSS evo2

with a Lowrance TotalScan transducer (www.simrad.com) in parallel transects spaced c. 30 m apart. These data were used to prepare depth contour maps using ordinary kriging in R (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, following methods of the European Committee of Standardization (CEN, 2015) for the sampling of lake fish communities with multimesh gillnets (0–2.9, 3–5.9, 6–11.9, 12–19.9 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 transects varied between 4 and 20 depending on the lake size. In each transect, the macrophyte coverage of each macrophyte depth stratum (0–1, 1–2, 2–4 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.

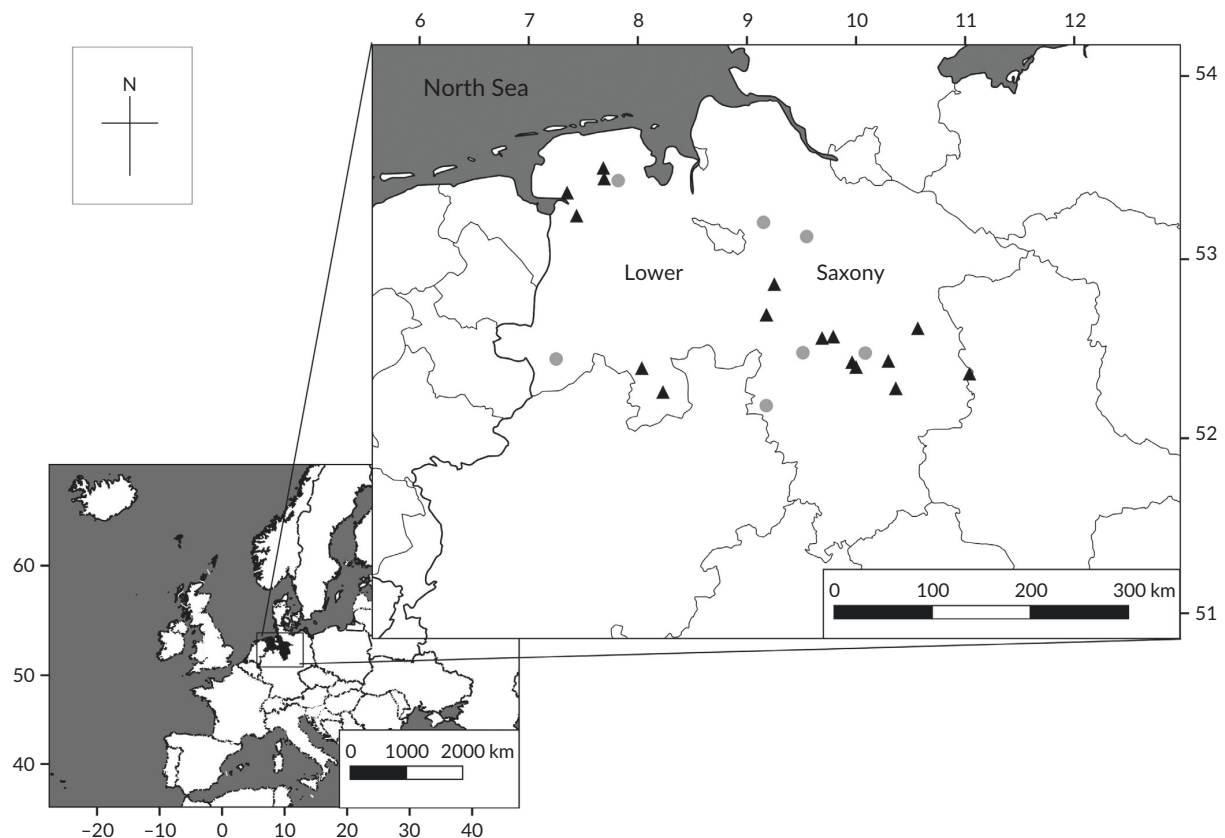


FIGURE 1 Location of the managed (▲) and unmanaged (●) gravel pit lakes in Lower Saxony, north-western Germany, sampled for the analysis of fish communities

The fish communities were sampled using day-time electrofishing in the littoral and multimesh gillnets in the benthic and profundal zones at night in autumn 2016 and 2017. During each fish sampling campaign, the lake's Secchi depth, conductivity and pH value were measured (Supporting Information Table S2) with a WTW Multi 350i sensor (www.wtw.com). 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 taken 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; Murphy & Riley, *et al.*, 1962) 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 an FEG 8000 electrofishing device (8 kW; 150 - 300V / 300 - 600V; EFKO Fischfängergeräte GmbH; www.efko-gmbh.de) 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 40 and 120 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 (c. 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 seven unmanaged lakes) were sampled by littoral electrofishing of the whole shoreline and multimesh gillnets following the same procedure as in 2016. Electrofishing data were standardised 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 in an 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, 19.5 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 otherwise captured (CEN, 2015). One pelagic multimesh gillnet was set in each of the following vertical depth strata: 0–1.5, 3–4.5, 6–7.5, 9–10.5 and 12–13.5 m, but only if the depth strata contained > 1 mg O₂ l⁻¹. We set benthic gillnets in anoxic conditions to confirm zero catches at oxygen levels below 1 mg O₂ 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 (L_T) of all fish captured was measured to the nearest mm and weighed (M_T) to the nearest g. In case of large fish catches, at least 10 fish per species and 2 cm length class were measured and weighed. Afterwards, fish were only measured for length and the mass was calculated with lake-specific $L_T - M_T$ 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 weighed, 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 (Emmrich *et al.*, 2014), number of threatened species [Red List of Lower Saxony, (LAVES, 2011), Red List of Germany (Freyhof, 2009) and European Red List (Freyhof & Brooks, 2011)] and number of non-native species in Germany (Wiesner *et al.*, 2010; 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. 1758) > 150 mm L_T and eel *Anguilla anguilla* (L. 1758) > 500 mm L_T were assigned to the piscivorous fish guild,

TABLE 1 Common and scientific names, frequency of occurrence (%) and relative frequency (%) of 23 fish species and one hybrid caught in 16 managed and 7 unmanaged gravel pit lakes. Fish were sampled using electrofishing in the littoral zone, and using benthic and pelagic gillnetting in the open water

Common name	Scientific name	Frequency of occurrence in managed lakes (%)	Frequency of occurrence in unmanaged lakes (%)	Relative littoral frequency in managed lakes (%)	Relative littoral frequency in unmanaged lakes (%)	Relative open water frequency in managed lakes (%)	Relative open water frequency in unmanaged lakes (%)
Perch [†]	<i>Perca fluviatilis</i> L., 1758	100.0	28.6	42.5	20.0	62.3	28.0
Roach	<i>Rutilus rutilus</i> (L., 1758)	100.0	14.3	7.1	1.2	24.3	14.1
Tench	<i>Tinca tinca</i> (L., 1758)	93.8	28.6	3.5	3.4	0.6	0.7
Eel ^{†§}	<i>Anguilla anguilla</i> (L., 1758)	93.8	0.0	13.2	0.0	0.0	0.0
Pike ^{†§}	<i>Esox lucius</i> L., 1758	87.5	14.3	3.9	5.4	0.3	0.0
Rudd	<i>Scardinius erythrophthalmus</i> (L., 1758)	68.8	42.9	14.5	16.8	1.7	17.0
Bream	<i>Abramis brama</i> (L., 1758)	68.8	14.3	6.8	0.0	5.2	0.2
Carp	<i>Cyprinus carpio</i> L., 1758	56.3	42.9	0.4	0.1	0.2	1.2
Ruffe [‡]	<i>Gymnocephalus cernua</i> (L., 1758)	56.3	0.0	0.3	0.0	2.7	0.0
Pikeperch [†]	<i>Sander lucioperca</i> (L., 1758)	50.0	0.0	0.01	0.0	0.7	0.0
White bream	<i>Blicca bjoerkna</i> (L., 1758)	43.8	0.0	1.9	0.0	1.7	0.0
Prussian carp	<i>Carassius gibelio</i> (Bloch, 1782)	12.5	28.6	2.7	2.8	0.2	9.1
European catfish ^{†§}	<i>Silurus glanis</i> L., 1758	12.5	14.3	0.06	0.0	0.02	0.0
Cyprinid hybrid	<i>Rutilus x Abramis</i>	12.5	0.0	0.0	0.0	0.0	0.0
Topmouth gudgeon ^{‡¶}	<i>Pseudorasbora parva</i> (Temminck & Schlegel, 1846)	6.3	14.3	0.01	0.01	0.0	0.0
Bitterling ^{‡§}	<i>Rhodeus amarus</i> (Bloch, 1782)	6.3	0.0	0.02	0.0	0.0	0.0
European whitefish	<i>Coregonus lavaretus</i> (L., 1758)	6.3	0.0	0.0	0.0	0.0	0.0
Spined loach ^{‡§}	<i>Cobitis taenia</i> L., 1758	6.3	0.0	0.4	0.0	0.0	0.0
Bleak [‡]	<i>Alburnus alburnus</i> (L., 1758)	6.3	0.0	2.8	0.0	0.0	0.0
Sunbleak [‡]	<i>Leucaspis delineatus</i> (Heckel, 1843)	0.0	42.9	0.0	27.5	0.0	15.2
Nine-spined stickleback [‡]	<i>Pungitius pungitius</i> (L., 1758)	0.0	42.9	0.0	21.8	0.0	6.0
Gudgeon [‡]	<i>Gobio gobio</i> (L., 1758)	0.0	28.6	0.0	0.7	0.0	4.7
Stone loach [‡]	<i>Barbatula barbatula</i> (L., 1758)	0.0	14.3	0.0	0.1	0.0	3.8
Brown bullhead ^{†¶}	<i>Ameiurus nebulosus</i> (Lesueur, 1819)	0.0	14.3	0.0	0.05	0.0	0.0

[†]Piscivorous species (perch > 15 cm total length (TL) and eel > 50 cm TL were classified piscivorous)

[‡]Small-bodied non-game fish

[§]Threatened species in Lower Saxony

[¶]Non-native species

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 α -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 coloniser of lakes; *e.g.*, sunbleak *Leucaspis delineatus* (Heckel 1843) (Kottelat & Freyhof, 2007). The number of threatened species was contrasted between the two management types to assess the potential effect 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 (Søndergaard *et al.*, 2018; Zhao *et al.*, 2016).

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 ($n\ 50\ m^{-1}$) or gillnet area ($n\ 100\ m^{-2}$) and as biomass per unit effort (BPUE) with biomass per shoreline length ($g\ 50\ m^{-1}$) or gillnet area ($g\ 100\ m^{-2}$). 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 also calculated the Shannon diversity index combining presence-absence and species-specific abundance (Shannon, 1948) and compared the indices between the two management types.

2.3 | Statistical analysis

A principle component analysis (PCA) was conducted to visualise 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), β -diversity of the fish communities in managed and unmanaged gravel pit lakes was visualised 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 (γ -diversity) and to further visualise average local diversity (α -diversity) and between management type variation in diversity (β -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 3.2.2 (www.r-project.org) 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 (Figure 2). The PCA (Figure 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; Figure 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 9066 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. 1758) 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. 1758, *A. anguilla* and pikeperch *Sander lucioperca* (L. 1758) were also regularly found in managed, but only occasionally or not at all in unmanaged gravel pit lakes (Table 1). Littoral species, such as *E. lucius*, *A. anguilla* and tench *Tinca tinca* (L. 1758), were mainly or even exclusively caught by electrofishing, while large individuals of less littoral-bound species such as *P. fluviatilis* and *R. rutilus* as well as *S. lucioperca* were better detected by gillnetting.

Of the species pool of 23 species, *A. anguilla*, *S. lucioperca*, ruffe *Gymnocephalus cernua* (L. 1758), white bream *Blicca bjoerkna* (L. 1758), bitterling *Rhodeus amarus* (Bloch 1782), European whitefish *Coregonus lavaretus* (L. 1758), spined loach *Cobitis taenia* L. 1758 and bleak *Alburnus*

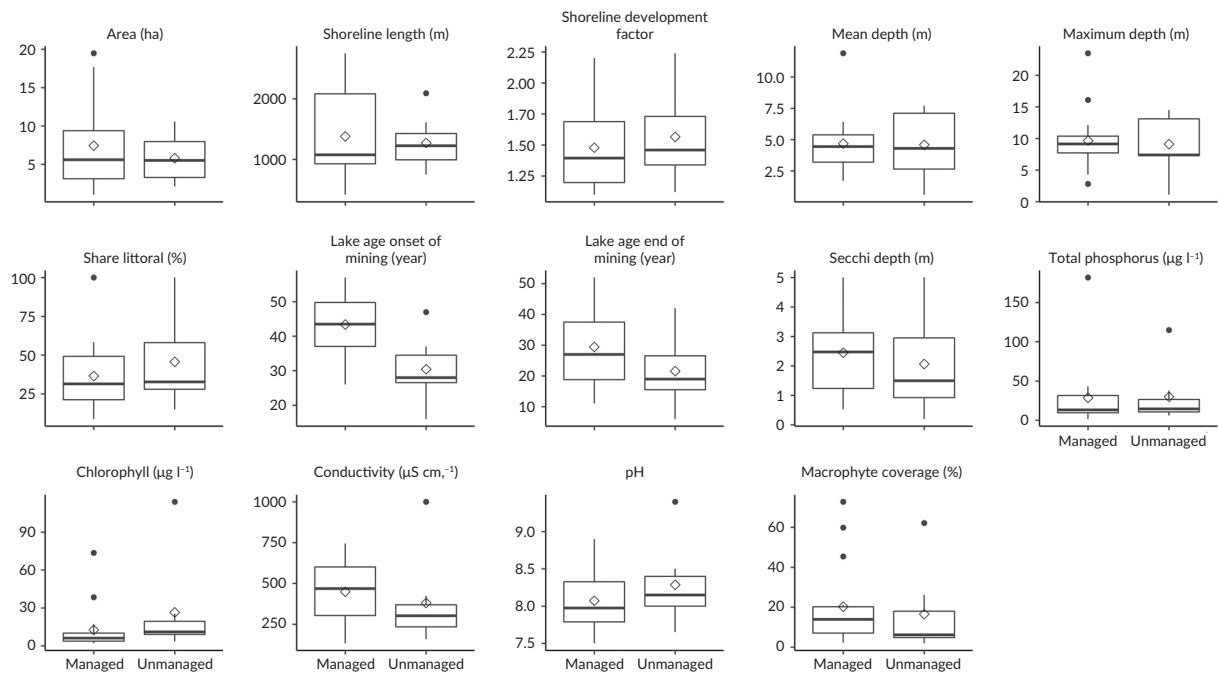


FIGURE 2 Univariate illustration of the environmental characteristics between managed ($n = 16$) and unmanaged ($n = 7$) gravel pit lakes to show the dimensions of each variable. \diamond , Mean; —, median; \square , the 25th to the 75th percentile; |, the extent of $1.5 \times$ inter-quartile range; \bullet , outliers

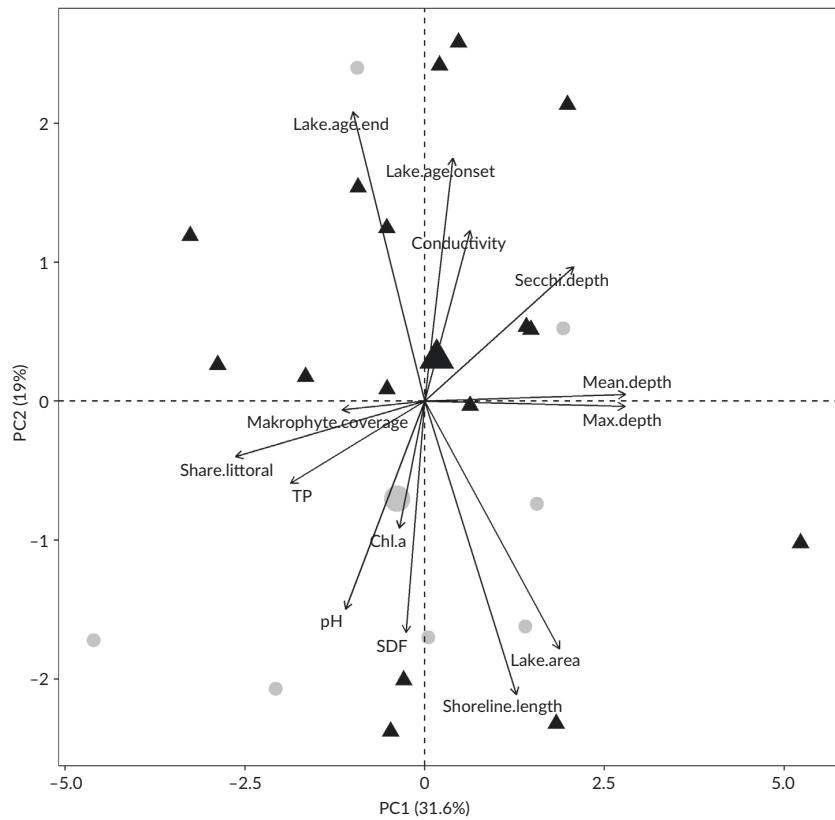


FIGURE 3 Principle component analysis (PCA) of the environmental variables in managed (\blacktriangle ; centroid enlarged) and unmanaged gravel pit lakes (\bullet ; centroid enlarged). \longrightarrow ; the vectors of the environmental variables

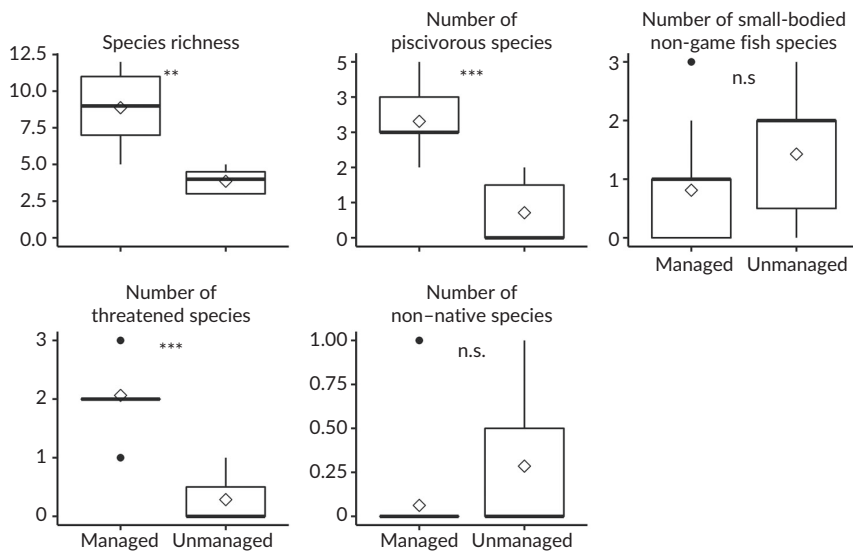


FIGURE 4 Descriptors of the fish community derived from electrofishing and multimesh gillnetting in managed ($n = 16$) and unmanaged ($n = 7$) gravel pit lakes. \diamond , Mean; —, median; \square , the 25th to the 75th percentile; \mid , the extent of $1.5 \times$ inter-quartile range; \bullet , outliers. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ and n.s., $P > 0.05$

alburnus (L. 1758) were only caught in managed gravel pits, while sunbleak *Leucaspius delineatus* (Heckel 1843), nine-spined stickleback *Pungitius pungitius* (L. 1758), gudgeon *Gobio gobio* (L. 1758), stone loach *Barbatula barbatula* (L. 1758) and brown bullhead *Ameiurus nebulosus* (Lesueur 1819) only occurred in unmanaged gravel pits (Table 1). Note that 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 with unmanaged lakes (Figure 4 and Supporting Information Table S3). No significant differences between the two management types were found in the numbers of small-bodied non-game fish species (Wilcoxon rank-sum test, $W = 37$, $P > 0.05$) and the number of non-native species (Wilcoxon rank-sum test, $W = 43.5$, $P > 0.05$). The Shannon index revealed an overall greater diversity of littoral fishes in terms of abundance (NPUE; $P < 0.05$) in managed gravel pit lakes compared with those that were unmanaged (Table 2).

To investigate differences of the fish communities regarding β -diversity, nMDS biplots were constructed using presence-absence data (Figure 5) and using abundance and biomass data (NPUE and BPUE) of each fishing gear separately (Figure 6). Strong variation in the fish diversity and the fish community composition was visually striking between the unmanaged lakes (Figures 5,6). By contrast, the managed gravel pit lakes 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 β -diversity for

unmanaged gravel pit lakes compared with managed lakes using presence-absence data ($F = 88.401$, $P < 0.001$; Figure 5), littoral species-specific fish abundance and biomass (NPUE: $F = 6.871$, $P < 0.05$; BPUE: $F = 12.856$, $P < 0.01$) and benthic species-specific fish abundance and biomass (NPUE: $F = 13.595$, $P < 0.001$; BPUE: $F = 10.106$, $P < 0.01$; Figure 6).

The same pattern of larger β -diversity in unmanaged lakes was visually recovered by the steeper slope of the species accumulation curve in the unmanaged lakes compared with the managed lakes (Figure 7), yet, as before, average local species richness was found to be greater in the managed compared with the unmanaged lakes (indicated by the greater intercept for managed lakes compared with unmanaged lakes in Figure 7). Importantly, γ -diversity was significantly larger when combining the species pools present in the managed and the unmanaged lakes (comparing the combined species accumulation curve relative with each management type separately, managed lakes $n = 16$; $V = 130$, $P < 0.001$, unmanaged lakes $n = 7$; $V = 28$, $P < 0.05$, Figure 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 with unmanaged lakes; however, after conservative Bonferroni correction differences were no longer significant (Table 2). 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 ($P < 0.01$) and biomasses ($P < 0.05$) were detected in managed lakes compared to unmanaged lakes.

TABLE 2 Comparison between the two management types for numbers per unit effort (NPUE) and biomass per unit effort (BPUE) of electrofishing and multimesh gillnet data on the total abundance and biomass as well as the abundance and biomass of selected fish community descriptors in gravel pit lakes in Germany

		Median (Range)			P-value ^a
		Managed lakes (n = 16)	Unmanaged lakes (n = 7)		
Littoral NPUE (electrofishing; n 50 m ⁻¹)	Total abundance	21.8 (6.3–97)	32.6 (3.5–3292)	W = 41	1.000
	Piscivorous fishes	1.4 (0.2–3.5)	0.0 (0.0–1.5)	W = 96	0.089
	Small-bodied non-game fishes	0.01 (0.0–6.3)	10.1 (0.0–3291)	W = 25	0.368
	Threatened species	3.0 (0.4–5.8)	0.0 (0.0–1.3)	W = 107	0.007
	Non-native species	0.0 (0.0–0.06)	0.0 (0.0–0.05)	W = 44.5	1.000
	Shannon index	1.1 (0.6–1.6)	0.6 (0.04–0.9)	t = 3.88 df = 13.32	0.022
Littoral BPUE (electrofishing; g 50 m ⁻¹)	Total biomass	682 (53.6–1731)	440 (20.7–1911)	W = 58	1.000
	Piscivorous fishes	283 (20.6–1294)	0.0 (0.0–339)	W = 94	0.131
	Small-bodied non-game fishes	0.04 (0.0–7.3)	11.5 (0.0–1318)	W = 24	0.308
	Threatened species	414 (24.9–1554)	0.0 (0.0–339)	W = 104	0.015
	Non-native species	0.0 (0.0–0.1)	0.0 (0.0–149)	W = 43.5	1.000
	Shannon index	1.1 (0.4–1.6)	0.7 (0.2–1.0)	t = 2.92 df = 12.63	0.147
Benthic NPUE (multimesh gillnet; n 100 m ⁻²)	Total abundance	91.8 (23.7–236)	77.1 (40.6–112)	W = 64	1.000
	Piscivorous fishes	6.0 (0.3–19.3)	0.0 (0.0–8.2)	W = 95	0.106
	Small-bodied non-game fishes	0.2 (0.0–6.6)	0.0 (0.0–33.5)	W = 48	1.000
	Threatened species	0.0 (0.0–1.2)	0.0 (0.0–0.0)	W = 73.5	1.000
	Non-native species	0.0 (0.0–0.0)	0.0 (0.0–0.0)		NA
	Shannon index	0.9 (0.04–1.4)	0.6 (0.07–1.0)	t = 1.86 df = 10.29	1.000
Benthic BPUE (multimesh gillnet; g 100 m ⁻²)	Total biomass	2919 (496–7,000)	3708 (98.3–4,682)	W = 62	1.000
	Piscivorous fishes	701 (12.1–2,602)	0.0 (0.0–1,858)	W = 95	0.106
	Small-bodied non-game fishes	1.6 (0.0–76.8)	0.0 (0.0–89.8)	W = 52	1.000
	Threatened species	142.0 (0.0–518)	0.0 (0.0–0.0)	W = 73.5	1.000
	Non-native species	0.0 (0.0–0.0)	0.0 (0.0–0.0)		NA
	Shannon index	1.2 (0.6–1.7)	0.7 (0.02–1.1)	t = 2.84 df = 9.29	0.226

^aBonferroni corrected P-value are from t-test and Wilcoxon rank-sum tests.

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

The SIMPER analysis revealed *L. delineatus*, *P. fluviatilis*, rudd *Scardinius erythrophthalmus* (L. 1758) and *P. 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, *L. delineatus* and *P. pungitius* were not detected in managed gravel pit lakes and they contributed

significantly to the differences in the littoral fish community among management types (*L. delineatus*: $P < 0.05$, *P. pungitius*: $P < 0.01$; Table 3). In terms of littoral fish biomass (BPUE), *A. anguilla*, Prussian carp *Carassius gibelio* (Bloch 1782) and *E. 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 *P. fluviatilis* biomass significantly differentiated among managed and unmanaged gravel pit lakes ($P < 0.05$), revealing significantly greater biomasses in managed lakes (Table 3).

When taking the multimesh gillnet data (NPUE and BPUE) as a metric of the benthic fish community, *P. fluviatilis* and *R.utilus* revealed the highest contribution to the difference in the fish community between

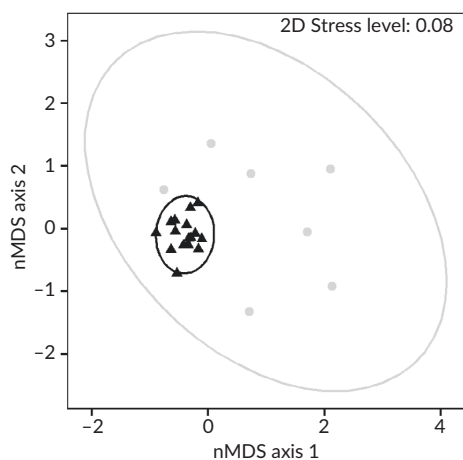


FIGURE 5 Non-metric multidimensional scaling (nMDS) plot of the fish community structures in managed (\blacktriangle ; $n = 16$) and unmanaged (\bullet ; $n = 7$) gravel pit lakes, shown for presence-absence data sampled through electrofishing in the littoral zone and gillnetting in the benthic zone. The ellipses show the 95% CI for managed lakes (—) and unmanaged lakes (—)

the two management types, with significantly higher biomasses of *P. fluviatilis* in managed gravel pit lakes ($P < 0.05$; Table 3). Furthermore, the benthic biomass of *S. erythrophthalmus* differed significantly among management types, with a greater average biomass detected in unmanaged lakes ($P < 0.05$; Table 3). In terms of abundance (NPUE), *L. delineatus* was a significantly discriminatory species, who was found in multimesh gillnet catches only in unmanaged lakes ($P < 0.05$; 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 (H1, H2, H4). 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 hypothesised, managed gravel pit lakes were found to contain a higher α -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 fourth hypothesis of lower β -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 homogenisation caused by recreational-fisheries management, particularly due to regular stocking.

4.2 | Robustness of results to sampling bias

Both groups of gravel pit lakes 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 (Jeppesen *et al.*, 2000; Mehner *et al.*, 2005; Persson *et al.*, 1991). 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 (Achleitner *et al.*, 2012; Barthelmes & Doering, 1996; Diekmann *et al.*, 2005; Jurajda *et al.*, 2009; Menezes *et al.*, 2013; Mueller *et al.*, 2017; Scharf *et al.*, 2009). 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 (Angermeier & Smogor, 1995; Lyons, 1992; 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 appears to be robust.

The benthic zone was sampled using multimesh gillnets following European standards (CEN, 2015). We adapted the gillnet numbers to lake size to harmonise 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 L_T more representatively. However, certain large-bodied species known to occur in Lower Saxonian gravel pit lakes (Schällicke *et al.*, 2012) and other angler-managed lakes in Germany (Borkmann, 2001), in particular large-bodied cyprinids such as *C. 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 is unlikely to have affected the species inventory as we regularly captured *C. carpio* in all lakes where the local fisheries managers reported regular stocking of this species. Longer panels of large mesh sizes are needed to sample large-bodied individuals of *C. carpio* and top predators (e.g., *E. lucius*, *S. glanis*, *S. lucioperca*) more effectively, 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 α -diversity in lakes managed by and for recreational fisheries has previously been demonstrated for gravel pit lakes in southern France (Zhao

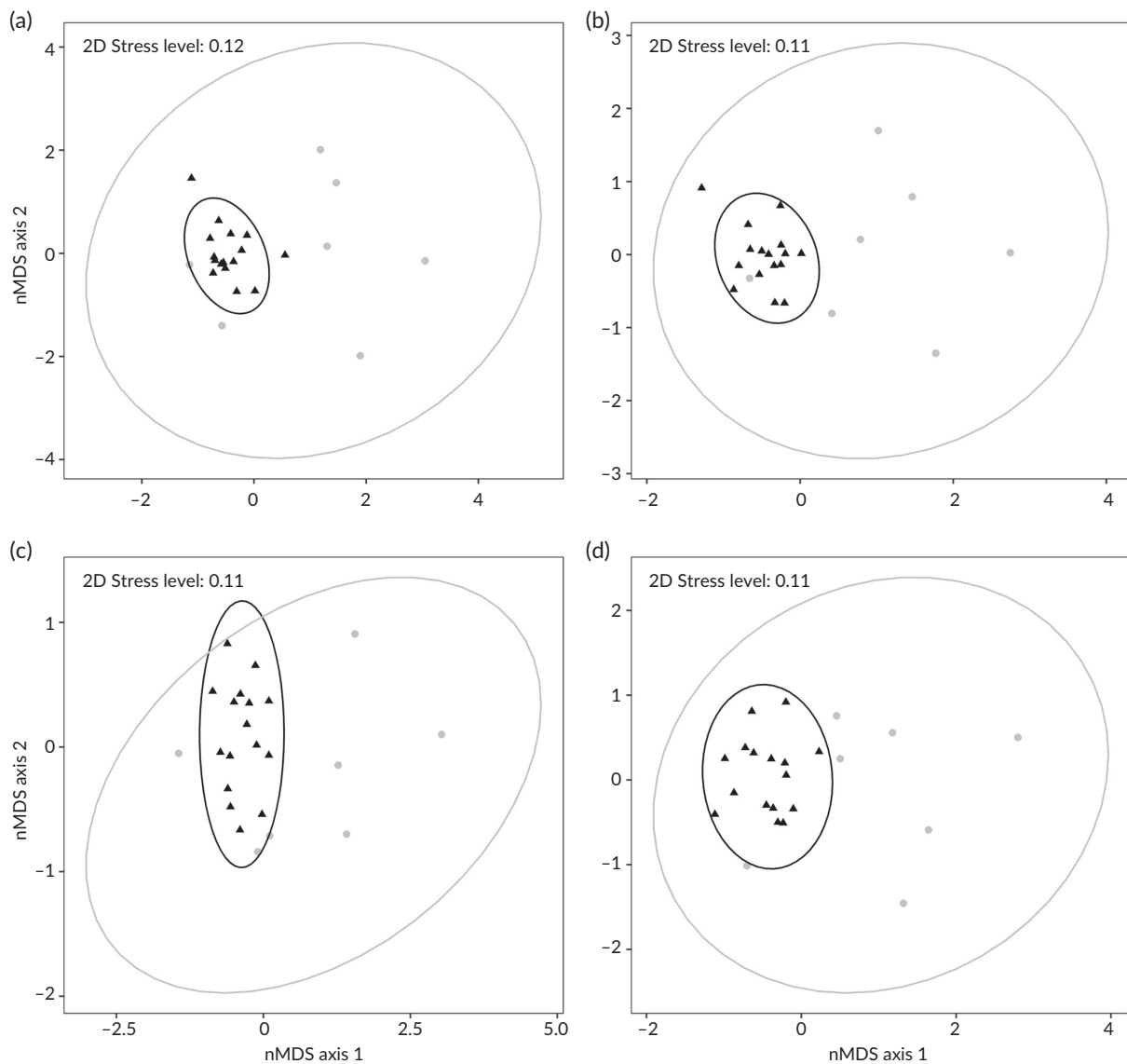


FIGURE 6 Non-metric multidimensional scaling (nMDS) plots of the fish community structures in managed (\blacktriangle ; $n = 16$) and unmanaged (\bullet ; $n = 7$) gravel pit lakes for: (a) species abundance in the littoral zone; (b) species biomass in the littoral zone; (c) species abundance in the benthic zone; (d) species biomass in the benthic zone. The ellipses show the 95% CI for managed lakes (—) and unmanaged lakes (---). The littoral and benthic zones were sampled through electrofishing and gillnetting, respectively

et al., 2016) and Minnesota (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 (Arlinghaus et al., 2015; Eby et al., 2006) and large-bodied cyprinid fish such as *C. carpio* and *T. 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 *A. anguilla*, *E. lucius* and *P. fluviatilis* were found in all or almost all managed gravel pits. While *E. lucius* and *P. fluviatilis* become established and reproduce naturally after introduction, the abundance of *A. anguilla* in the gravel pits we studied (which all lacked connections to nearby rivers) clearly indicates ongoing stocking. Correspondingly, no *A. anguilla* and hardly any top predators, which are popular as game fishes, were found in unmanaged lakes. Accordingly, presence-absence of *A. anguilla* was one of the major dissimilarities between the two management types following our SIMPER analyses (Supporting Information Table S6). In gravel pit lakes managed for recreational fisheries, a higher relative frequency of

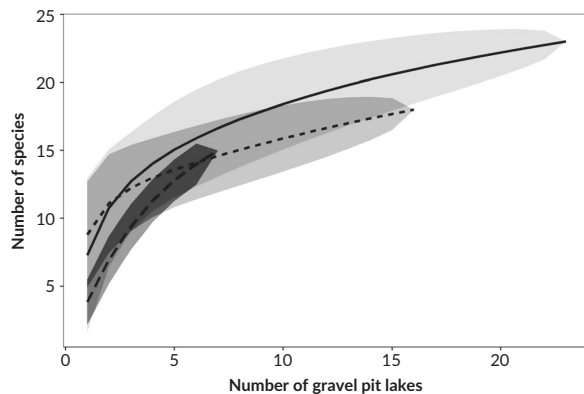


FIGURE 7 Species accumulation curve for the average expected species numbers in a given number of gravel pit lakes for both management types (—), only managed (---) and only unmanaged (····). The variance of the average expected species number is represented through the corresponding ribbon of each line

A. anguilla has previously been reported compared with natural lakes predominantly managed for commercial fisheries (Arlinghaus *et al.*, 2016; Emmrich *et al.*, 2014), 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 *A. anguilla* (Bark *et al.*, 2007; Dekker, 2016), continuous stocking of this species into isolated lakes is problematic from a conservation perspective.

4.4 | Small-bodied non-game fish and threatened species

Small-bodied *R. rutilus*, *A. alburnus* or *P. fluviatilis* are considered forage fish for predators and are therefore regularly stocked in Germany (Arlinghaus *et al.*, 2015). We found *R. rutilus* and *P. 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 (Emmrich *et al.*, 2014; Mehner *et al.*, 2005; Ritterbusch *et al.*, 2014). Already widespread species have, when becoming translocated to new water bodies, the highest fauna-homogenising effects (Sommerwerk *et al.*, 2017). Therefore, fisheries management fosters faunal homogenisation 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. *G. cernua*, *R. amarus*, *C. taenia* and *A. alburnus* exclusively occurred in managed lakes, while *L. delineatus*, *P. pungitius*, *G. gobio* and *B. barbatula* were only caught in unmanaged lakes. *L. delineatus* and *P. 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. At first sight, this rather surprising finding probably 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 with 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 colonisation (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 German Red List of freshwater fishes (Freyhof, 2009). Only *A. 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 hypothesised 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., *C. carpio*, *S. lucioperca* and *S. glanis*. In our study, only two individuals of non-native *P. parva* were found in one of 16 managed lakes, which were most probably introduced unintentionally through poorly sorted stocking of pond-reared *C. carpio* or poorly sorted stocking of wild-captured cyprinids (Copp *et al.*, 2005b; Wiesner *et al.*, 2010). In comparison, in two out of seven unmanaged lakes, one individual of either non-native *P. parva* or non-native *A. 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 *S. erythrophthalmus* found in one unmanaged lake, have been reported vectors for fish dispersal around the globe (Copp *et al.*, 2005a; Hirsch *et al.*, 2018; Johnson *et al.*, 2009). Indeed, illegal releases, 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 homogenisation caused by fisheries management

In agreement with our hypothesis, recreational-fisheries management collectively contributed to the homogenisation of fish faunas, reducing

TABLE 3 Similarity percentage analysis (SIMPER) for fish species numbers per unit effort (NPUE) and fish species biomass per unit effort (BPUE) in managed and unmanaged gravel pit lakes sampled through electrofishing in the littoral zone and multimesh gillnetting in the benthic zone. Only the six species contributing most to the average dissimilarity are presented

	Species	Average contribution to overall dissimilarity	Cumulative contribution %	Mean managed \pm S.D.	Mean unmanaged \pm S.D.	P-value
Littoral NPUE (electrofishing; n 50 m^{-1})	<i>Leucaspis delineatus</i>	25.2	28.8	0.0 \pm 0.0	485.9 \pm 1229.0	0.019
	<i>Perca fluviatilis</i>	14.3	45.2	8.2 \pm 6.3	2.1 \pm 4.8	0.460
	<i>Scardinius erythrophthalmus</i>	14.1	61.3	7.0 \pm 20.9	5.4 \pm 11.4	0.546
	<i>Pungitius pungitius</i>	11.8	74.8	0.0 \pm 0.0	5.8 \pm 11.1	0.009
	<i>Anguilla anguilla</i>	4.6	80.1	2.3 \pm 1.8	0.0 \pm 0.0	0.345
	<i>Rutilus rutilus</i>	4.0	84.7	3.1 \pm 7.7	0.4 \pm 1.0	0.946
Littoral BPUE (electrofishing; g 50 m^{-1})	<i>Anguilla anguilla</i>	27.3	29.2	363.0 \pm 386.6	0.0 \pm 0.0	0.160
	<i>Carassius gibelio</i>	17.1	47.5	9.7 \pm 34.3	375.2 \pm 705.0	0.079
	<i>Esox lucius</i>	12.4	60.7	139.7 \pm 176.0	4.0 \pm 10.7	0.323
	<i>Leucaspis delineatus</i>	8.3	69.6	0.0 \pm 0.0	187.9 \pm 465.8	0.119
	<i>Scardinius erythrophthalmus</i>	6.9	77.0	22.1 \pm 56.8	60.6 \pm 92.9	0.120
	<i>Perca fluviatilis</i>	6.6	84.1	66.5 \pm 41.8	21.7 \pm 46.4	0.033
Benthic NPUE (multimesh gillnet; n 100 m^{-2})	<i>Perca fluviatilis</i>	33.1	40.2	64.3 \pm 59.3	24.4 \pm 43.9	0.138
	<i>Rutilus rutilus</i>	16.4	60.1	24.5 \pm 23.5	11.6 \pm 30.6	0.136
	<i>Scardinius erythrophthalmus</i>	9.1	71.2	0.5 \pm 1.3	15.8 \pm 27.0	0.079
	<i>Leucaspis delineatus</i>	6.2	78.7	0.0 \pm 0.0	9.0 \pm 14.2	0.013
	<i>Carassius gibelio</i>	4.0	83.6	0.4 \pm 1.6	5.3 \pm 13.8	0.183
	<i>Abramis brama</i>	3.0	87.3	6.9 \pm 17.6	0.1 \pm 0.4	0.767
Benthic BPUE (multimesh gillnet; g 100 m^{-2})	<i>Perca fluviatilis</i>	20.0	24.0	1240.3 \pm 1032.8	435.0 \pm 834.7	0.020
	<i>Rutilus rutilus</i>	16.5	43.9	988.7 \pm 763.9	243.2 \pm 643.4	0.153
	<i>Cyprinus carpio</i>	14.9	61.8	552.2 \pm 791.0	848.7 \pm 1191.5	0.152
	<i>Scardinius erythrophthalmus</i>	11.0	75.1	26.6 \pm 70.6	690.3 \pm 1332.1	0.031
	<i>Carassius gibelio</i>	9.0	86.0	18.7 \pm 74.6	683.0 \pm 1724.4	0.202
	<i>Abramis brama</i>	4.5	91.4	358.3 \pm 724.0	0.9 \pm 2.4	0.875

β -diversity in fish communities compared with unmanaged lakes. Homogenisation 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 effects, 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 (Bruet *et al.*, 2013; Diekmann *et al.*, 2005; Mehner *et al.*, 2005; 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 currently or in the past.

In conclusion, 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 fostered 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 probably 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 (γ -diversity), because recreational-fisheries management in gravel pits fosters local species richness, at the cost of biotic homogenisation.

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CONTRIBUTIONS

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Paper II

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Fish community composition in small lakes: the impact of lake genesis and fisheries management.

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Fish community composition in small lakes: The impact of lake genesis and fisheries management

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Abstract

1. Gravel pit lakes are common across Europe. These novel ecosystems serve as model systems to study human-induced and natural colonisation of isolated lakes by fish. Fisheries-management activities can quickly spread species over large distances, possibly homogenising fish communities across ecosystems, while fostering local fish diversity.
2. Our objective was to evaluate the effects of lake genesis (gravel pit lakes < 100 years old vs. natural lakes of glacial genesis ~10,000 years old) and fisheries management (fish stocking activities present vs. absent) on the fish community in small lakes, while controlling for key environmental variables known to affect lake fish communities.
3. We sampled fish communities by electrofishing and multimesh gillnetting in 47 isolated lakes managed for fisheries, and 19 unmanaged and isolated lakes of both natural and artificial origin in northern Germany. Unmanaged lakes were used as reference to assess fisheries-management impacts in small natural and artificial lakes.
4. We caught 178,506 fish from 30 species and found that the accumulation of native lake fish species in lakes was associated with fisheries management, which increased local species richness (α -diversity) and number of predatory species, and reduced among-lake variation in fish community composition (β -diversity; i.e., homogenisation). The homogenisation-effect associated with fisheries happened with introduced native fish species, whereas non-native species were rarely detected.
5. In unmanaged gravel pit lakes, the littoral fish community composition was substantially different to the communities present in both types of managed lakes and unmanaged natural lakes. Therefore, the relatively young unmanaged gravel pit lakes revealed evidence of ongoing, stochastic colonisation processes that resulted in comparatively species-poor fish communities.

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6. We concluded that fisheries management by anglers speeds up the colonisation of gravel pit lakes with native fish species in the study area. For planning initial fish introductions in newly created gravel pit lakes, it is recommended that fish communities from ecologically similar natural lakes within the same geographical region are used as references to maintain the biotic integrity of newly created fish communities.

KEYWORDS

biodiversity, fish assemblage, fish colonisation, gravel pit lake, lake origin, quarry lake, stocking

1 | INTRODUCTION

Humans are shaping an epoch: the Anthropocene (Crutzen, 2006). Among other issues, this epoch is characterised by a strong decline in biodiversity (Barnosky et al., 2011; Díaz et al., 2019). Freshwater biodiversity is especially threatened (Reid et al., 2018; Tickner et al., 2020), including fishes that are experiencing particularly rapid declines (Freyhof & Brooks, 2011; Tickner et al., 2020). Habitat loss and fragmentation, pollution, warming, and the spread of non-natives have been identified as major threats for freshwater fishes (Aarts et al., 2004; Rahel, 2000; Villéger et al., 2011). Overfishing, fish introductions and regular stocking with native fish can also have strong impacts on freshwater fish communities, and contribute to faunal homogenisation and biomass decline in the case of overharvest (Allan et al., 2005; Johnson et al., 2009; Lewin et al., 2006; Rahel, 2002).

Within the European Union, the Water Framework Directive (WFD) sets good ecological status or potential (in heavily modified and artificial waters) as mandatory environmental targets for all surface water bodies, to be achieved by 2027 (EU, 2000). In this context, the fish community became an obligatory component for assessing the ecological status of freshwaters (Birk et al., 2012). However, the WFD monitoring is mandatory only for lakes ≥ 50 ha. Thus, the highly abundant and socially relevant small lakes (≤ 20 ha; Downing et al., 2006; Meyerhoff et al., 2019; Nikolaus et al., 2020; Kaemingk et al., 2022) are not necessarily covered by regular environmental monitoring, and there remains a widespread lack of knowledge about fish communities in small lakes. In central Europe, small lakes are regularly managed by recreational-angling communities, often in club contexts (Deadlow et al., 2011; Fujitani et al., 2020; Gee, 1978; Umweltbundesamt, 2021). In this context, fish stocking is by far the most important fisheries-management tool, which is used for various reasons including establishment of fish in newly created waters through introductory stocking, stock enhancement and conservation of threatened populations (Arlinghaus et al., 2015; Cowx, 1994; Cucherousset et al., 2021; Lorenzen et al., 2012). Owing to the popularity and intensity of stocking of lakes managed by recreational fisheries, the fish community composition of small and managed lakes often is shaped by stocking (Matern et al., 2019; Skeate et al., 2021; Zhao et al., 2016). However, illegal stocking and introduction activities are possible in all types of lakes, including fish

transfer through the aquarium and garden pond trade and voluntarily release by ornamental fish keepers, and hence, anthropogenic traces of past human-mediated introductions also can be expected in unmanaged lakes (Copp et al., 2005; Johnson et al., 2009; Matern et al., 2019; Patoka et al., 2017).

Most natural lakes in central Europe were formed during the last ice age, which ended roughly 10,000 years ago, and were naturally recolonised by fishes from various glacial refugia since then (Bernatchez & Wilson, 1998; Håkanson, 2012; Mandrak & Crossman, 1992). The natural colonisation of lakes by fishes was determined primarily by hydrological connectivity (Borcherding et al., 2002; Kristensen et al., 2020), but isolated lakes also can be colonised via natural and anthropogenic pathways. For example, floodings can provide temporary connectivity with nearby waters (Olden et al., 2010; Pont et al., 1991) and other rare events (such as so-called fish rains resulting from hurricanes; Bajkov, 1949) might serve as stochastic colonisation events. Furthermore, fish eggs can be distributed by waterfowl (Lovas-Kiss et al., 2020; Silva et al., 2019) and mobile invertebrates (Suetsugu & Togashi, 2020). However, only a small fraction of eggs passing through the guts of waterfowl can hatch (Lovas-Kiss et al., 2020; Silva et al., 2019), therefore the spatial pattern of water bodies scattered across the landscape is of great relevance for the dispersal speed of aquatic organisms by birds (Anastácio et al., 2014). Accordingly, natural fish colonisation of isolated lakes mediated by waterfowl and insects usually is a slow and quite erratic process (Barbour & Brown, 1974). Therefore, greater fish diversity can be expected in older lakes because of the much longer natural colonisation time compared to young gravel pit or quarry lakes (hereafter collectively called gravel pit lakes).

Human-induced transfer of fish has been widespread since at least Roman times 2,000 years ago (Hoffmann, 1995). Human-induced fish colonisation of lakes can significantly speed up the establishment of fishes in artificial standing water bodies (Cowx, 1994; Johnson et al., 2009) and lead to rapid homogenisation of fish communities across natural lakes (Cazelles et al., 2019; Rahel, 2000; Villéger et al., 2011). Fish stocking is the most common fisheries-management measure in many countries worldwide, aiming at establishing and promoting species of relevance to fisheries (typically top predators and other large-bodied fish; Zhao et al., 2016; Matern et al., 2019; Skeate et al., 2021), but it may also include the release of small-bodied baitfish and endangered

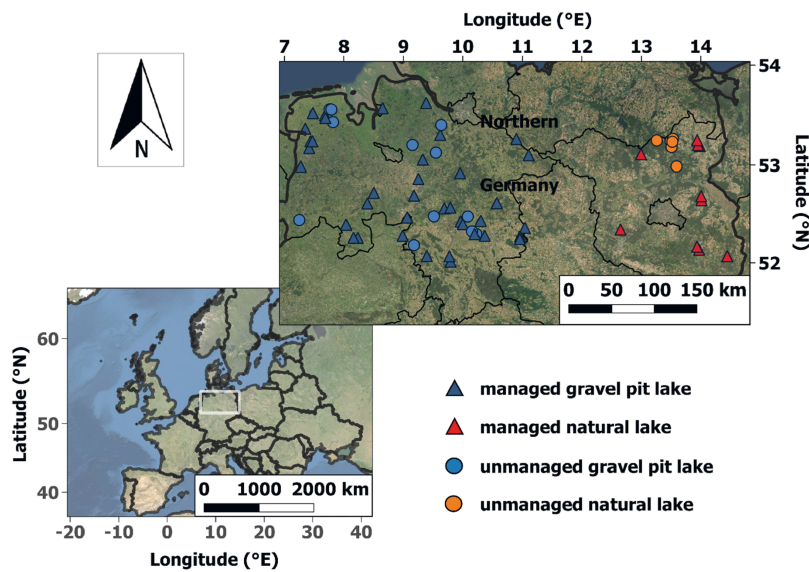


FIGURE 1 Map of all sampled gravel pit and natural lakes in northern Germany

species for conservation reasons (Arlinghaus et al., 2015; Cazelles et al., 2019; Eby et al., 2006). This practice can lead to intentional (Hickley & Chare, 2004; Johnson et al., 2009) or unintentional (e.g., as a consequence of poorly sorted stocking material) introduction and subsequent establishment and spread of possibly maladapted and non-native species (Gozlan et al., 2002; Zhao et al., 2016). Stocking and fisheries management more generally has thus been identified as a driver for increased local species richness (α -diversity), at the cost of homogenisation of fish communities across regions and continents in freshwaters (β -diversity; Rahel, 2002; Olden, 2006; Cazelles et al., 2019; Matern et al., 2019). Illegal introduction by individual anglers and aquarists can further contribute to the spread of fish species (Cambray, 2003; Hirsch et al., 2021; Johnson et al., 2009; Patoka et al., 2017). Especially in densely populated areas, illegal releases of ornamental and garden pond fishes have become the main vector for species introductions (Copp et al., 2005, 2010; Patoka et al., 2017).

After introduction and establishment of various fish species, the biomass and composition of fish communities will be shaped by local environmental conditions, such as nutrient level, lake morphology, spawning habitat and predation refuge availability (Jeppesen et al., 2000; Mehner et al., 2005; Persson et al., 1991). A lakes' trophic state is impacted by groundwater exchange and various nutrient input sources, and typically increases with age (Callisto et al., 2014; Mollema & Antonellini, 2016). In European lakes with increasing nutrient levels, fish communities shift from Salmoniformes-dominated, to Perciformes- and ultimately to Cypriniformes-dominated (de Leeuw et al., 2003; Hartmann & Nümann, 1977; Jeppesen et al., 2000; Persson et al., 1991). Lake size and the availability of habitats also impact species richness, with larger lake size and a more diverse shoreline promoting a higher number of fish species as a result of the greater availability of niches and opportunities for species to segregate across them (Barbour & Brown, 1974; Browne, 1981; Eckmann, 1995; MacArthur & Wilson, 1967).

Gravel pit lakes are artificially created, novel water bodies, which originate from the excavation of sand, gravel and other mineral resources. These lakes often are isolated from other water bodies and characterised by their young age of less than 100 years (Matern et al., 2019; Seelen et al., 2021; Søndergaard et al., 2018; Zhao et al., 2016). Gravel pit lakes managed for recreational fisheries typically host higher fish species richness than unmanaged gravel pit lakes (Matern et al., 2019; Zhao et al., 2016), with some exceptional gravel pit lakes lacking fishes at all (Søndergaard et al., 2018; Werneke et al., 2018). While the first comparison of the littoral fish community in managed natural and managed gravel pit lakes in Germany revealed no significant differences (Emmrich et al., 2014), a comparison of the benthic fish community among natural and gravel pit lakes is still necessary. Also, the fish community composition of unmanaged natural lakes has not yet been characterised, which is essential to analyse the probable human-assisted colonisation history in young gravel pit lakes compared to significantly older natural lakes. Indeed, unmanaged natural lakes constitute an important reference for assessing the impact of past fisheries management in both managed gravel pit and natural lakes. Comparative analyses of fish community differences between gravel pit and natural lakes, both with and without fisheries management, can shed light on whether fisheries management (mainly representing traces of past fish stocking) leads to homogenisation of fish communities in gravel pit lakes (Matern et al., 2019), and whether it fosters the establishment of fish communities that are similar in richness and composition to those of small natural lakes as previously hypothesised for littoral fish communities by Emmrich et al. (2014).

We compared fish communities from small and isolated gravel pit and natural lakes in northern Germany, each with and without recent fisheries management. We hypothesised, firstly, that fisheries management (with fish stocking as major management tool) influences fish communities in both gravel pit and natural lakes by enhancing local fish diversity (α -diversity) and shaping diversity of regional fish

community composition (β -diversity) relative to unmanaged reference lakes, and secondly, that α -diversity is higher and β -diversity lower in unmanaged natural lakes compared to unmanaged gravel pit lakes because of the longer colonisation time of natural lakes.

2 | METHODS

2.1 | Sampling location and environmental variables

We sampled fish communities and environmental variables in 66 isolated lakes, of which 50 were gravel pit lakes and 16 natural lakes. All gravel pit lakes were located in north-western Germany, mainly in the Federal State of Lower Saxony (Figure 1). Owing to the low number of natural lakes in this area, we sampled ecologically comparable natural lakes in the Federal State of Brandenburg, which is located at the same latitude in north-eastern Germany at a distance of about 400 km. Data for this study were collected from different projects and all available data were gathered to a coherent and comparable set of environmental and fishing data. The investigated gravel pit lakes were in an advanced succession stadium and we categorised all lakes based on their genesis as either gravel pit lakes (mean lake age at fishing event: 29 ± 12 years; Table S1) or natural lakes (lake age ~ 10,000 years). Data on stocking numbers and species composition of stocked fish were not available for all lakes, and we therefore categorised the lakes as either managed for fisheries with legal fish stocking ($n_{\text{managed gravel pit lakes}} = 37$ and $n_{\text{managed natural lakes}} = 10$) or unmanaged without legal fish stocking ($n_{\text{unmanaged gravel pit lakes}} = 13$ and $n_{\text{unmanaged natural lakes}} = 6$). It is possible that lakes with no current fishing rights and no current legal stocking might have experienced some level of legal or illegal stocking in the past. However, it is certain that the lakes without legal fish stocking were not under active fisheries management since their genesis in the case of gravel pit lakes and the same was true for natural lakes, at least since the German reunification in 1989. Because the set of sampled lakes was from different projects, only a small set of environmental variables was available for all lakes, specifically total phosphorus (TP), pH value and lake morphology (lake size and depth). These variables are known to be decisive indicators of mixing regime and productivity of lakes (Schindler, 1977, 1978), and thus probably captured the most important covariates affecting abundance and fish community composition of our study lakes.

The key difference among our categorisation of managed and unmanaged lakes was whether the fishing right that is tied to water body ownership or a lease contract by the water body owner was used for commercial or recreational fisheries (Table S1). In Germany, the holder of the fishing right is entitled to catch and harvest fish, but also entitled (and in fact legally forced) to ensure near-natural fish communities and to avoid overharvesting through sustainable management. The management obligation by fishing rights holders typically is enforced by engaging in stocking and by strengthening state-level harvest regulations (e.g., minimum-length limits, daily bag limits or protected seasons). Of course harvesting, harvest regulations and

habitat enhancement is conducted in managed lakes, too (Arlinghaus et al., 2002; Arlinghaus, Müller, et al., 2017), but the key impact on the community composition is likely to originate from past and current fish stocking, which often is done annually by the vast majority of German angling clubs (Arlinghaus et al., 2015). The fishing right holders in our study for the managed systems encompassed small angling clubs in western Germany, and the state angling organisation and local fishers in eastern Germany. By contrast, the unmanaged lakes lacked any active use of fishing rights and hence neither exploitation nor stocking practices were reported in the unmanaged gravel pit lakes or at least for the last 30 years in the case of unmanaged natural lakes. Furthermore, no other planned management measures (e.g., habitat management) were conducted in the riparian area of the unmanaged lakes. Thus, we can conclude that besides origin, the key difference of managed and unmanaged lakes was the presence of organised, legal stocking and exploitation of fish.

All gravel pit lakes and all unmanaged natural lakes were sampled between 2016 and 2019. Managed natural lakes were sampled between 2007 and 2011, apart from a single lake in 2002. We measured lake size and shoreline length for all lakes using QGIS (QGIS Development Team, 2019) at a scale of 1: 1,000 and calculated the shoreline development factor (SDF) after Hutchinson (1957) as an index of shoreline complexity and extension following recommendations for enhanced comparison by Seekell et al. (2022). We used contour maps, derived from echo sounder data, to extract mean lake depth and shares of the different depth strata (0–3; 3–6; 6–12; 12–20 and 20–35 m). Mean lake depth is correlated with temperature, degree of stratification and nutrient mixing and affects fish community composition and leading indicator species as well as productivity of lakes (Mehner et al., 2005). TP concentrations were analysed as a proxy for lake productivity in terms of primary production (Schindler, 1978) using the molybdenum blue method (ISO, 2004; Murphy & Riley, 1962). TP was measured during spring circulation for all managed natural lakes and a subset of managed and unmanaged gravel pit lakes, but as a consequence to the aforementioned issue of compiling data from different projects done by different institutions not for unmanaged natural lakes. For all lakes lacking a spring TP measurement ($N = 29$), TP values at the time of the fishing events in late summer/early autumn were used, which were sufficiently correlated to the spring values (Spearman-rank correlation: $r = 0.63$ and $p < 0.001$; Table S2 and Figure S1). Furthermore, pH value was measured at each fishing event to assure generally suitable conditions for fishes (E.I.F.A.C., 1969).

2.2 | Fish community sampling

Fish communities were sampled by boat electrofishing and multimesh gillnetting to cover the major habitat types of lakes and knowing that both methods sample different taxa effectively (Achleitner et al., 2012; Diekmann et al., 2005; Mueller et al., 2017). In all lakes the shorelines were subdivided in electrofishing transects of varying length between 30 and 300 m. In all gravel pit lakes and all unmanaged natural lakes,

TABLE 1 Median and range of the main environmental characteristics of all gravel pit lakes and natural lakes with and without fisheries management examined in this study (SDF = shoreline development factor, TP = total phosphorus)

	Managed gravel pit lake	Managed natural lake	Unmanaged gravel pit lake	Unmanaged natural lake
Lake size (ha)	6.2 (0.7–21.1)	12.1 (3.2–18.4)	4.1 (1.1–16.5)	4 (1.3–10.5)
Shoreline length (m)	1,457 (417–3,113)	1,768 (776–2,510)	1,072 (492–3,944)	930 (461–2,038)
SDF	1.4 (1.1–2.7)	1.4 (1.1–1.9)	1.5 (1.1–2.7)	1.6 (1.1–2)
Mean lake depth (m)	3.7 (0.5–13)	3.2 (0.5–4.3)	4.3 (0.6–9.6)	2.3 (0.7–4.4)
TP ($\mu\text{g/L}$)	19 (4–235)	51 (30–125)	19 (12–78)	27 (14–160)
pH value	8.3 (6.8–10.1)	7.5 (6.8–8.5)	8.3 (7.3–9.9)	7.8 (7.5–8.6)

all transects were fished, whereas in the larger managed natural lakes a randomly selected subset of transects was fished.

The gillnetting data differed slightly between the different datasets. All nets were benthic multimesh gillnets with 1.5 m standard height in the following length/mesh size combinations: Type I, standard WFD (CEN, 2015), 30 m long with 2.5 m panels of 43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 35, 29, 5 mm mesh size; Type II, 32.5 m long, standard WFD (CEN, 2015) plus 2.5 m with 70 mm mesh size; Type III, standard WFD (CEN, 2015) plus an additional 50 m gillnet with 70 mm mesh size; and Type IV, 40 m long, standard WFD (CEN, 2015) plus four panels of 2.5 m with 70, 90, 110 and 135 mm mesh size. Among the managed natural lakes, one was fished with Type I gillnets and the other nine lakes were fished with Type II gillnets. Three unmanaged natural lakes were sampled with Type III gillnets and the catches of the 50 m net were adjusted to 2.5 m effort corresponding to Type II. All other lakes were sampled using Type IV gillnets with the number of gillnets depending on lake size (compare Matern et al., 2019, for methodological details). For 41 of 66 lakes, the catches on mesh sizes ≥ 70 mm were noted separately. A total of 322 gillnet nights yielded just 29 fish caught on the ≥ 70 mm panels of the Type IV nets, which allowed us to standardise catch per unit effort (CPUE) to Type II (32.5 m) nets without biasing the results. As robustness check, re-running the analyses with original data of the Type IV (40 m) gillnets yielded similar results and patterns.

For analyses, CPUE was calculated based on fish numbers per 50 m sampled shoreline (fish $\times 50 \text{ m}^{-1}$) for electrofishing and per 100 m^2 gillnet area and night (fish $\times 100 \text{ m}^{-2}$) for multimesh gillnets. Gillnet CPUE was calculated in a stratified manner using depth strata as recommended for the WFD monitoring (0–3, 3–6, 6–12, 12–20 and 20–35 m; CEN, 2015). However, owing to the small size of some gravel pit lakes, not all depth strata were sampled. For these lakes, gillnets were treated as random sample. The unmanaged gravel pit lake “Kiessee Isums klein” was removed from the gillnet data analysis, because no fish were caught.

To describe the fish species inventory, we calculated the total fish species richness, the number of piscivorous species and the number of non-native species for each lake combining data from electrofishing and gillnetting. Piscivorous species included perch >150 mm total length and eel >500 mm total length following Emmrich et al. (2014) and Matern et al. (2019), and species were assigned as non-native in Germany according to Wiesner et al. (2010) and Wolter and Röhr (2010).

2.3 | Data analysis

We checked the residuals of the environmental variables, total fish species richness (α -diversity) and number of predatory species for normality using Shapiro–Wilk tests. Depending on normality or not, we used either Kruskal–Wallis tests and Bonferroni-corrected pairwise Wilcoxon tests or analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) *post hoc* test to check for differences between the lake and management types. We ran redundancy analyses (RDA) using all available environmental variables (Table 1) and fisheries management (present/absent) and lake genesis (gravel pit lake/natural lake) followed by model selections (selection direction = both) using the function ‘ordiR2step’ from the vegan package to evaluate the effect of environmental variables most strongly associated with the fish community (Oksanen et al., 2019). As robustness check, we ran an additional RDA on the data with available lake age information, using lake age as covariate instead of lake genesis, and received similar results. The among-lake fish community variation (β -diversity) of all four combinations of lake genesis and fisheries management was visualised using non-metric multidimensional scaling (nMDS; Kruskal, 1964) to investigate homogenisation effects. Permutation tests were conducted to reveal differences in β -diversity between lake and management types (permutations: $n = 9,999$), and a similarity percentage analysis (SIMPER; permutations: $n = 999$; Clarke, 1993) was performed to reveal species-specific abundance effects on the differences in fish community composition. All analyses and visualisations were conducted using the software R (R Core Team, 2019) and the packages vegan (Oksanen et al., 2019) and ggplot2 (Wickham, 2016).

3 | RESULTS

3.1 | Lake environment

The lakes ranged in size from 0.7 to 21.2 ha, and their shoreline lengths varied between 417 and 3,944 m (Table 1). The SDF varied between 1.1 and 2.7 for all lakes, and mean lake depth was between 0.5 and 13 m. No significant differences were detected for lake size, shoreline length, SDF and mean lake depth between the four groups of lake types. TP concentration ranged between 4 and

235 $\mu\text{g L}^{-1}$ with highest median TP concentration in managed natural lakes (51 $\mu\text{g L}^{-1}$). In managed natural lakes, TP concentrations were significantly higher than in managed gravel pit lakes (median: 19 $\mu\text{g L}^{-1}$; Bonferroni-corrected pairwise Wilcoxon test, $p = 0.035$), elevated compared to unmanaged gravel pit lakes (median: 19 $\mu\text{g L}^{-1}$; Bonferroni-corrected pairwise Wilcoxon test, $p = 0.085$) and did not differ (median: 27 $\mu\text{g L}^{-1}$; Bonferroni-corrected pairwise Wilcoxon test, $p = 0.265$) from unmanaged natural lakes (Table 1). The pH values ranged between 6.8 and 10.1 and were somewhat elevated in managed gravel pit lakes compared to managed natural lakes (Bonferroni-corrected pairwise Wilcoxon test, $p = 0.056$). All other pairwise comparisons were not significantly different between lake types (Table 1).

3.2 | Description of catches and frequency of occurrence

In total, we caught 178,506 fish from 30 species (143,263 individuals from 26 species by electrofishing; 35,243 individuals from 25 species by multimesh gillnetting). Perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) were the most frequent species that occurred in all managed gravel pit lakes and in 80% of all managed natural lakes. Roach and perch were also caught in 83% and in 50% of the unmanaged natural lakes, respectively (Table 2). The species pike (*Esox lucius*), tench (*Tinca tinca*) and rudd (*Scardinius erythrophthalmus*) were frequent in managed gravel pit lakes (pike: 95%; tench: 81%; rudd: 68%), managed natural lakes (pike: 90%; tench: 90%; rudd: 90%) and in unmanaged natural lakes (pike: 83%; tench: 100%; rudd: 83%). Tench was the only species present in all unmanaged natural lakes (Table 2). In unmanaged gravel pit lakes, the fish species with the highest frequency of occurrence were perch (46%), followed by roach, rudd and common carp (*Cyprinus carpio*; all 39%; Table 2). Eel (*Anguilla anguilla*) was caught in most managed lakes (gravel pit lake: 95%; natural lake: 70%), but some individuals also were found in unmanaged natural lakes (17%) and unmanaged gravel pit lakes (31%). Crucian carp (*Carassius carassius*) was found in only one managed gravel pit lake (3%), but was relatively frequent in managed (40%) and unmanaged (50%) natural lakes. Small-bodied, often pioneer species such as sunbleak (*Leucaspis delineates*) and ninespine stickleback (*Pungitius pungitius*) were most frequently detected in unmanaged gravel pit lakes (31% and 23%, respectively).

The fishes that we sampled were overwhelmingly native species, which in Germany includes common carp. We detected three non-native species, each with only few individuals. In total, three individuals of topmouth gudgeon (*Pseudorasbora parva*) were found in one managed and one unmanaged gravel pit lake; a single brown bullhead (*Ameiurus nebulosus*) individual was caught in an unmanaged gravel pit lake and a single rainbow trout (*Oncorhynchus mykiss*) was detected in a managed natural lake. No non-native species were found in unmanaged natural lakes. We further detected the riverine fish species ide (*Leuciscus idus*) and chub (*Squalius cephalus*) in low frequencies in managed gravel pit lakes (both 5%).

Total fish species richness (α -diversity) and number of predatory species was significantly greater in lakes with fisheries management (gravel pit and natural lakes) compared to lakes without management (gravel pit and natural lakes; Figure 2 and Table 3). Unmanaged gravel pit lakes did not differ from unmanaged natural lakes in terms of total fish species richness and number of predatory species.

3.3 | Fish community composition and its descriptors

After model selection the RDA revealed lake genesis, fisheries management and TP as significant descriptors of the fish communities sampled by electrofishing (littoral; Table 4) and multimesh gillnets (benthic; Table 4 and Figure S2), whereas no significant effects of lake size, shoreline length, mean lake depth, SDF and pH value were found. In unmanaged gravel pit lakes, the littoral fish communities were highly variable (Figure 3a). Accordingly, the β -diversity was significantly higher in unmanaged gravel pit lakes than in both managed gravel pit lakes (Table 5; permutation test, $p = 0.003$) and unmanaged natural lakes (permutation test, $p = 0.016$), and also tended to strongly differ from managed natural lakes (permutation test, $p = 0.063$). The benthic fish community significantly differed in β -diversity between managed and unmanaged gravel pit lakes (permutation test, $p = 0.006$), whilst differences were found neither among natural and gravel pit lakes, nor among unmanaged gravel pit lakes and unmanaged natural lakes (Figure 3b and Table 5). SIMPER analysis revealed three fish species, namely rudd, perch and roach, explaining most of the differences between fish communities (Table 6 for condensed results, and Table S3 and S4 for full results). Rudd was caught in highest abundance in unmanaged natural lakes (mean NPUE = $98.2 \pm 212.7 \text{ N} \cdot 50 \text{ m}^{-1}$) and contributed most to the differences relative to managed gravel pit lakes (mean NPUE = $6.5 \pm 20.8 \text{ N} \cdot 50 \text{ m}^{-1}$; contribution to difference = 37.4%), managed natural lakes (mean NPUE = $12.0 \pm 17.9 \text{ N} \cdot 50 \text{ m}^{-1}$; contribution to difference = 35.1%) and unmanaged gravel pit lakes (mean NPUE = $5.1 \pm 10.1 \text{ N} \cdot 50 \text{ m}^{-1}$; contribution to difference = 30%) using electrofishing data. Perch and roach were the two species that contributed most to differences between all pairwise comparisons using gillnet data for the SIMPER analysis. Roach was caught in highest abundance in managed natural lakes (mean NPUE = $64.7 \pm 71.9 \text{ N} \cdot 100 \text{ m}^{-2}$) and contributed most to the differences relative to managed gravel pit lakes (mean NPUE = $51.7 \pm 73.1 \text{ N} \cdot 100 \text{ m}^{-2}$; contribution to difference = 28%), unmanaged natural lakes (mean NPUE = $32.6 \pm 25.7 \text{ N} \cdot 100 \text{ m}^{-2}$; contribution to difference = 22.7%) and unmanaged gravel pit lakes (mean NPUE = $40.6 \pm 68.6 \text{ N} \cdot 100 \text{ m}^{-2}$; contribution to difference = 28.2%). Perch was more important for the differences between managed gravel pit lakes (mean NPUE = $63.5 \pm 60.4 \text{ N} \cdot 100 \text{ m}^{-2}$) and unmanaged natural lakes (mean NPUE = $20.7 \pm 42.4 \text{ N} \cdot 100 \text{ m}^{-2}$; contribution to difference = 31.3%), between managed

TABLE 2 Frequency of occurrence (%) of all 30 fish species sampled by littoral electrofishing and multimesh gillnetting in the lake types studied

Common name	Scientific name	Managed gravel pit lakes (N = 37)	Managed natural lakes (N = 10)	Unmanaged gravel pit lakes (N = 13)	Unmanaged natural lakes (N = 6)
Perch ^a	<i>Perca fluviatilis</i> L., 1758	100.0	80.0	46.2	50.0
Roach	<i>Rutilus rutilus</i> (L., 1758)	100.0	80.0	38.5	83.3
Eel ^a	<i>Anguilla anguilla</i> (L., 1758)	94.6	70.0	30.8	16.7
Pike ^a	<i>Esox lucius</i> (L., 1758)	94.6	90.0	30.8	83.3
Tench	<i>Tinca tinca</i> (L., 1758)	81.1	90.0	15.4	100.0
Bream	<i>Abramis brama</i> (L., 1758)	75.7	50.0	15.4	33.3
Rudd	<i>Scardinius erythrophthalmus</i> (L., 1758)	67.6	90.0	38.5	83.3
Ruffe	<i>Gymnocephalus cernua</i> (L., 1758)	54.1	60.0	7.7	33.3
Pikeperch ^a	<i>Sander lucioperca</i> (L., 1758)	48.6	30.0	15.4	0.0
White bream	<i>Blicca bjoerkna</i> (L., 1758)	45.9	70.0	15.4	33.3
Common carp	<i>Cyprinus carpio</i> L., 1758	45.9	20.0	38.5	0.0
Sunbleak	<i>Leucaspis delineatus</i> (Heckel, 1843)	16.2	60.0	30.8	16.7
Prussian carp	<i>Carassius gibelio</i> (Bloch, 1782)	13.5	0.0	23.1	0.0
Gudgeon	<i>Gobio gobio</i> (L., 1758)	10.8	20.0	30.8	0.0
Spined loach	<i>Cobitis taenia</i> (L., 1758)	8.1	10.0	7.7	0.0
European catfish ^a	<i>Silurus glanis</i> (L., 1758)	8.1	10.0	7.7	0.0
Ide	<i>Leuciscus idus</i> (L., 1758)	5.4	0.0	0.0	0.0
Bitterling	<i>Rhodeus amarus</i> (Bloch, 1782)	5.4	20.0	0.0	0.0
Chub	<i>Squalius cephalus</i> (L., 1758)	5.4	0.0	0.0	0.0
Bleak	<i>Alburnus alburnus</i> (L., 1758)	5.4	50.0	0.0	16.7
Topmouth gudgeon ^b	<i>Pseudorasbora parva</i> (Temminck & Schlegel, 1846)	2.7	0.0	7.7	0.0
Three-spined stickleback	<i>Gasterosteus aculeatus</i> (L., 1758)	2.7	0.0	0.0	0.0
Crucian carp	<i>Carassius carassius</i> (L., 1758)	2.7	40.0	0.0	50.0
European whitefish	<i>Coregonus lavaretus</i> (L., 1758)	2.7	0.0	0.0	0.0
Vendace	<i>Coregonus albula</i> (L., 1758)	2.7	0.0	0.0	0.0
Sterlet sturgeon	<i>Acipenser ruthenus</i> L., 1758	2.7	0.0	0.0	0.0
Stone loach	<i>Barbatula barbatula</i> (L., 1758)	0.0	0.0	7.7	0.0
Brown bullhead ^{a,b}	<i>Ameiurus nebulosus</i> (Lesueur, 1819)	0.0	0.0	7.7	0.0
Ninespine stickleback	<i>Pungitius pungitius</i> (L., 1758)	0.0	0.0	23.1	0.0
Rainbow trout ^{a,b}	<i>Oncorhynchus mykiss</i> (Walbaum, 1792)	0.0	10.0	0.0	0.0

^aPiscivorous species (perch >15 cm total length [TL] and eel >50 cm TL were classified piscivorous).

^bNon-native species.

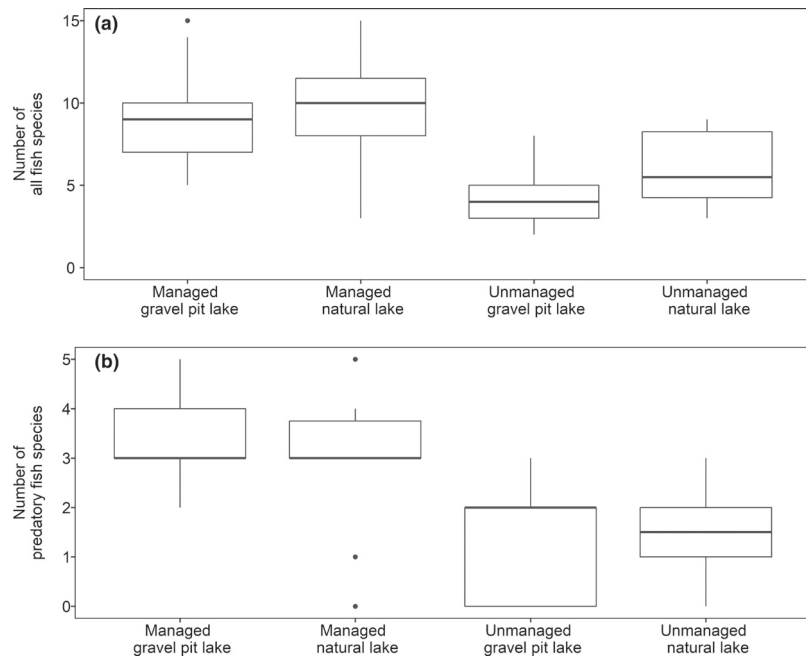
gravel pit lakes and unmanaged gravel pit lakes (mean NPUE $49.2 \pm 70.1 \text{ N} \cdot 100 \text{ m}^{-2}$; contribution to difference = 34%), and between unmanaged natural lakes and unmanaged gravel pit lakes (contribution to difference = 25.3%).

4 | DISCUSSION

We found fish communities in small lakes in northern Germany to be influenced by traces of fisheries management, lake genesis and nutrient level. By contrast, we found no impact of lake size, lake depth, SDF or pH value variation among lakes on fish communities, probably

because the gradients of these variables in the small lakes that we examined were insufficiently large to exert impacts. Supporting our first hypothesis, we found that fisheries management enhanced local fish diversity (α -diversity) in both natural lakes and gravel pit lakes, but did not significantly affect among-lake variability in fish community composition (β -diversity) compared to unmanaged natural lakes as reference. Support for the second hypothesis was mixed. We expected species richness to be lower in unmanaged gravel pit lakes than in unmanaged natural lakes as a result of the shorter colonisation time of gravel pit lakes. However, we detected no differences in species richness (i.e., α -diversity) between unmanaged lakes of both genesis types. By contrast, and in line with the second hypothesis, the

FIGURE 2 Boxplots of total fish species richness (a) and number of predatory species (b) for gravel pit lakes and natural lakes with and without fisheries management. Results from pairwise comparison are presented in Table 3.



β -diversity of the littoral fish communities in unmanaged gravel pit lakes was significantly higher than in all other three lake types, indicating greater stochasticity in fish species colonisation and establishment in unmanaged gravel pit lakes. No such differences among the two unmanaged lake types were found for the benthic fish communities, probably because the electrofishing captured a greater diversity of species (Diekmann et al., 2005; Mueller et al., 2017) increasing statistical power to detect richness-based community differences.

4.1 | Impact of lake genesis on fish communities

Natural lakes in the north German lowlands resulted from the last ice age that ended roughly 10,000 years ago (Håkanson, 2012). By contrast, gravel pit lakes in the same region and in other European areas are relatively young, most of them being created during the last century (Matern et al., 2019; Seelen et al., 2021; Søndergaard et al., 2018; Zhao et al., 2016). Hence, the impact of lake genesis on β -diversity, as evidenced from higher β -diversity in the unmanaged gravel pit lakes relative to the unmanaged natural lakes, probably was caused by differences in lake age. Furthermore, the number of species colonising a lake rises with lake age (Barbour & Brown, 1974; Peel et al., 2019). Hence, the high variation in fish community composition in newly created unmanaged gravel pit lakes most probably resulted from the stochastic colonisation process as evidenced by presence of small-bodied pioneer species, such as sunbleak and ninespine stickleback (Gozlan et al., 2003; Merilä, 2013; Mobley et al., 2011) and highly variable (among lakes), yet overall species-poor community composition. Importantly, the colonisation process

of unmanaged gravel pit lakes is influenced not only by stochastic natural colonisation, but also by human assistance, specifically illegal stocking, which also shares stochastic elements (Matern et al., 2019; for details see below). The probabilities for both colonisation processes rise with time (lake age) even in relatively young gravel pit lakes. Accordingly, we detected fish in all of our isolated gravel pit lakes (mean age of available data: 29 ± 12 years), whereas other isolated gravel pit lakes with an age of only a few years that were rarely covered in our study sometimes host no fish species at all (Søndergaard et al., 2018; Werneke et al., 2018). Both processes—natural and anthropogenic colonisation—can further create stronger variation in fish communities among different unmanaged gravel pit lakes, whereas fisheries management with regular stocking tends to homogenise communities (Matern et al., 2019).

4.2 | Impact of fisheries management on fish communities

We detected higher species richness (α -diversity) and greater numbers of predatory species in managed lakes compared to unmanaged lakes. Many of these predatory fish species are popular targets of anglers (Donaldson et al., 2011) and, therefore, typically introduced and stocked in managed lakes (Arlinghaus et al., 2015; Cucherousset et al., 2021). We found typical central European lake fish species such as roach, perch, pike, rudd and tench to occur frequently in all managed lakes as well as unmanaged natural lakes, with very few traces of non-native fishes. By contrast, none of the mentioned native fish species were found in more than half of the unmanaged

Comparison	Variable	Diff	<i>p</i> .adj
Managed natural lake vs. Managed gravel pit lake	Total fish species richness	0.473	0.955
Unmanaged gravel pit lake vs. Managed gravel pit lake	Total fish species richness	-4.642	0.000
Unmanaged natural lake vs. Managed gravel pit lake	Total fish species richness	-3.027	0.046
Unmanaged gravel pit lake vs. Managed natural lake	Total fish species richness	-5.115	0.000
Unmanaged natural lake vs. Managed natural lake	Total fish species richness	-3.500	0.051
Unmanaged natural lake vs. Unmanaged gravel pit lake	Total fish species richness	1.615	0.584
Managed natural lake vs. Managed gravel pit lake	Number of predatory species	-0.559	0.347
Unmanaged gravel pit lake vs. Managed gravel pit lake	Number of predatory species	-2.075	0.000
Unmanaged natural lake vs. Managed gravel pit lake	Number of predatory species	-1.959	0.000
Unmanaged gravel pit lake vs. Managed natural lake	Number of predatory species	-1.515	0.002
Unmanaged natural lake vs. Managed natural lake	Number of predatory species	-1.400	0.027
Unmanaged natural lake vs. Unmanaged gravel pit lake	Number of predatory species	0.115	0.995

Note: Significant differences are presented in bold.

Method	Variable	<i>R</i> ² adj	<i>df</i>	AIC	<i>F</i>	Pr (> <i>F</i>)
Electrofishing	Lake genesis	0.0469	1	214.7955	2.1427	0.001
Electrofishing	Fisheries management	0.0594	1	214.8631	1.8421	0.005
Electrofishing	TP	0.0299	1	215.0029	3.0004	0.015
Multimesh gillnet	Lake genesis	0.0356	1	209.7997	2.0008	0.002
Multimesh gillnet	TP	0.0203	1	209.8642	2.3243	0.010
Multimesh gillnet	Fisheries management	0.0448	1	210.1170	1.5998	0.019

gravel pit lakes, again indicating more sporadic colonisation and establishment. In originally fish-free gravel pit lakes subjected to private fishing rights (as it is common in Germany; Arlinghaus, Müller, et al., 2017), fish stocking regularly is conducted to introduce a fishable stock and maintain captures of popular species (Arlinghaus et al., 2015; Cowx, 1994). In Germany, typical lake fish species stocked by recreational-fisheries managers include predatory species and larger-bodied Cypriniformes, such as tench and carp, but also common baitfish species, such as roach or rudd, and small-bodied non-game fish species for conservation purpose (Arlinghaus et al., 2015; Cucherousset et al., 2021), with some species of those that are introduced establishing self-reproducing populations. Hence, and in line with our findings, lakes managed for fisheries were found to host increased numbers of fish species and predatory species relative to unmanaged lakes, similar to previous findings (Matern et al., 2019; Tammi et al., 2003; Zhao et al., 2016).

We detected eel in all lake types with higher frequencies in managed lakes compared to unmanaged lakes, common carp in 46% of the managed, but also in close to 40% of the unmanaged gravel pit lakes, and a single rainbow trout in a managed natural lake. Given that natural reproduction is sporadic (carp) or absent (eel, rainbow trout, sometimes carp) in isolated still waters in Germany (Souza et al., 2022), all three species strongly depend on continued stocking. Their occurrence in isolated lakes indicates past and ongoing stocking activities. Indeed, all three species are regularly stocked in high abundances and biomasses all over Europe, specifically in angler-managed water bodies (Aas et al., 2018; Arlinghaus et al., 2015; Cucherousset et al., 2021; FAO, 2005) and are, therefore, more likely to occur in managed lakes. However, carp were detected in managed lakes less frequently than expected, which most probably resulted from typical underestimation of this species in fish community sampling gear (Ravn et al., 2019). However, natural recruitment is not

TABLE 3 Results from ANOVA comparisons and subsequent *post hoc* tests of total fish species richness and number of predatory species in natural lakes and gravel pit lakes with and without fisheries management

TABLE 4 Redundancy analysis models after variable selection describing fish communities sampled by electrofishing and multimesh gillnets (TP = Total phosphorus)

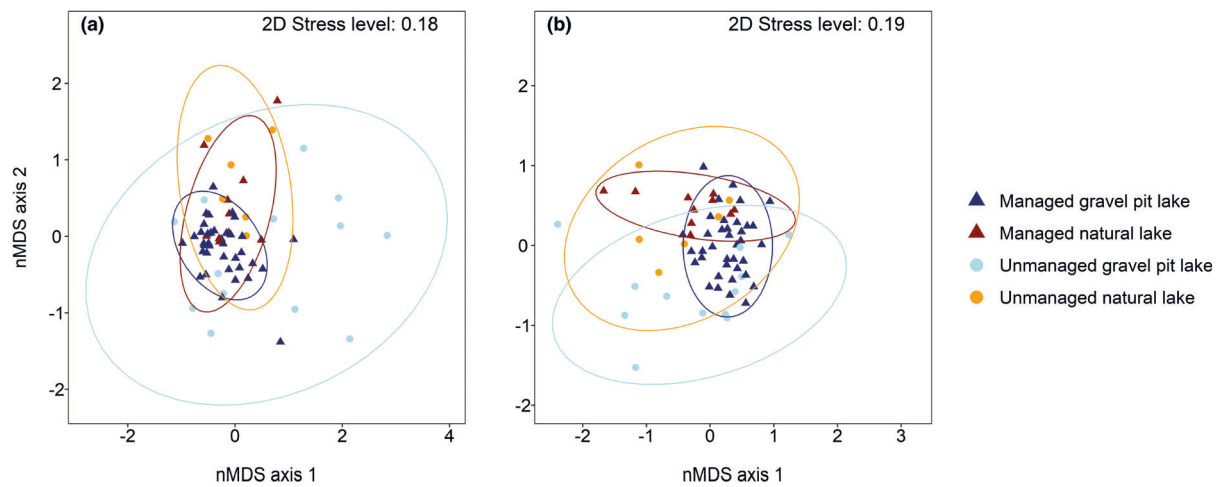


FIGURE 3 Non-metric multidimensional scaling plot of the fish community structure in gravel pit lakes ($n_{\text{managed}} = 37$ and $n_{\text{unmanaged}} = 13$ [electrofishing] and 12 [multimesh gillnetting]) and natural lakes ($n_{\text{managed}} = 10$ and $n_{\text{unmanaged}} = 6$) with (a) displaying the littoral fish community revealed by electrofishing and (b) displaying the benthic fish community revealed by multimesh gillnetting. The ellipses represent the 95% confidence interval.

TABLE 5 Pairwise comparison results from the permutation test to reveal differences in β -diversity between lake types

Comparison	Method	<i>p</i> -value
Managed gravel pit lake vs. Managed natural lake	Electrofishing	0.309
Managed gravel pit lake vs. Unmanaged gravel pit lake	Electrofishing	0.003
Managed gravel pit lake vs. Unmanaged natural lake	Electrofishing	0.666
Managed natural lake vs. Unmanaged gravel pit lake	Electrofishing	0.063
Managed natural lake vs. Unmanaged natural lake	Electrofishing	0.738
Unmanaged gravel pit lake vs. Unmanaged natural lake	Electrofishing	0.016
Managed gravel pit lake vs. Managed natural lake	Multimesh gillnets	0.737
Managed gravel pit lake vs. Unmanaged gravel pit lake	Multimesh gillnets	0.006
Managed gravel pit lake vs. Unmanaged natural lake	Multimesh gillnets	0.203
Managed natural lake vs. Unmanaged gravel pit lake	Multimesh gillnets	0.136
Managed natural lake vs. Unmanaged natural lake	Multimesh gillnets	0.552
Unmanaged gravel pit lake vs. Unmanaged natural lake	Multimesh gillnets	0.427

Note: Significant differences are marked in bold.

consistent for German carp stocks (Souza et al., 2022), which can contribute to the lack of long-term establishment after stocking in managed lakes, especially when recapture rates are high as is commonly observed (Arlinghaus, Hühn, et al., 2017).

We detected only single individuals of three non-native species across the entire set of lakes, even when managed, in agreement with our previous work in the study region (Matern et al., 2019). Of those, only rainbow trout is of fisheries importance and intentionally released. The other two species, brown bullhead and top-mouth gudgeon, usually are unintentionally released when poorly sorted fish from pond aquaculture are stocked (Kinzelbach, 1995; Waterstraat, 2002). Although studies in England and France reported fisheries management and stocking to be associated with the spread of non-native fish species in lakes (Hickley & Chare, 2004;

Skeate et al., 2021; Zhao et al., 2016), we could not detect similar outcomes in our study area. One difference might be that many of those fish established in French gravel pit lakes are warm-water fish, and the spring temperature in northern Germany might not be high enough to guarantee regular recruitment (Souza et al., 2022).

The fish community composition in both managed lake types was surprisingly similar to that found in unmanaged natural lakes. This finding might result from past fisheries management as most lakes in the study area were subjected to fisheries and stocking several decades ago (Anwand, 1973). Alternatively, the finding also might indicate that a similar lake type-specific fish community will establish over very long colonisation periods with the general ecological features of a lake (such as food availability and habitat features as well as predation level) driving the final species composition and

TABLE 6 Results from SIMPER analyses to reveal species-specific abundance effects on the differences in fish community composition between lake types for electrofishing and gillnetting with average abundances (mean CPUE \pm SD)

A vs. B	Electrofishing				Gillnetting			
	Species	Group A	Group B	Cumulative contribution (%)	Species	Group A	Group B	Cumulative contribution (%)
Managed gravel pit lake vs. Unmanaged natural lake	Rudd	6.5 \pm 20.8	98.2 \pm 212.7	37.4	Perch	63.5 \pm 60.4	20.7 \pm 42.4	31.3
	Tench	1.5 \pm 4.8	10.8 \pm 14.5	55.5	Roach	51.7 \pm 73.1	32.6 \pm 25.7	51.8
	Perch	8.8 \pm 9.0	4.3 \pm 5.4	67.8	Rudd	8.5 \pm 31.6	24.0 \pm 28.3	64.4
Managed gravel pit lake vs. Managed natural lake	Rudd	6.5 \pm 20.8	12.0 \pm 17.9	25	Roach	51.7 \pm 73.1	64.7 \pm 71.9	28
	Perch	8.8 \pm 9.0	5.8 \pm 5.7	46.5	Perch	63.5 \pm 60.4	38.7 \pm 35.0	50.8
	Roach	4.7 \pm 10.1	5.3 \pm 11.2	59.2	Sunbleak	22.5 \pm 105.2	85.5 \pm 252.8	66.8
Managed gravel pit lake vs. Unmanaged gravel pit lake	Perch	8.8 \pm 9.0	2.7 \pm 5.2	21.8	Perch	63.5 \pm 60.4	49.2 \pm 70.1	34
	Sunbleak	0.7 \pm 3.1	265.1 \pm 903.7	42.2	Roach	51.7 \pm 73.1	40.6 \pm 68.6	61.1
	Roach	4.7 \pm 10.1	12.2 \pm 29.3	61.2	Rudd	8.5 \pm 31.6	14.2 \pm 27.0	71.5
Unmanaged natural lake vs. Managed natural lake	Rudd	98.2 \pm 212.7	12.0 \pm 17.9	35.1	Roach	32.6 \pm 25.7	64.7 \pm 71.9	22.7
	Tench	10.8 \pm 14.5	7.1 \pm 19.6	52.5	Perch	20.7 \pm 42.4	38.7 \pm 35.0	41.5
	Perch	4.3 \pm 5.4	5.8 \pm 5.7	61.2	Sunbleak	30.7 \pm 75.1	85.5 \pm 252.8	59.8
Unmanaged natural lake vs. Unmanaged gravel pit lake	Rudd	98.2 \pm 212.7	5.1 \pm 10.1	30	Perch	20.7 \pm 42.4	49.2 \pm 70.1	25.3
	Sunbleak	0.3 \pm 0.6	265.1 \pm 903.7	45.6	Roach	32.6 \pm 25.7	40.6 \pm 68.6	47.8
	Tench	10.8 \pm 14.5	0.1 \pm 0.3	60.1	Rudd	24.0 \pm 28.3	14.2 \pm 27.0	61.2
Managed natural lake vs. Unmanaged gravel pit lake	Sunbleak	12.5 \pm 37.7	265.1 \pm 903.7	23.5	Roach	64.7 \pm 71.9	40.6 \pm 68.6	28.2
	Rudd	12.0 \pm 17.9	5.1 \pm 10.1	44.4	Perch	38.7 \pm 35.0	49.2 \pm 70.1	50.6
	Roach	5.3 \pm 11.2	12.2 \pm 29.3	59.5	Sunbleak	85.5 \pm 252.8	12.8 \pm 24.3	65.5

structure. The lack of typically riverine species (e.g., chub or ide) that were obviously occasionally stocked most probably via poorly sorted stocking material, underlined that these species do not form stable populations in lentic water bodies. Such stocking “errors” seemed to self-correct over time and only lentic species ultimately established reproducing populations in gravel pit lakes. Our finding of only minor traces of non-native or ecologically maladapted fish also implies that German fisheries managers rely mainly on native fishes for their stocking programme, in line with legal requirements (Arlinghaus et al., 2015).

β -diversity in managed lakes of both genesis types was particularly low, indicating faunal homogenisation in response to fisheries management (Matern et al., 2019). This finding agrees with previous work describing homogenised fish communities in lakes as a result of fish stocking across the temperate zone (Olden et al., 2006; Rahel, 2002; Villéger et al., 2011) and especially underlines the importance of translocated native species for faunal homogenisation (Sommerwerk et al., 2017). By contrast, unmanaged gravel pit lakes revealed the highest β -diversity of all lake types studied. Their littoral fish communities lacked typical lake fish species and were species-poor. The higher β -diversity and highly variable fish community composition in unmanaged gravel pit lakes indicate stochastic natural colonisation events, as discussed above. However, in unmanaged gravel pit lakes also traces of past introductions were found, probably via private illegal releases (e.g., golden phenotypes of rudd or carp; Matern et al., 2019). Thus, we conclude that restricting fisheries and the associated planned fish stocking from gravel pit lakes will not guarantee that these lakes remain fish-free in the long term. Natural colonisation processes and in densely populated regions also illegal fish introductions are likely to happen nevertheless. Accordingly, even rare examples of fish-free gravel pit lakes in Germany (Werneke et al., 2018) have later been colonised by fish (Jost Borcherdig, personal communication).

4.3 | Impact of environmental conditions on fish communities

Nutrient concentrations (represented by TP) strongly affected lake fish communities. With increased nutrient levels we found higher fish abundance, especially of Cypriniformes. We also found TP concentrations to be higher in managed natural lakes compared to managed gravel pit lakes, most probably because of their young age and because gravel pit lakes are generally fed by nutrient-poor ground water (Mollema & Antonellini, 2016). Our findings of elevated nutrient levels in natural small lakes relative to gravel pit lakes agrees with previous work in central and northern Europe (Emmrich et al., 2014; Søndergaard et al., 2018). Nutrient level impacts European lake fish communities in two ways. On the one hand, the amount of phosphorus determines productivity and general standing fish biomass in a lake (Downing et al., 1990; Hanson & Leggett, 1982; Lemmens et al., 2018). On the other hand, TP and eutrophication

more generally determine community dominance structure in lakes through effects of turbidity, oxygen concentrations, and availability of zooplankton and benthos. Typically, with increasing trophic state European lake fish communities shift from a dominance of Salmoniformes over Perciformes (particularly perch) to a dominance of Cypriniformes (Jeppesen et al., 2000; Mehner et al., 2005; Persson et al., 1991). In line with these well-established relationships, we found Cypriniformes (mainly roach and tench) to benefit from higher trophic levels, whereas the opposite was true for perch based on our gillnet catches.

We found no significant impact of mean lake depth, lake size, shoreline length, SDF and pH value on lake fish communities in our study, which disagreed with previous work from lakes that reported impacts of these variables on fish diversity and species-specific abundance (Eckmann, 1995; Mehner et al., 2005). However, the gravel pit lakes studied ranged in dimension between 0.7 and 21.2 ha, in mean depth from 0.5 to 13.0 m and were compared with natural lakes of similar morphology. Accordingly, the gradients of morphological lake characteristics were rather narrow in our work, which might explain the lack of discriminatory power.

4.4 | Fish species richness and communities in small lakes

We detected 30 different fish species in small lakes in northern Germany and species richness varied between two and 15 species per lake, which agreed with previous findings from small natural lakes in the same ecoregion of Germany (Eckmann, 1995). Perch, roach and rudd acted as most discriminatory between all four lake types. Perch and roach typically are found in European lakes independent of lake size (Eckmann, 1995; Ritterbusch et al., 2014; Tammi et al., 2003) and are also typically found in European gravel pit lakes (Emmrich et al., 2014; Zhao et al., 2016), with species-specific abundance depending primarily on nutrient level and lake morphology (Jeppesen et al., 2000; Mehner et al., 2005; Persson et al., 1991). Accordingly, in our study perch dominated fish communities in mesotrophic gravel pit lakes, whereas roach were more abundant in eutrophic natural lakes. Alongside large perch, the phytophilic pike is a key predator of mesotrophic lentic water bodies and regularly found all over northern Europe (Craig, 1996). The phytophilic rudd and tench are less widely distributed in northern Europe (Olin et al., 2002; Tammi et al., 2003), but typically found in central European lakes (Emmrich et al., 2014; Ritterbusch et al., 2014). Pike, rudd and tench are also typically found in gravel pit lakes (Emmrich et al., 2014; Matern et al., 2019) with their abundances being strongly bound to the extension of emerged and submerged macrophytes (Lewin et al., 2014; Matern et al., 2021). Overall, we detected typical fish communities in the natural lakes and the fish communities in the gravel pit lakes were similar to those. Although this finding was previously reported for the littoral fish community by Emmrich et al. (2014), our work also includes the benthic fish community. Thus, fish communities from natural lakes can be used as reference for the expected fish

communities that establish in gravel pit lakes after the first assemblage is formed.

4.5 | Study limitations

We used littoral electrofishing and multimesh gillnetting to sample lake fish communities, in line with literature recommendations (Achleitner et al., 2012; Barthelmes & Doering, 1996; Jurajda et al., 2009; Mueller et al., 2017). Šmejkal et al. (2015) recommended the use of larger mesh sizes than the mesh sizes of the experimental gillnets used in the Water Framework Directive (CEN, 2015; maximum 55 mm mesh size) to more effectively sample larger fishes—a recommendation that we also followed albeit with smaller panel lengths than recommended in the cited study. However, these additional larger mesh sizes resulted only in very low additional fish captures. It is possible that larger net dimensions with large mesh sizes are needed to catch larger-bodied fish like large pike or large carp. Alternatively, those body sizes may be relatively rare in exploited gravel pit lakes. A potential underestimation of large specimens, however, would affect all lakes similarly, so our key results on the comparison of lakes following the impact of fisheries management and lake genesis should be robust.

We found no differences in fish community composition between managed lakes and unmanaged natural lakes. This might indicate a lack of impact of fisheries management on established fish communities, yet we cannot exclude that the unmanaged natural lakes in our analysis had faced a former management history prior to German reunification. The unmanaged natural lakes that we sampled have been protected by nature conservation regulations and projects, which took place after German reunification in 1989. However, in the former German Democratic Republic, where these lakes are located, almost all available waters were subjected to fisheries management and fish production (Anwand, 1973). Therefore, we cannot exclude past human influences on the fish community structure in contemporarily unmanaged natural lakes. However, we could not detect signs of contemporary stocking (e.g., non-native fishes or carp) and there was a tendency for unmanaged lakes to be species-poorer and more variable in composition than managed lakes. The unmanaged lakes that we sampled represent the best sample of unmanaged natural lakes in our study area and our results therefore should be as unbiased as possible.

Fish species survival after introduction, reproduction, population dynamics and ultimately abundance are strongly governed by local environmental conditions (Anas & Mandrak, 2021; Mehner & Brucet, 2022). Combining data from different projects for this study led to a reduced dataset of environmental variables. We used the variables TP and mean lake depth as surrogates to display information on lake productivity and morphology, which further effect mixing regime and oxygen depletion. TP and mean lake depth have been found to be key indicators on fish productivity and community composition (Downing et al., 1990; Mehner et al., 2005) and therefore should lead to robust results. We were, however, lacking

information on littoral habitat characteristics (e.g., macrophyte coverage), which impact species-specific abundance in lakes (Lewin et al., 2014; Matern et al., 2021). However, mean depth and nutrient state specifically are correlated with macrophyte abundance and also water clarity (Søndergaard et al., 2017, 2022), and have been found in cross-lake studies to be decisive determinants of lake fish communities (Diekmann et al., 2005; Jeppesen et al., 2000; Mehner et al., 2005). We further included SDF as a quantitative measurement of available littoral habitat. We thus believe that we have covered the most important co-variates and that the remaining variation in our lake fish assemblage can quite safely be related to the degree of management by fishing clubs.

Spatial separation is a further factor that can lead to changes in the fish community structure, even within the same ecoregion (Mehner et al., 2014). In our study, gravel pit lakes were located in north-western Germany, which is characterised by a low number of natural lakes. Natural lakes from lake-rich north-eastern Germany represented the best comparison possible within the same ecoregion and lowest spatial distances in similar latitudes. Although both lake sets were from the same ecoregion, it is possible that glacial refugia affected the two environments differentially (Griffiths, 2006). However, as we detected the species pool that generally would be expected in Germany, we do not believe that spatial separation strongly affected our results.

5 | CONCLUSIONS AND IMPLICATIONS

By comparing natural lakes and gravel pit lakes in similar ecological conditions and in the same ecoregion (northern German lowlands), our study suggested an impact of lake genesis (via differences in lake age; gravel pit lakes <100 years and natural lakes ~10,000 years) and fisheries management (most probably via regular stocking programmes) on species richness and fish community composition. We found fisheries management to increase fish species richness in both natural and gravel pit lakes. Yet, this human-assisted colonisation did not lead to different fish community compositions in gravel pit lakes compared to managed and unmanaged natural lakes. By contrast, unmanaged gravel pit lakes lacked typical lake fish species and showed large differences in fish community composition among lakes, in particular in the littoral zone. High β -diversity in unmanaged gravel pit lakes indicates an ongoing, rather stochastic colonisation process in novel and isolated ecosystems. Our study suggests that recreational-fisheries management of gravel pit lakes shortens the colonisation process with fishes, resulting in species-rich and naturally composed fish communities that are similar in abundance and richness to (unmanaged and managed) natural lakes. We recommend fisheries and aquatic ecosystem managers to use fish communities in ecologically similar natural lakes as reference communities for planning initial stocking practices in newly created gravel pit lakes. Without initial fish stocking, the colonisation of gravel pit lakes by fish will be slow and stochastic, but all investigated lakes were colonised by fishes and, thus, keeping gravel pit lakes (≥ 1 ha) fish-free in

the long term seems difficult. The resulting, stochastically formed fish communities in unmanaged gravel pit lakes then may radically depart from the conditions expected in unmanaged natural lakes, specifically when influenced by illegal fish releases by private people, without necessarily hosting lower fish biomass (Matern et al., 2019).

Our work has implications for the wider discussion of whether recreational fisheries as activity and recreational-fisheries management more generally negatively shapes biodiversity, including via the management practice of fish stocking (Eby et al., 2006; Lewin et al., 2006; Schafft et al., 2021). Our work shows that in the case of fish species diversity as conservation target, recreational fisheries will increase local fish diversity and “speed up” the colonisation time of newly created gravel pit lakes with native fishes introduced via stocking. However, fishes can negatively impact other taxa via predation (Eby et al., 2006; Lemmens et al., 2013; Schmidt et al., 2021). Yet, in previous studies in the same study area, recreational-fisheries management and stocking in gravel pit lakes did not negatively affect local species richness and the presence of threatened taxa across a wide range of riparian and aquatic taxa (e.g., dragonflies, macrophytes; Nikolaus et al., 2021). However, predation impacts on selected species of zooplankton and macrozoobenthos (not studied by Nikolaus et al., 2021) are still plausible, as the presence of fish repeatedly has been shown to shape composition, size structure and abundance of lower trophic levels in previously fish-free lake ecosystems (Knapp et al., 2001; Lemmens et al., 2015). Some taxa, such as amphibians, are particularly sensitive to fish predation and thus would benefit from fish-free waters (Leu et al., 2009; Schmidt et al., 2021). However, our work showed that fish-free gravel pit lakes are unlikely and the biomass of fish were identical at entirely different species composition in unmanaged and managed gravel pit lakes (Matern et al., 2019). Therefore, and because of the reduced littoral zones, the studied gravel pit lakes seem unsuitable for amphibian conservation. Instead, small temporary ponds and kettle holes constitute superior amphibian habitats as these systems are more likely to remain fish-free (Søndergaard et al., 2005). Such outcomes are unlikely in permanent lake ecosystems that are large enough to attract humans for recreation, such as the gravel pit lakes studied in our work. Such systems may then be managed preferentially to support high local diversity of fishes and recreational fisheries as an ecosystem service.

AUTHOR CONTRIBUTIONS

Conceptualisation: SM, TK, CW and RA; Developing methods: SM, TK, AM, JS, CW and RA; Conducting the research: SM, TK, AM, JS; Data analysis: SM; Data interpretation: SM, TK, CW, RA; Preparation figures & tables: SM; Writing: SM, TK, AM, JS, CW and RA.

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DATA AVAILABILITY STATEMENT

The analysed data are available at the repository “figshare”: <https://doi.org/10.6084/m9.figshare.14958258>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Paper III

Matern S.*, Robichon C.*, Nikolaus R., Monk C., Arlinghaus R.

Deadwood recruitment in gravel pit lakes.

Manuscript

*shared first authorship

Recruitment of coarse woody debris in gravel pit lakes

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Contributions

Sven Matern: conceptualization of the study, data analysis and interpretation, manuscript preparation; Charlotte Robichon: conceptualization of the study, data generation, data analysis and interpretation, manuscript preparation; Robert Nikolaus: conceptualization of the study, data generation, data analysis and interpretation, manuscript editing; Christopher T. Monk: data analysis and interpretation, manuscript editing; Robert Arlinghaus: conceptualization of the study, data interpretation, manuscript preparation, funding.

Abstract

Coarse woody debris (CWD) is an important structural component and habitat in freshwater ecosystems. In natural lakes, CWD accumulates over centuries alongside the succession of littoral tree communities. Newly created aquatic ecosystems, such as gravel pit or quarry lakes, have difficulties in accumulating CWD due to their young age. Additionally, in natural and artificial lakes, CWD presence might be negatively affected by shoreline development, where wood is removed to facilitate recreational activities, such as fishing, housing or pleasure boating. To understand the factors affecting CWD recruitment and retention in young man-made ecosystems, we studied 26 gravel pit lakes in Lower Saxony, Germany and assessed the impact of environmental conditions on CWD density, specifically lake

morphology, lake age, wind direction, abundance of riparian trees and the presence or absence of fisheries management. We sampled small and large CWD in the littoral zone of the study lakes using a transect-based approach. Density of CWD was lower in German gravel pit lakes than in natural lakes from the USA. In gravel pit lakes, we detected increasing densities of small CWD with increasing numbers of large trees on the shore and with increasing littoral slopes in lakes managed for recreational fisheries, suggesting that recreational fisheries or other human actions remove wood in shallow water zones. Large CWD density was positively affected by lake age, by the density of large trees on the shore with wind from land and again by steep littoral slopes in lakes managed for recreational fisheries. We recommend recreational fisheries managers to maintain CWD also in shallow littoral zones and increase efforts in outreach to inform anglers about the possible downsides of CWD removal in lakes that are naturally devoid of structural elements such as wood due to their young age.

Keywords: quarry lakes; deadwood; riparian zone; littoral structure; habitat complexity; fisheries management

Introduction

Littoral zones link terrestrial and aquatic ecosystems (Naiman & Décamps, 1997; Schindler & Scheuerell, 2002; Pusey & Arthington, 2003) and provide structural heterogeneity and habitat complexity in aquatic ecosystems (Eadie & Keast, 1984; Kovalenko, Thomaz & Warfe, 2012). In addition to emerged and submerged macrophytes, coarse woody debris (CWD) represents a third littoral structure that can generate suitable habitats for colonization by various species (Sass, 2009; Czarnecka, 2016). Invertebrates, such as Gammaridae and Chironomidae, regularly use CWD, with the highest diversity and biomasses found on highly decayed deadwood (Benke & Wallace, 2003; Smokorowski *et al.*, 2006; Dossi, Leitner & Graf, 2020). Lake fish also use CWD regularly (Lewin, Okun & Mehner, 2004; Lewin *et*

al., 2014; Matern *et al.*, 2021), for purposes such as spawning (Nash, Hendry & Cragg-Hine, 1999; Lawson, Gaeta & Carpenter, 2011), feeding (Czarnecka, Pilotto & Pusch, 2014), and importantly refuging from predation (Newbrey *et al.*, 2005; Roth *et al.*, 2007; Smokorowski & Pratt, 2007; Ahrenstorff, Sass & Helmus, 2009). Hence, CWD abundance and complexity in lentic waters impact fishes' abundance, spatial distribution and feeding ecology (Newbrey *et al.*, 2005; Ahrenstorff *et al.*, 2009; Sass *et al.*, 2012; Matern *et al.*, 2021).

Gravel pit lakes, also known as quarry lakes, are created through anthropogenic excavation of littoral resources such as sand or gravel (Soni, Mishra & Singh, 2014; Blanchette & Lund, 2016; Mollema & Antonellini, 2016). In regions with a sparse abundance of natural lakes, gravel pit lakes dominate the lake landscape and can constitute the most frequent lentic water body type (Søndergaard *et al.*, 2018; Nikolaus *et al.*, 2020; Seelen *et al.*, 2021b). Novel lake ecosystems, such as gravel pit lakes, are quickly colonized by organisms and can act as important secondary habitats for biodiversity conservation in agriculture-dominated landscapes (Santoul, Figuerola & Green, 2004; Rey-Boissezon & Joye, 2012; Biggs, Fumetti & Kelly-Quinn, 2017; Nikolaus *et al.*, 2021). However, due to the young age of less than 100 years (Søndergaard *et al.*, 2018; Matern *et al.*, 2019; Seelen *et al.*, 2021b), the colonization and succession of the gravel pit lakes is ongoing (Müllerová, Řehouňková & Prach, 2022). The density and complexity of CWD densities can thus be expected to be lower than in natural lakes, because CWD in lakes is known to accumulate over time, typically remaining in lakes for several centuries depending on the type of tree and branch complexity and density (Guyette & Cole, 1999).

The recruitment of CWD has been intensively studied in rivers (Naiman *et al.*, 2002; Gregory, Boyer & Gurnell, 2003; Comiti, Lucía & Rickenmann, 2016), not only because it is an important fish habitat in lotic systems (e.g. Whiteway *et al.*, 2010; Roni *et al.*, 2015), but also because the presence of deadwood is associated with various impacts and hazards, such as

floodings and blocking of waterways (e.g. Gurnell, Gregory & Petts, 1995; Wohl *et al.*, 2016). By contrast, few studies have focused on CWD recruitment in natural lakes (e.g. Christensen *et al.*, 1996; Marburg, Turner & Kratz, 2006) and none exists for gravel pit lakes. Lake size, littoral water depth, riparian tree density, wind intensity, beaver presence and human-induced shoreline development have all been identified as relevant factors impacting CWD recruitment, abundance and complexity in lentic ecosystems (Christensen *et al.*, 1996; Mallory *et al.*, 2000; Bozek, 2001; Marburg *et al.*, 2006; Sass, 2009). In this context, residential development and other human actions, such as fishing site construction, have been reported to reduce CWD density in North American lakes (Christensen *et al.*, 1996; Marburg *et al.*, 2006). As many gravel pit lakes in Germany are intensively used by humans (Meyerhoff, Klefoth & Arlinghaus, 2019), it is possible that CWD density is negatively affected by both - the young age of man-made lakes and by shoreline development actions.

Many gravel pit lakes in Europe are managed by and for recreational fisheries (Arlinghaus *et al.*, 2015; Zhao *et al.*, 2016; Seelen *et al.*, 2021a; Umweltbundesamt, 2021). Fisheries management, in particular stocking activities, have been found to foster fish species richness in gravel pit lakes relative to unmanaged lakes (Matern *et al.*, 2019, 2022), to contribute to regional fish species homogenization (Matern *et al.*, 2019) and in some countries establishment of non-native species (Zhao *et al.*, 2016). However, in northwestern Germany, fish communities in angler-managed gravel pit lakes have been found to be similar to the fish communities present in natural lakes (Emmrich *et al.*, 2014; Matern *et al.*, 2022). In addition to stocking, the intensive use of nearshore habitats by anglers and other recreationists can negatively affect littoral wildlife and change the habitat quality of the littoral zone (O'Toole, Hanson & Cooke, 2009; Kaufmann *et al.*, 2014b; Meyer *et al.*, 2021; Schafft *et al.*, 2021; Nikolaus *et al.*, 2022). As angling activities are often shore-bound, it is also possible that anglers, or fishing clubs more generally, remove CWD to clean shorelines in an attempt to

reduce the potential for snagging of fishing lines or hooks. One indication for such effects would be a greater accumulation of CWD in steeper sloped shorelines where shoreline anglers have less access to sunk CWS than in shallower shorelines.

The objective of this study was to investigate the CWD recruitment in the littoral zones of 26 gravel pit lakes in Lower Saxony, Germany. We tested three hypotheses: 1) the CWD density in the littoral zone of gravel pit lakes is positively influenced by lake size, lake age and riparian tree abundance, especially with wind exposure; 2) the presence of recreational-fisheries management negatively influences the amount of CWD, especially in shallow areas due to CWD removal as management action for improved angling access; and 3) due to their young age CWD density in gravel pit lakes is lower than in natural lakes.

Methods

Sampling locations and management of the lakes

All 26 sampled gravel pit lakes were located in Lower Saxony, Germany (Table 1) with 16 gravel pit lakes managed by angling clubs and ten unmanaged gravel pit lakes owned by private persons or nature conservation agencies (Appendix Table 1). Angling clubs buy or rent the fishing rights of gravel pit lakes often during or shortly after the excavation process. Subsequent utilization and management encompass: introductory fish stocking with a desired native species mix (Matern *et al.*, 2019), recreational angling including harvest regulations (e.g. minimum-length and daily bag limits) (Arlinghaus *et al.*, 2016) and habitat management (e.g. creating angling sites or deadwood supplement for fish) (Arlinghaus & Mehner, 2005; Sass, 2009). In the unmanaged lakes recreational fishing was prohibited and the lakes did not receive initial fish stocking or shoreline development to create fishing sites. However, the vast

majority of our gravel pit lakes were accessible to the public, and recreational visitors (e.g. walkers and dog walkers) were documented at all lakes.

Data collection

We sampled littoral CWD abundance and environmental variables in each lake either during June and July 2017 or August 2018 at multiple transects per lake, following two approaches: 1) for all lakes, prior to sampling, the location for the first transect was chosen randomly and subsequently other transects were placed equidistantly along the whole shoreline. Distances between sampling points were constant within each lake and varied between 100 and 200 m depending on lake size; 2) in eight of the studied lakes, additional transects were placed randomly within the lake (six to nine per lake) based on objectives in other studies not reported here. Thus, mainly due to variation in lake size but also due to the additional transects sampled, the number of transects varied across lakes. We kept the additionally sampled transects in the data set to increase the sample size of transects. We divided each transect into a riparian zone plot and littoral zone plot (Figure 2). The riparian plot measured 10 x 10 m and all trees were counted and classified into three height categories (<3 m, 3-10 m and >10 m). The littoral zone plot measured 6 m in width and was investigated to a maximum water depth of 3 m, in cases of shallow zones plot length was set to maximum 10 m. In the six lakes investigated in August 2018 the littoral zone plot measured only 2 m in width because of sampling time constraints. Water depth after every meter was measured with a tape measure attached to a stick to calculate the littoral slope. The total length of the littoral plot was noted to calculate the size of the littoral plot. We assessed all CWD structures including tiny sticks (Figure 3) by snorkeling. We defined three criteria for CWD classification: 1) CWD length ≥ 50 cm; 2) CWD diameter ≥ 5 cm and 3) complexity ≥ 2 . Complexity was determined according to the maximum number of branch orders (1 = main trunk / 1st order branch; 2 = 2nd order branch; 3 = 3rd order branch; 4 = 4th order branch and 5 = 5th order

branch; following Newbrey *et al.* (2005)). Each CWD structure that fulfilled at least two of the three criteria was classified as large CWD and measured in detail (length, diameter, complexity and percentage of submersion). All other CWD structures were classified as small CWD and their length was noted.

We measured lake area using QGIS (QGIS Development Team, 2019) and used contour maps to extract information on mean and maximum lake depth (compare Matern *et al.*, 2019; Nikolaus *et al.*, 2021). We measured pH value, Secchi depth at the water surface in the middle of the lake and took a water sample to analyze total phosphorus concentration in the lab (ISO, 2004). With respect to lake age, either the start of excavation and the end of excavation could be chosen to calculate the age of gravel pit lakes. For this study, we used the end of excavation to ensure that all sampling locations within each lake already existed. The share of wood within 100 m around each lake (buffer zone) was calculated in QGIS 3.4.1 with GRASS 7.4.2 using ATKIS® land use data with a 10 x 10 meter grid scale (© GeoBasis-DE/BKG 2013; AdV - Working Committee of the Surveying Authorities of the States of the Federal Republic of Germany, 2006). We used the ATKIS®-objects categorized as forest (economically) and wood (naturally) which included six object-categories.

The general wind direction at each lake was calculated using data from the DWD (Deutscher Wetterdienst, www.dwd.de; DWD Climate Data Center (CDC), 2018), which provides historical station observations at 10 minutes interval for Germany. We used data running from 2015 to 2017 to have a measure of wind direction representing multiple years before this study. For each lake, we used the data of the nearest meteorological station (mean distance \pm SD: 22.1 \pm 10.3 km). Wind directions were categorized according to the eight cardinal and ordinal directions. To break branches off trees, a wind power of 8 Beaufort or higher is needed (Deutscher Wetterdienst, www.dwd.de), and we therefore considered the most occurring wind direction with a power of 8 Beaufort or higher as the general wind direction

for each lake. For each plot, the wind exposure was assessed by calculating the angle ($^{\circ}$) between the general wind direction and the shoreline of the plot (0° ; 45° ; 90° ; -45° ; -90°). Positive values indicate wind coming from land (90° being orthogonal to the shoreline) and negative value indicate wind coming from water (-90° being orthogonal to the shoreline). An angle of 0° indicates wind parallel to the shoreline.

Data analysis

We calculated the density of small and large CWD per area ($N\ m^{-2}$) of each littoral plot. We tested all environmental variables (lake area, lake age, wind direction, 100 m wood buffer around the lake, littoral slope of the plot, transect water depth, density of small riparian trees, density of medium-sized riparian trees, density of tall riparian trees and density of all riparian trees) for collinearity using a stepwise Variance Inflation Factor (VIF) selection. Based on the results from the VIF ($VIF > 5$), we removed the following variables: transect water depth, density of small riparian trees and density of all riparian trees from the further analysis. We ran two linear mixed effects models to predict the number of small and large CWD separately as a function of lake age, wind direction, 100 m wood buffer around the lake, density of medium-sized riparian trees, density of tall riparian trees, littoral slope of the plot and fisheries management (present/absent) by offsetting log transformed littoral sampling area and using the package *glmmTMB* with negative binomial distribution: linear parameterization as family (version 1.0.1; Brooks *et al.*, 2017). We also included interaction effects between density of medium-sized riparian trees and wind direction, density of tall riparian trees and wind direction and the littoral slope of the plot and management in both models to test hypothesis 1) and 2), and used lake as random factor to avoid the pseudo replication of transects within lakes. We used the ‘AICstep’ function from the package *MASS* for model selection (version 7.3-51.4; Venables & Ripley (2002)). All statistical analyses were conducted using the software R 3.6.2 (R Core Team, 2019).

We compared CWD densities in gravel pit lakes and natural lakes by extracting data on CWD densities (defined by a bole diameter ≥ 5 cm) in natural lakes in Northern Wisconsin and Upper Michigan, USA from Christensen *et al.* (1996) and CWD densities (defined by a bole diameter ≥ 10 cm) in natural lakes in Ontario, Canada from Pearce, Mallory & Smokorowski (2022). No data were available from German natural lakes. We included all large CWD structures from the sampled gravel pit lakes with matching bole diameter definitions to achieve a comparable data sets and compared CWD densities by using a non-parametric Wilcoxon-test (Wilcoxon, 1945).

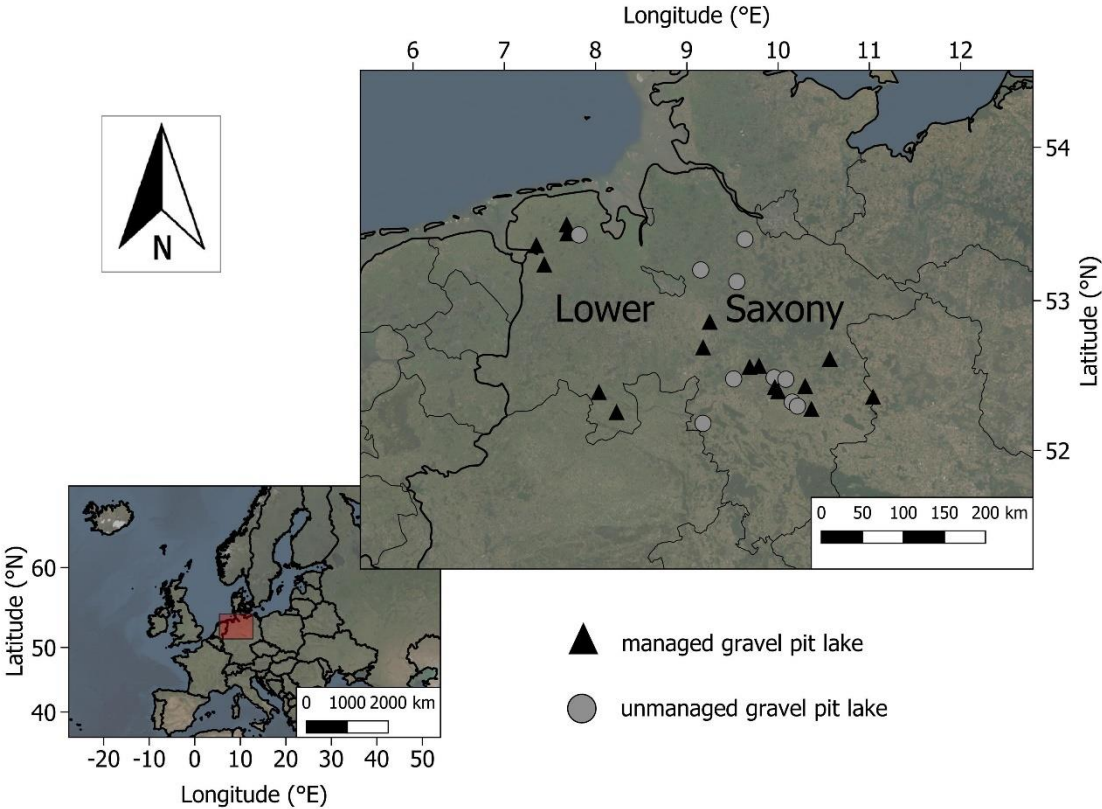


Figure 1: Map of all sampled gravel pit lakes in Lower Saxony, Germany.

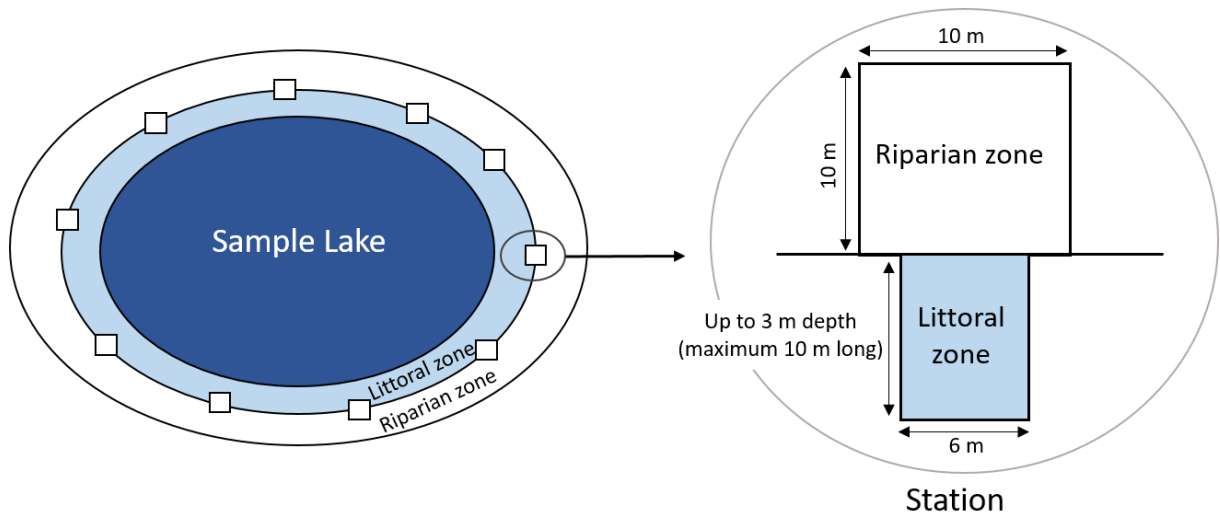


Figure 2: Sampling design adapted and modified after Newbrey *et al.* (2005) and Kaufmann *et al.* (2014a). In 2018 the width of the littoral zone plot was reduced to two meters due to time constraints.

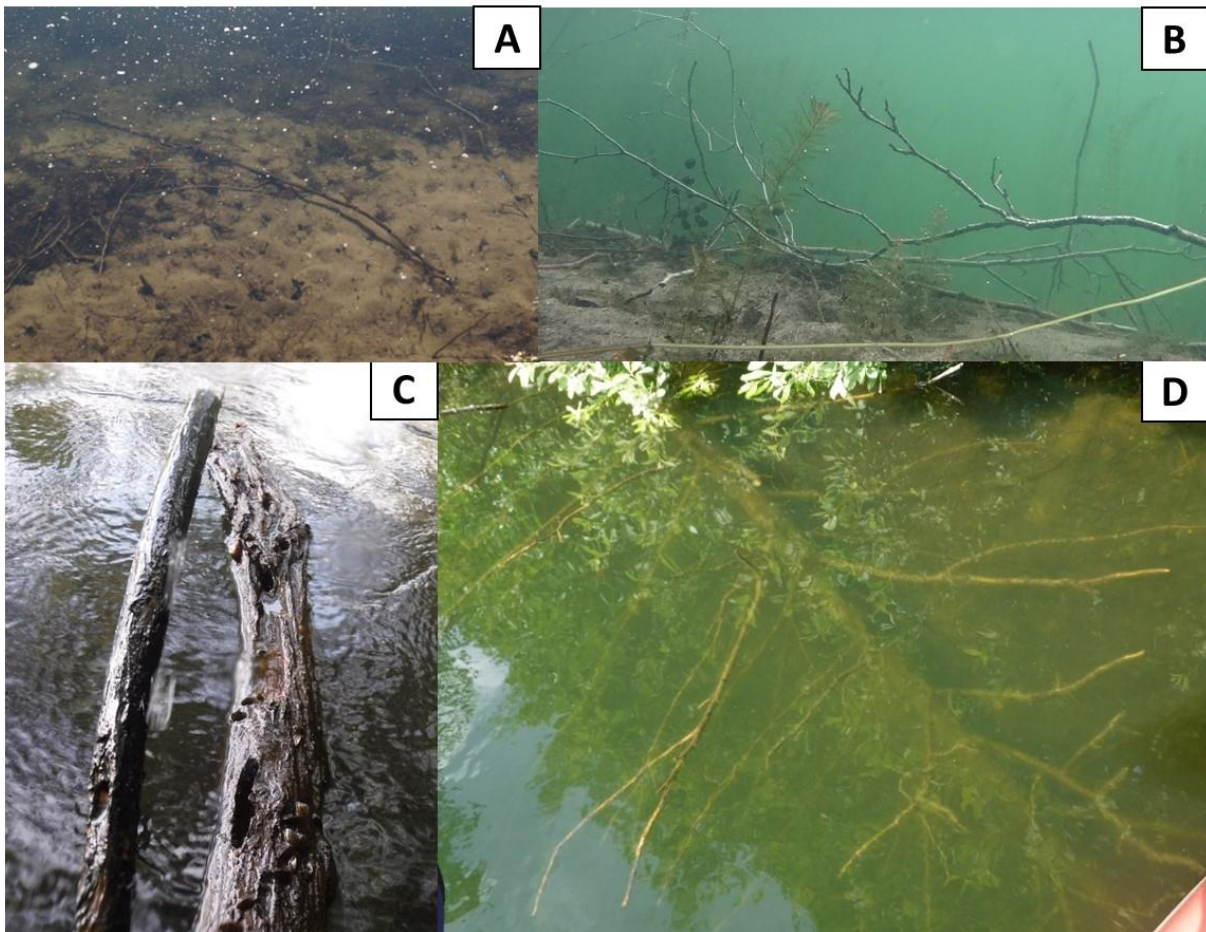


Figure 3: Diversity of coarse woody debris (CWD) structures in gravel pit lakes: (A) and (B) small CWD, (C) and (D) large CWD.

Results

Lake environments and CWD abundance

The sampled gravel pit lakes varied in size between 0.9 ha and 19.5 ha (mean \pm SD: 6.5 ± 5.2 ha) with a mean lake depth between 0.6 and 11.9 m (mean \pm SD: 4.6 ± 2.5 m; Table 1). The gravel pit lakes were on average mesotrophic with a total phosphorus concentration of $29.9 \pm 30.6 \mu\text{g l}^{-1}$ (mean \pm SD) and a Secchi depth of 2.7 ± 1.5 m (mean \pm SD). The age of the gravel pit lakes ranged from seven to 55 years (mean \pm SD: 27.5 ± 13.2 years). The slope of the littoral plot varied between 1.1° and 40.6° on transect level and 4.8° and 27.2° on lake level. The 100 m wood buffer around the lakes varied between 0 % and 72.6 % (mean \pm SD: 16.1 ± 21.5 %; Table 2). The density of medium-sized riparian trees was $0.06 \pm 0.05 \text{ N m}^{-2}$ (mean \pm SD) and ranged from 0.01 to 0.25 N m^{-2} on lake level, while the density of tall riparian trees was $0.05 \pm 0.04 \text{ N m}^{-2}$ (mean \pm SD) and ranged from 0 to 0.21 N m^{-2} on lake level.

We detected 12,160 small CWD structures distributed over all gravel pit lakes with 259 out of 291 transects containing small CWD structures. 4,012 of the 'small CWD' structures (33.0 %) measured between 1 and 20 cm, 4,791 small CWD structures (39.4 %) measured between 21 and 50 cm and 3,357 small CWD structures (27.6 %) were longer than 50 cm. The density of small CWD was $1.47 \pm 1.77 \text{ N m}^{-2}$ (mean \pm SD) and ranged from 0.17 to 6.18 N m^{-2} in the gravel pit lakes. We further found 620 large CWD structures distributed over all gravel pit lakes and in 193 out of 291 sampled transects. Large CWD structures measured 181 ± 149 cm (mean \pm SD) in length with a bole diameter of 4.8 ± 6.9 cm (mean \pm SD). The complexity of the large CWD structures was 2.5 ± 1.3 (mean \pm SD) with 93.0 ± 16.4 % (mean \pm SD) being

submerged. The density of large CWD was $0.07 \pm 0.10 \text{ N m}^{-2}$ (mean \pm SD) and ranged from 0.004 to 0.53 N m^{-2} in the gravel pit lakes.

Predictors of CWD recruitment

For both models no variables were dropped after model selection (Table 3 and Table 4). We detected large CWD density in gravel pit lakes to be significantly affected by lake age ($p = 0.049$) and the interaction of littoral slope and management ($p < 0.001$, Table 3). Densities of large CWD increased with lake age, and in managed lakes large CWD densities increased with increasing littoral slope, while large CWD densities in unmanaged lakes were not affected by littoral slope (Figure 4). Furthermore, large CWD densities were positively affected by tall trees on the shore ($p = 0.06$) and also in interaction with the wind direction ($p = 0.07$, Table 3, Figure 4), however effects were not significant at a significance level of 0.05. Small CWD density in gravel pit lakes was significantly affected by tall trees on the shore ($p < 0.001$) and the interaction of littoral slope and management ($p < 0.001$; Table 4). Densities of small CWD increased with the number of large trees on the shore and similar to large CWD, the density of small CWD increased in managed lakes with increasing littoral slope, while small CWD densities in unmanaged lakes were not affected by littoral slope (Figure 5). Furthermore, and similar to large CWD densities, small CWD densities were positively affected by lake age, but the effect was not significant ($p = 0.09$; Table 4: Model output from the linear mixed effects model predicting densities of small, coarse woody debris (CWD) in gravel pit lakes. Variables with a p value < 0.1 are in bold and variables with a p value < 0.05 are also marked with an asterisk.; Figure 5).

We detected significantly lower densities of CWD structures with a bole diameter ≥ 5 cm in gravel pit lakes in Germany compared to natural lakes in the USA (Wilcoxon-test: $W = 126$, $p = 0.035$) and significantly lower densities of CWD structures with a bole diameter ≥ 10 cm compared to natural lakes in Canada (Wilcoxon-test: $W = 9$, $p < 0.001$, Figure 6).

Table 1: Environmental description of the studied gravel pit lakes.

Lake name	Management	Lake size (ha)	Mean lake depth (m)	Max lake depth (m)	pH value	Secchi depth (m)	Total phosphorus ($\mu\text{g l}^{-1}$)	Lake age (years)	Number of sampled transects	Station slope ($^{\circ}$)	Station wind exposure ($^{\circ}$)
Chodhemster Kolk	managed	3.2	5.6	10.1	8	2.5	14	46	6	12.7 \pm 6.8	7.5 \pm 66.2
Collrunge	managed	4.3	4	8.6	9	2.7	16	35	14	13.7 \pm 4.8	3.2 \pm 64.8
Donner Kiesgrube 3	managed	1	3.3	5.2	7.9	2.1	49	17	13	23.3 \pm 4.2	-6.9 \pm 48.1
Goldbeck	unmanaged	2.3	2.5	5	6.9	0.8	34	26	7	17.1 \pm 4.8	0 \pm 63.6
Handorf	unmanaged	13.6	9.6	23	8.6	4.2	14	14	10	22.2 \pm 5.9	0 \pm 56.1
Hänigsen	unmanaged	6.2	7.7	12.3	8.5	4.1	14	7	10	11.2 \pm 5.7	4.5 \pm 49.5
Heeßel	unmanaged	0.9	3.8	7.4	7.8	3.1	15	55	4	27.2 \pm 11.3	0 \pm 73.5
Hopels	unmanaged	5.5	6.7	14.5	8.3	5.8	10	19	13	13.7 \pm 7.7	3.5 \pm 46.7
Kiesteich Brelingen	managed	8.5	3.2	8.7	8	1.7	22	18	17	17.8 \pm 10.5	13.2 \pm 56.8
Kolshorner Teich	managed	4.3	6.4	16.1	7.7	3.5	14	37	12	23.1 \pm 7.4	0 \pm 54.3
Linner See	managed	17.7	5.1	11.2	8.9	2.1	21	17	20	15.8 \pm 8.8	-6.8 \pm 46.8
Lohmoor	unmanaged	4.1	2.2	7.4	8.6	1.1	62	27	13	13.1 \pm 7.1	-3.5 \pm 53.4
Meitzer See	managed	19.5	11.9	23.5	8.3	5.3	10	11	20	21.1 \pm 6.5	-6.8 \pm 42
Neumanns Kuhle	managed	6.9	3.1	6.2	9.2	0.5	111	47	8	4.8 \pm 2	0 \pm 58.9
Pfütze	unmanaged	10.6	4.3	7.3	8.4	4.5	12	17	13	17.1 \pm 3.4	13.8 \pm 49.9
Plockhorst	managed	14.3	3.2	8.2	8.7	1.3	53	19	12	14.4 \pm 8.4	-11.2 \pm 39
Saalsdorf	managed	9	5.3	9.2	8.4	2.3	27	22	11	20.5 \pm 8.6	8.2 \pm 56.3
Schleptruper See	managed	4	4.9	10.1	8.4	2.1	15	52	6	15.8 \pm 8.9	-7.5 \pm 52.6
Schwicheldt	unmanaged	1.7	4	10	8.1	3.2	10	11	7	13.8 \pm 7.7	19.3 \pm 62.9
Stedorfer Baggersee	managed	1.9	1.7	2.8	8.2	2.2	33	34	5	10 \pm 2.2	-18 \pm 40.2
Steinwedeler Teich	managed	10.4	5.3	9.1	8.2	3.9	16	39	17	24.4 \pm 7.2	2.6 \pm 51.5
Tongrube Bülstedt	unmanaged	2.4	0.6	1.1	9.3	0.2	134	27	9	6.2 \pm 1.6	-10 \pm 70.4
Wahle	managed	8.1	5.9	12.1	8.4	2.5	19	27	13	19.7 \pm 8	6.9 \pm 63.2
Weidekampsee	managed	2.9	2.3	4.3	8.5	4.4	15	23	13	12.8 \pm 3.2	10.4 \pm 55.6
Wiesedermeer	managed	2.9	3.7	9.2	8.3	2.4	18	27	11	13.6 \pm 6.6	-4.1 \pm 51.1
Xella	unmanaged	2.1	3.1	7.3	8.3	0.9	20	42	7	18.8 \pm 7.7	6.4 \pm 48.1

Table 2: Riparian wood and tree descriptors and coarse woody debris (CWD) densities of the studied gravel pit lakes.

Lake name	Trees in a 100 m buffer around the lake (%)	Medium-sized tree density (N m ⁻²)	Tall tree density (N m ⁻²)	Small CWD density (N m ⁻²)	Large CWD density (N m ⁻²)	Total CWD density (N m ⁻²)
Chodhemster Kolk	0	0.02 ± 0.02	0 ± 0	0.16 ± 0.16	0.01 ± 0.01	0.17 ± 0.16
Collrunge	0	0.03 ± 0.03	0.02 ± 0.03	1.01 ± 0.82	0.03 ± 0.05	1.05 ± 0.83
Donner Kiesgrube 3	0	0.08 ± 0.08	0.03 ± 0.04	1.73 ± 1.98	0.07 ± 0.09	1.8 ± 2.05
Goldbeck	5.6	0.02 ± 0.02	0.03 ± 0.03	6.07 ± 3.99	0.11 ± 0.06	6.18 ± 4.01
Handorf	0	0.06 ± 0.07	0.05 ± 0.06	4.1 ± 2.7	0.09 ± 0.13	4.19 ± 2.73
Hänigsen	5.5	0.02 ± 0.05	0.02 ± 0.03	0.71 ± 1.24	0.07 ± 0.09	0.78 ± 1.26
Heeßel	15.4	0.02 ± 0.02	0.02 ± 0.02	5.45 ± 3.03	0.53 ± 0.45	5.98 ± 2.94
Hopels	0	0.15 ± 0.13	0.07 ± 0.04	1.93 ± 1.42	0.05 ± 0.03	1.98 ± 1.41
Kiesteich Brelingen	66.3	0.05 ± 0.05	0.07 ± 0.07	0.3 ± 0.37	0.04 ± 0.05	0.33 ± 0.41
Kolshorner Teich	72.6	0.03 ± 0.03	0.07 ± 0.03	0.39 ± 0.2	0.09 ± 0.09	0.48 ± 0.27
Linner See	11.2	0.06 ± 0.03	0.1 ± 0.1	1.87 ± 1.81	0.05 ± 0.05	1.92 ± 1.81
Lohmoor	0	0.25 ± 0.12	0.02 ± 0.02	0.78 ± 1.4	0.02 ± 0.02	0.79 ± 1.4
Meitzer See	68.4	0.04 ± 0.04	0.08 ± 0.06	0.25 ± 0.47	0.07 ± 0.09	0.32 ± 0.48
Neumanns Kuhle	8.4	0.04 ± 0.03	0.02 ± 0.02	0.21 ± 0.27	0.03 ± 0.04	0.24 ± 0.26
Pfütze	8	0.1 ± 0.04	0.21 ± 0.09	0.43 ± 0.34	0.05 ± 0.05	0.48 ± 0.37
Plockhorst	17.2	0.06 ± 0.07	0.09 ± 0.05	1.66 ± 2.17	0.09 ± 0.11	1.75 ± 2.27
Saalsdorf	5.9	0.03 ± 0.05	0.06 ± 0.06	0.98 ± 1.75	0.08 ± 0.08	1.06 ± 1.8
Schlepstruper See	24.3	0.04 ± 0.03	0.05 ± 0.03	0.61 ± 0.33	0.11 ± 0.06	0.72 ± 0.29
Schwicheldt	24.3	0.03 ± 0.06	0 ± 0	1.32 ± 3.5	0.01 ± 0.04	1.34 ± 3.53
Stedorfer Baggersee	11.9	0.11 ± 0.06	0.01 ± 0.01	0.2 ± 0.17	0.02 ± 0.02	0.23 ± 0.16
Steinwedeler Teich	25.9	0.05 ± 0.02	0.04 ± 0.04	0.39 ± 0.58	0.03 ± 0.03	0.42 ± 0.59
Tongrube Bülstedt	0	0.02 ± 0.02	0.03 ± 0.03	4.58 ± 8.57	0.1 ± 0.12	4.68 ± 8.55
Wahle	9.1	0.01 ± 0.01	0.04 ± 0.02	0.5 ± 0.51	0.03 ± 0.03	0.54 ± 0.51
Weidekampsee	1.7	0.06 ± 0.06	0.1 ± 0.05	0.23 ± 0.38	0.03 ± 0.05	0.26 ± 0.43
Wiesedermeer	29.7	0.06 ± 0.06	0.01 ± 0.02	0.36 ± 0.38	0 ± 0.01	0.36 ± 0.38
Xella	6.3	0.17 ± 0.17	0.05 ± 0.04	0.22 ± 0.19	0.03 ± 0.03	0.25 ± 0.21
Mean	16.1	0.06 ± 0.05	0.05 ± 0.04	1.4 ± 1.49	0.07 ± 0.07	1.47 ± 1.5

Table 3: Model output from the linear mixed effects model predicting densities of large, coarse woody debris (CWD) in gravel pit lakes. Variables with a p value < 0.1 are in bold and variables with a p value < 0.05 are also marked with an asterisk.

	Value	Std.Error	z value	p value
(Intercept)	-5.25986	0.59883	-8.78362	0.00000
Medium-sized tree density	0.01643	1.18111	0.01391	0.98890
Station wind exposure	-0.00296	0.00194	-1.52866	0.12635
Tall tree density	2.26030	1.21540	1.85971	0.06293
Lake size	0.03538	0.03043	1.16277	0.24492
Station slope	0.05440	0.01085	5.01343	0.00000*
Management	1.53213	0.48315	3.17112	0.00152*
Lake age	0.02430	0.01233	1.97027	0.04881*
Trees in a 100 m buffer around the lake	-0.00012	0.00627	-0.01919	0.98469
Medium-sized tree density : Station wind exposure	0.00055	0.01953	0.02797	0.97768
Station wind exposure : Tall tree density	0.03050	0.01689	1.80609	0.07090
Station slope : Management	-0.04994	0.02239	-2.23042	0.02572*

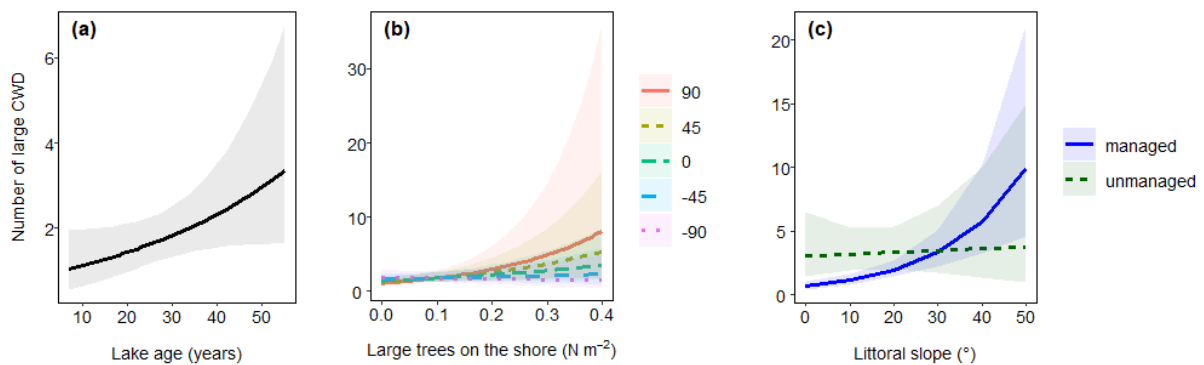


Figure 4: Marginal effect plots for the densities of large, coarse woody debris (CWD) in gravel pit lakes impacted by lake age (a), the interaction of large tree density on the shore and wind direction (b) and the interaction of littoral slope and lake management (c). The shaded region indicates the confidence intervals.

Table 4: Model output from the linear mixed effects model predicting densities of small, coarse woody debris (CWD) in gravel pit lakes. Variables with a p value < 0.1 are in bold and variables with a p value < 0.05 are also marked with an asterisk.

	Value	Std.Error	z value	p value
(Intercept)	-2.482721	0.679202	-3.655348	0.00026
Medium-sized tree density	-0.717571	0.983994	-0.729243	0.46585
Station wind exposure	-0.001389	0.001539	-0.901969	0.36707
Tall tree density	4.555846	0.977813	4.659219	0.00000*
Lake size	0.034892	0.036842	0.947076	0.34360
Station slope	0.062685	0.008368	7.491183	0.00000*
Management	1.897706	0.454250	4.177667	0.00003*
Lake age	0.024861	0.014489	1.715834	0.08619
Trees in a 100 m buffer around the lake	-0.012355	0.007906	-1.562785	0.11810
Medium-sized tree density : Station wind exposure	-0.001733	0.016050	-0.108001	0.91399
Station wind exposure : Tall tree density	0.015211	0.014398	1.056451	0.29076
Station slope : Management	-0.064092	0.016378	-3.913215	0.00009*

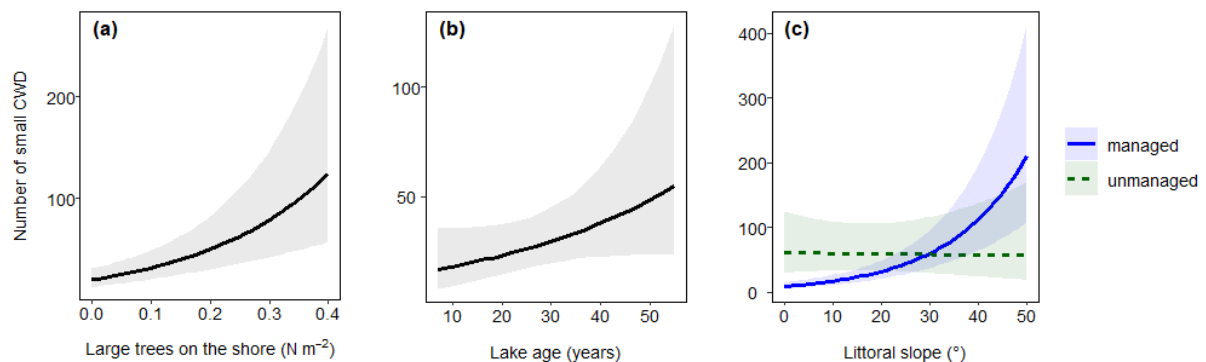


Figure 5: Marginal effect plots for the densities of small, coarse woody debris (CWD) in gravel pit lakes impacted by large tree density on the shore (a), lake age (b) and the interaction of littoral slope and lake management (c). The shaded region indicates the confidence intervals.

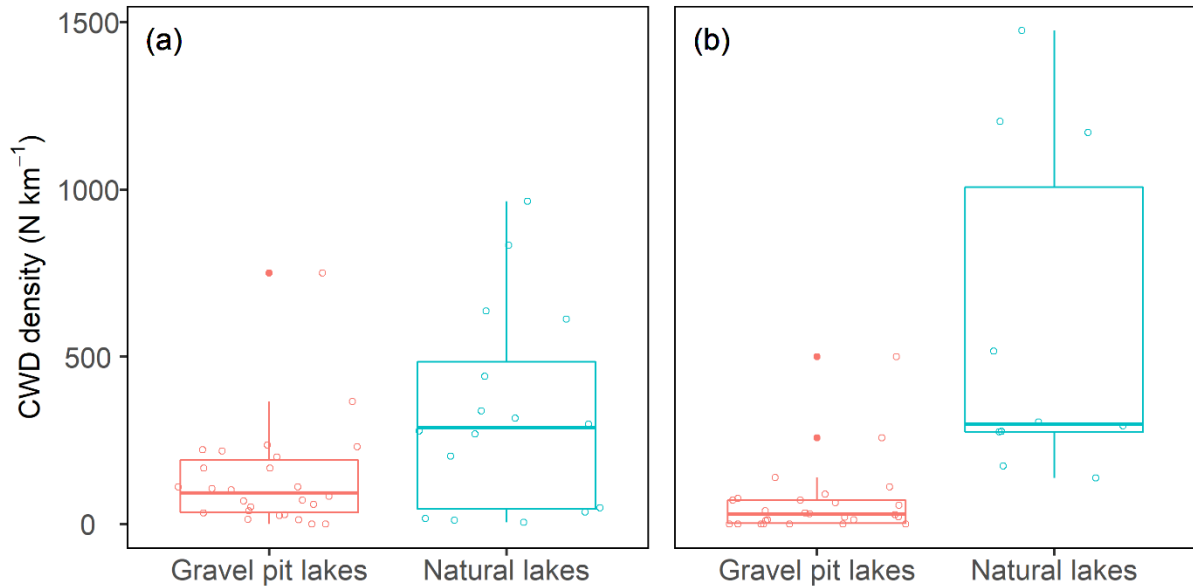


Figure 6: Comparison of coarse woody debris (CWD) densities in gravel pit lakes in Lower Saxony, Germany and (a) natural lakes in Northern Wisconsin and Upper Michigan, USA with a bole diameter ≥ 5 cm (data extracted from Christensen *et al.* (1996)) and (b) natural lakes in Ontario, Canada with a bole diameter ≥ 10 cm (data extracted from Pearce *et al.* (2022)). Boxes represent the 25th to the 75th percentile with the median represented by the thick horizontal line, whiskers display 1.5 times the inter-quantile range and filled dots display outliers. Circles represent the observed data.

Discussion

We studied the recruitment of small and large CWD in gravel pit lakes and found, in agreement with H1, that lake age and the number of tall trees especially with wind exposure to affect CWD densities. We further detected in support of H2 an influence of recreational-fisheries management on CWD with lowest densities in shallow water areas of managed lakes. Finally, and agreeing with H3, CWD densities were significantly lower in German gravel pit lakes compared to natural lakes in Wisconsin and Ontario. Therefore, all three hypotheses received empirical support in our work.

We detected tall trees on the shore as one of the main drivers for CWD densities in gravel pit lakes, especially in combination with wind direction (and power). Broken branches of riparian trees and trees felled by wind are a key source of littoral deadwood in littoral habitats of lakes (Sass, 2009) and expectedly they influence CWD also in gravel pit lakes. Relatedly, forest cover as well as riparian coarse woody debris have been reported to positively affect CWD density in lakes in Wisconsin, USA (Jennings *et al.*, 2003; Marburg *et al.*, 2006). However, our variable of forest cover - wood in a 100 m buffer - did not add significant information to the model, most likely because only trees in the immediate riparian zone contribute to littoral CWD densities. Furthermore, the succession in the riparian zone of gravel pit lakes is often still in progress (Müllerová *et al.*, 2022) and potentially outdated land use data are not useful as descriptor of littoral CWD. In addition to riparian trees, beavers have been identified as a further important source of littoral CWD in lakes and rivers (Sass, 2009). However, we only detected beavers at a single gravel pit lake in our dataset and, therefore, did not integrate this in our analysis. Lake shape has also been revealed as a good predictor of littoral CWD (Marburg *et al.*, 2006), but we did not include lake shape in our analysis as we used a transect-based sampling design and lake shape has only been used as a predictor of whole lake CWD densities (Marburg *et al.*, 2006).

The gravel pit lakes in our study varied in age between seven and 55 years, and as expected we found increased CWD densities with increasing lake age, most likely because an older age allows trees to develop and branches and other structures to occasionally die off and fall into the lake. In line with this argument, we detected significantly higher CWD densities in natural lakes in North America that already exist for more than 10.000 years (Mandrak & Crossman, 1992) compared to the relatively young gravel pit lakes. Both findings demonstrate the effect of lake age on littoral CWD densities. Gravel pit lakes are free of CWD recently after their excavation and CWD must accumulate in gravel pit lakes (over time) through riparian

vegetation. In North American lakes wood input rates ranged from 0.5 to 1.9 logs km⁻¹ year⁻¹ (Marburg *et al.*, 2009) with retention times of up to several centuries (Guyette & Cole, 1999). Similar to aquatic systems, studies focusing on deadwood in terrestrial ecosystems found increased densities in long-established reserves compared to recently-established reserves (Christensen *et al.*, 2005). Hence, our findings are in line with the literature and we can conclude that CWD densities in gravel pit lakes are impacted by lake age.

CWD densities in gravel pit lakes managed for recreational fisheries were strongly impacted by littoral slope, while no effect of littoral slope on CWD densities was found in unmanaged gravel pit lakes. In North American lakes, shoreline development typically for housing and to support boating has been detected as major factor on littoral CWD (Christensen *et al.*, 1996; Jennings *et al.*, 2003; Marburg *et al.*, 2006). Our gravel pit lakes were largely free from boating and housing. However, in Germany, angling clubs regularly meet to complete annual clean-up activities on the shoreline, and in this context very likely remove fallen trees and other deadwood to improve access to anglers for shoreline fishing. Moreover, individual anglers likely remove wood that is entangled in the fishing line during fishing operations or may otherwise remove wood that is accessible in shallow water through wading into the shallow littoral. It is likely that these actions are explaining the significant interaction term we found among fisheries management and littoral slope, as the clean-up activities are more easily completed in shallow near-shore areas, leaving wood at steeply-sloped shores but not in shallow sloped ones. In line with our findings Mallory *et al.* (2000) also found higher CWD densities in deeper areas of the littoral zone and human impacts on CWD density and distribution. Our findings support the assumption that the littoral CWD densities were lowest in shallow and easily reachable parts of the lake, while CWD densities increased with steeper slopes of the banks.

Limitations

We sampled environmental data as representatively as possible, but weather stations were sometimes several kilometers away from lakes (mean distance \pm SD: 22.1 \pm 10.3 km). However, our sampling area is characterized by an overall wind direction from west, which was also true for all weather stations. Accordingly, our wind data should appropriately represent the wind conditions at each lake. However, wind and wave action could relocate tree-specific CWD after it enters the lakes (Christensen *et al.*, 1996; Marburg *et al.*, 2006), but we were unable to measure these details within our study lakes.

Our analysis revealed a significant effect of lake age on large CWD densities, however the effect was not significant for small CWD. In addition, the effect of large trees was only significant for small CWD densities, but not for large CWD densities. A larger dataset including very old and highly vegetated gravel pit lakes might have revealed these effects to be significant at a significance level of 0.05 in all models. Nevertheless, and in line with the literature our study demonstrated that lake age and trees on the shoreline affect CWD recruitment in gravel pit lakes.

Conclusions and implications

We conclude that CWD densities in the littoral zone of gravel pit lakes are mainly driven by lake age and the number of tall trees on the shore especially with wind exposure. We further conclude that recreational-fisheries management negatively affects CWD densities, especially in shallow areas. CWD in the littoral zone represents an important habitat for fishes and other aquatic organisms in gravel pit and natural lakes (Sass *et al.*, 2012; Czarnecka, 2016; Matern *et al.*, 2021). Under certain situations, the removal of littoral CWD has been found to decrease the abundance of typical lake fish species (Helmus & Sass, 2008; Gaeta, Sass & Carpenter, 2014) and can also negatively affect aquatic invertebrates (Benke & Wallace, 2003; Czarnecka, 2016), especially when alternative habitats are missing (Smokorowski *et al.*, 2020). We thus recommend anglers and fisheries managers to pay attention to retain, and if

possible, increase the presence of CWD in the small and low structured littoral zones of gravel pit lakes. Moreover, planting of shorelines to increase the presence of trees and fostering rehabilitation of beavers could increase the CWD density in gravel pit lakes.

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Compliance with ethical standards

This study is in compliance with all ethical standards. The study was designed and performed without specific human or animal interactions.

Conflict of interest

The authors have no conflict of interest.

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Paper IV

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Environmental determinants of fish abundance in the littoral zone of gravel pit lakes

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Abstract The type and extent of habitats along the shoreline specify the distribution of fish in the littoral zone of lakes, but effects are likely species and size-specific and might be overwhelmed by lake-level environmental factors that drive fish abundance (e.g. trophic state). We applied a replicated transect-sampling design by electrofishing assessing fish abundance and distribution along the banks of 20 gravel pit lakes in Lower Saxony (Germany). Boosted regression trees were used to analyse the impact of different characteristic habitat types (e.g. vegetated, woody or

open water zones), shoreline water depth and lake-level environmental variables on species-specific fish abundances. In contrast to earlier studies, lake-level environment and transect-level habitat type similarly influenced the abundances of differently sized fish species in the littoral zone of gravel pit lakes. The abundance of almost all fish species increased with lake productivity and extent of structured littoral habitats, mostly following non-linear relationships. Our work suggests that investments into the quality of littoral habitat, and not merely the control of nutrient inputs or other lake-level environmental factors, can promote abundance of most gravel pit lake fish species, in particular those who depend on the littoral zone for at least part of their life-cycle.

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Introduction

Littoral zones and the associated ecotones connect terrestrial and aquatic habitats (Schindler & Scheuerell, 2002) and provide key habitat for many taxa in rivers and lakes (Pusey & Arthington, 2003; Winfield, 2004; Strayer & Findlay, 2010). Accordingly, littoral

zones provide manifold biological, chemical and physical functions, serving as spawning, feeding and refuge habitats for fishes and wildlife, enabling nutrient cycling, buffering waves and offering substrate for the colonization by plants (Radomski & Goeman, 2001; Pusey & Arthington, 2003; Winfield, 2004; Strayer & Findlay, 2010; Vander Zanden et al., 2011). The high structural complexity and heterogeneity of littoral zones is known to promote biodiversity, production and food web complexity (Benson & Magnuson, 1992; Sass et al., 2006; Carey et al., 2010; Ziegler et al., 2017; Cunha et al., 2019).

Most lake fish use the littoral zone on diel, seasonal or ontogenetic scales (Hofmann & Fischer, 2001; Amundsen et al., 2003; Westrelin et al., 2018) for feeding, spawning, nursery or as refuge habitat (Hölker et al., 2002; Lewin et al., 2004; Winfield, 2004). Yet, comparative studies across lakes, and time series analysis from individual lakes, have shown that lake-level environmental characteristics, in particular trophic state, morphology or water clarity, have stronger structuring effects on most lake fish communities than the quality and quantity of the habitats present in the littoral zone (Persson et al., 1991; Jeppesen et al., 2000; Diekmann et al., 2005; Mehner et al., 2005; Lewin et al., 2014). However, the characteristics of littoral habitats have been found to co-determine the abundance of selected fish species in the littoral zone (Fischer & Eckmann, 1997; Brosse et al., 1999; Helmus & Sass, 2008; Lewin et al., 2014), because availability and quality of littoral habitats may fundamentally constrain certain life-history stages (Scheuerell & Schindler, 2004; Ahrenstorff et al., 2009).

In cultural landscapes, artificially created lentic water bodies, in particular gravel pit lakes, have become common landscape elements (Soni et al., 2014; Blanchette & Lund, 2016). These artificial water bodies are often characterized by steep slopes, sandy habitats and high water depth (Gee, 1978; Blanchette & Lund, 2016; Nikolaus et al. 2020). Correspondingly, the littoral zone of gravel pit lakes appears functionally simplified relative to those of natural lakes (Emmrich et al., 2014). An increased relative importance of littoral zones has been reported to affect the abundance of selected fish species in lakes with limited littoral zones (Gasith, 1991; Hampton et al., 2011; Lewin et al., 2014). Hence, the relevance of littoral habitat features for driving the fish abundance

in the limited littoral zone of gravel pit lakes might overrule the effect of environmental lake-level characteristics. However, this has not been quantified, yet.

Littoral habitat structures mainly encompass wood, coarse woody debris, reeds and submerged macrophytes, which are known to affect the abundances of fish species in the littoral zone of lakes (e.g. Okun & Mehner, 2005; Sass et al., 2012; Lewin et al., 2014). For example, after controlling for lake-level impacts rudd (*Scardinius erythrophthalmus* (Linnaeus, 1758)), tench (*Tinca tinca* (Linnaeus, 1758)) and northern pike (*Esox lucius* Linnaeus, 1758) have been found to be more abundant in complex habitats formed by submerged and emerged macrophytes, while European eel (*Anguilla anguilla* (Linnaeus, 1758)), perch (*Perca fluviatilis* Linnaeus, 1758) and roach (*Rutilus rutilus* (Linnaeus, 1758)) have been preferentially found in woody habitats (Perrow et al., 1996; Lewin et al., 2004, 2014). Ecological processes such as preferences for spawning substrate and foraging habitat might explain these findings. At the same time, too dense structures can also limit foraging success (Savino & Stein, 1982, 1989; Diehl, 1988) and, thus, non-linear relationships with a peak at intermediate levels can be expected for the relationship of the extent of specific habitat structures and the abundance of selected species in the littoral zone of lakes.

In particular small fish face a trade-off between foraging and shelter seeking to avoid predation, which is at the cornerstone of classical ecological theory explaining habitat choice as a function of a growth-survival trade-off (Werner & Hall, 1988; Ahrens et al., 2012). Risk-sensitive foraging is under strong natural selection, and fish have evolved a sensitive repertoire to balance shelter seeking with foraging (Ahrens et al., 2012). Highly structured habitat is usually safe as is very shallow water for small-bodied fish, and these habitats are thus preferred by larval and juvenile fishes (e.g. Brosse & Lek, 2002; Okun & Mehner, 2005). As fish grow, risk of predation by gape-limited predators decreases (Lorenzen, 2000; Gaeta et al., 2018), which might loosen the attachment of larger-bodied fish to shelter habitat (Říha et al., 2015). Therefore, in particular larval and juvenile fish of several species should benefit from functional littoral zones with shallow areas and structural complexity to cope with the growth-survival trade-off mentioned above by switching among foraging and refuge habitats (Brosse & Lek, 2002).

In lentic waters comparative studies of microhabitat use by fish have mainly focused on the effects of littoral substrates (e.g. sand or rocks) rather than littoral structures (e.g. submerged macrophytes or deadwood; Fischer & Eckmann, 1997; Brosse et al., 1999; Brosse & Lek, 2002; Šmejkal et al., 2014; Říha et al., 2015). Lewin et al. (2014) examined the relative importance of lake-level and shoreline-level environmental determinants of the abundance of fish species across German lakes. However, this study did not consider how the littoral zone might affect different size classes of fish. Abundances of small individuals should be more dependent on littoral habitat and shoreline characters (Poizat & Pont, 1996; Grift et al., 2003; Pierce & Tomcko, 2005), whereas the abundances of large individuals should be better predicted by lake-level environmental factors (Persson et al., 1991; Jeppesen et al., 2000; Mehner et al., 2005). To test this proposition, a species- and size-specific analysis was performed of fish distributions in the littoral zone (here the nearshore margin up to a maximum depth of 2 m) of small gravel pit lakes, one of the most abundant and at the same time most understudied water body type in many cultural landscapes (Saulnier-Talbot & Lavoie, 2018; Søndergaard et al., 2018).

We hypothesized that (I) the relative importance of lake-level vs. littoral-level environmental descriptors in driving fish abundance differs between species and size-classes, (II) increasing amounts of complex, littoral habitats and shallow areas positively affect abundances of small fish, and (III) the impact of different littoral structures on abundances of large fish is non-linear and species-specific, with thresholds expected in the relationship of littoral habitat and fish abundance.

Methods

Sampling location and data collection

We sampled the littoral fish abundance in 20 gravel pit lakes in the lowlands of Lower Saxony, North Western Germany, located in the Central Plains ecoregion (Fig. 1). For littoral electrofishing, we divided the entire shoreline of each lake into transects. The number of transects varied between 4 and 27 per lake. The individual transect length ranged from 30 to

244 m. All transects were sampled by boat electrofishing (FEG 8000 electrofishing device; 8 kW; 150–300 V/300–600 V; EFKO Fischfanggeräte GmbH; www.efko-gmbh.de) with one anodic hand net (40 cm diameter and mesh size 6 mm) once per year in autumn from 2016 to 2019. This configuration enabled an effective electric fishing field of about 5 m diameter. Accordingly, along each transect the activated anode was swiftly immersed every three to five meter and all immobilized fish were netted. In rare cases, the number of transects varied between sampling years for some lakes for logistical reasons, varying water levels and due to ongoing habitat management actions. In each transect, all fish were identified and total length was measured to the nearest mm.

The transect-based sampling design was chosen to produce robust density estimates and to avoid zero-inflation of the data (e.g. Reid, 2011). Transect-based sampling further allowed the estimation of the relative composition of certain habitat types, e.g. the relative fraction of reed vs. woody habitat for a given transect. Electrofishing data were processed, and the catch per unit effort (CPUE) on transect-level was quantified for each year, lake and transect as individuals caught per 50 m electrofishing. Lake-level CPUE values were calculated as individuals caught per 50 m electrofishing per year and lake by summing up all catches and dividing them by the sum of all transect lengths. We then studied the effect of littoral structure on fish abundance (using transect-level CPUE in fish per 50 m as an abundance index), with transect-based CPUE values by size class and species nested as samples within lakes.

We confined our analysis of the relative impact of littoral structures, littoral water depth and lake-level environmental factors to six fish species, which regularly use and partly depend on the littoral zone in temperate European lakes: European eel, a relevant fisheries resource, the predators perch and pike, the benthivorous tench and the smaller-bodied “forage fish” roach and rudd. These species are common in German gravel pit lakes and naturally reproduce there, except for the stocked eel (Emmrich et al., 2014; Matern et al., 2019). To study the size-structured utilization of the littoral zone by fishes, all species except pike were separated into “small” and “large” size classes. For perch, roach, rudd and tench the threshold was set to 100 mm total length (TL).

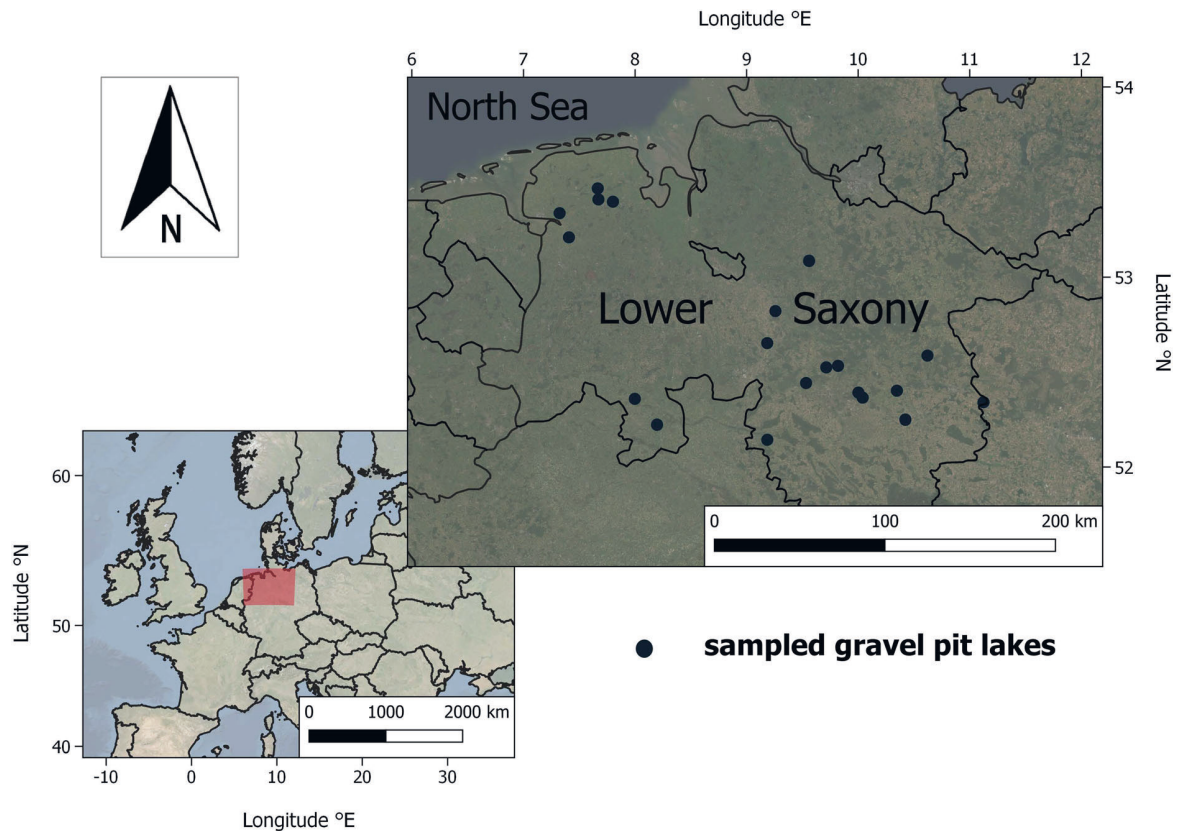


Fig. 1 Map of the gravel pit lakes in Lower Saxony, north-western Germany

Fish ≤ 100 mm TL are particularly vulnerable to predators (Gaeta et al., 2018) and should especially use structured habitats in the littoral zone. For the larger-bodied eel, the threshold was set at 300 mm TL. Pike was the only species analysed in three size classes: small (≤ 200 mm TL), medium (> 200 and ≤ 400 mm TL), and large (> 400 mm TL) to account for size-related habitat choice as a consequence of decreasing risk of cannibalism with increasing length (Nilsson, 2006) and size-dependent reliance on submerged macrophytes previously reported in the literature (Casselman, 1996; Casselman & Lewis, 1996).

Environmental lake-level variables

Lake area and shoreline length of the gravel pit lakes were calculated using QGIS (QGIS Development Team, 2019). The shoreline development factor (SDF) was calculated after Hutchinson (1957) as an index of

shoreline complexity and extent. Mean and maximum lake depth and the percentage of shallow lake areas (less than 3 m depth) were extracted from depth contour maps that were calculated by ordinary kriging in R following Monk and Arlinghaus (2017). Conductivity and Secchi depth were measured at each sampling event above the deepest point of the lake. Furthermore, water samples of the epilimnion were taken to analyse the total phosphorus concentration (TP) and the chlorophyll a concentration (Chl a) of the lakes to indicate trophic state. TP determination was conducted following the molybdenum blue method (Murphy & Riley, 1962; ISO, 2004), and the Chl a concentration was determined using high performance liquid chromatography (Mantoura & Llewellyn, 1983; Wright et al., 1991). To control for annual variation, Secchi depth, Chl a and TP values from two additional summer samplings (2017 and 2018) and one additional sampling in early spring (2017) were used to calculate a more robust mean for each lake.

Transect variables and habitat structures along the shoreline

The extent of different shoreline structures and average transect depth were visually determined for each transect at every sampling event. We differentiated the extent (in percentage of transect length) of reeds, wood, deadwood, submerged macrophytes and the absence of structure, termed “open littoral”. Reed habitats were mainly created by common reed (*Phragmites australis*) and in minor fractions by cattail (*Typha* sp.) and rush (*Juncus* sp.). The category “wood” was mainly represented by branches of living trees (various species) that extended from above the surface into the water column. Deadwood and roots were assigned to the category “deadwood” as they create a wooden structure in the water column and on the lake bottom. The category “submerged macrophytes” was represented by various species. For simplicity, some rare floating-leaved macrophytes, mainly water lilies (*Nymphaea* sp.), were also included in the category “submerged macrophytes”. The fifth category “open littoral” represented littoral areas without any structures and open, mostly soft bottom or sandy substrates such as sandy beaches or unstructured angling sites. The average fished depth in each transect was estimated and noted as “littoral depth”. Transects with a littoral depth of more than 2 m were removed from the analysis due to a reduced catchability of the electrofishing device (Zalewski & Cowx, 1990). The variable littoral depth contained three levels: very shallow (VS; < 0.5 m); shallow (S; 0.5–1.0 m) and deep (D; 1.0–2.0 m).

Data analysis

We first conducted a principal component analysis (PCA) of the z-transformed lake-level variables mean lake depth, maximum lake depth, share of shallow lake area (0–3 m depth), TP, Chl a, Secchi depth, SDF and conductivity to reduce the dimensionality of the environmental data (Table S1 and Fig. S1 in Supplementary Information). The broken stick method was chosen as stopping rule in the PCA (Jackson, 1993). Only one relevant PC axis was retained, which displayed information about the lake’s productivity. SDF and conductivity loaded on separate axes (Table S1 and Fig. S1 in Supplementary Information). PC scores from PC 1 were extracted and used for

further analysis (Table 1). Two gravel pit lakes showed “unusual” productivities (one very high, the other very low), however, both lakes were kept for further analysis to cover a larger productivity gradient.

To model the influence of environmental predictors (lake-level and transect-level) on the abundances of the different size classes of the six fish species, we used boosted regression trees (BRTs), similar to Lewin et al. (2014). BRTs are a machine-learning technique that produces several simple models (trees) and combines (boosts) them to produce a model with an improved predictive performance (Elith et al., 2008; Busto & Elith, 2011). BRTs are superior to other statistical methods (e.g. generalized mixed models and generalized additive models) in identifying the relative importance of different predictor variables when relationships are non-linear (Elith et al., 2006; Leathwick et al., 2006). Importantly, they are able to detect non-linear effects of the predictor variables on the dependent variable (Elith et al., 2008). BRTs were modelled separately by species and size class. We also used linear mixed effects models and found qualitatively similar results, and for the sake of space and comparability with Lewin et al. (2014) opted to only present the BRT results here.

Lake-level predictor variables included PC scores representing productivity and raw values of SDF and conductivity. SDF was used in the BRTs as it represents shoreline quantity. Conductivity was integrated in the analysis as it corrects for electrofishing gear effects, i.e. lower efficiency at low conductivity, and species-specific reactivity to electrofishing at different conductivity. Transect variables describing the littoral habitat comprised the extent (in percentage of each transect) of different shoreline structures as well as average transect depth (as categorical variable with three levels). The BRTs calculated a species- and size-class specific relative importance for each variable for fish abundance. These relative importance values were scaled so that all variables summed to 100 (Elith et al., 2008) and can be compared between all lake-level and all transect-level variables to reveal the overall importance of lake vs. transect effects for the abundance of each species and size-class.

The bag fraction determines the proportion of the dataset that is used to build a single tree. It should be set between 0.5 and 0.75 to receive robust results (Elith et al., 2008). In our analysis, the bag fraction for all BRTs was set at 0.75 to ensure highest accuracy

Table 1 Sampling effort and environmental lake data for all sampled gravel pit lakes

Lake	Maximum number of transects	Lake area (ha)	Shoreline length (m)	Shoreline development factor (SDF)	Mean lake depth (m)	Share shallow area (%)	Start year of lake excavation	End year of lake excavation	Conductivity ($\mu\text{S cm}^{-1}$)
Chodhemster Kolk	7	3.2	693	1.1	5.6	37.4	1968	1971	218
Collrunge	11	4.3	838	1.1	4.0	21.9	1970	1982	206
Donner Kiesgrube 3	5	1.0	417	1.2	3.3	30.9	1977	2000	603
Hopels	11	5.5	1072	1.3	6.7	19.1	1980	1998	219
Kiesteich Brelingen	20	8.5	2271	2.2	3.2	43.1	1980	1999	400
Kolshorner Teich	11	4.3	1095	1.5	6.4	21.9	1965	1980	587
Linner See	27	17.7	2752	1.8	5.1	19.2	1969	2000	308
Lohmoor	16	4.1	1611	2.2	2.2	67.0	1989	1991	170
Meitzer See	23	19.5	2028	1.3	11.9	8.6	1980	2006	628
Neumanns Kuhle	10	6.9	1045	1.1	3.1	48.1	1964	1970	614
Pfütze	19	10.6	2091	1.8	4.3	28.2	1985	2000	333
Plockhorst	22	14.3	2242	1.7	3.2	52.1	1980	1998	340
Saalsdorf	14	9.0	1414	1.3	5.3	16.9	1969	1995	599
Schleptruper See	9	4.0	954	1.3	4.9	39.7	1960	1965	512
Stedorfer Baggersee	5	1.9	590	1.2	1.7	24.4	1981	1983	360
Steinwedeler Teich	20	10.4	2247	2.0	5.3	19.8	1963	1978	744
Wahle	14	8.1	1457	1.4	5.9	23.9	1981	1990	738
Weidekampsee	8	2.9	964	1.6	2.3	58.3	1991	1994	409
Wiesedermeer	10	2.9	1055	1.7	3.7	34.1	1980	1990	138
Xella	7	2.1	749	1.5	3.1	53.5	1970	1975	1004

Table 1 continued

Lake	Total phosphorus (TP; $\mu\text{g l}^{-1}$)	Chlorophyll a (Chl a; $\mu\text{g l}^{-1}$)	Secchi depth (m)	PC scores productivity
Chodhemster Kolk	18	5	1.5	- 0.3
Collrunge	13	4	3.0	- 0.8
Donner Kiesgrube 3	36	9	1.5	0.7
Hopels	18	3	4.4	- 2.4
Kiesteich Brelingen	27	8	1.2	0.9
Kolshorner Teich	11	4	3.7	- 2.2
Linner See	17	6	2.6	- 1.0
Lohmoor	49	24	1.0	2.6
Meitzer See	9	2	4.3	- 4.7
Neumanns Kuhle	183	59	0.5	4.2
Pfütze	13	13	2.7	- 0.1
Plockhorst	39	32	0.9	2.0
Saalsdorf	23	16	1.4	- 0.2
Schleptruper See	12	6	2.8	- 0.6
Stedorfer Baggersee	55	27	1.0	2.0
Steinwedeler Teich	9	4	2.9	- 1.1
Wahle	13	7	3.1	- 1.4
Weidekampsee	11	6	3.2	0.8
Wiesedermeer	19	6	2.1	0.1
Xella	18	10	0.8	1.2

even for datasets with a low number of observations (e.g. large pike). The tree complexity was set to 5 to account for potential interaction effects in all BRT models. The learning rate was adjusted by species and size class to ensure at least 1000 trees per BRT model as recommended by Elith et al. (2008). The BRT output was displayed by using partial dependence plot to show the effect size of a variable on the response after accounting for the average effect of all other variables (Elith et al., 2008).

Fish abundances in neighbouring transects within a lake might be spatially autocorrelated violating assumptions of independence of data within lakes. Therefore, the spatial autocorrelation index Moran's I was separately estimated by fish species, lake and sampling event. Due to multiple comparisons, *P*-values were Šidák-corrected (Šidák, 1967). We found no evidence for spatial autocorrelation with just three detected events out of a total of 338 analyses (Table S2 in Supplementary Information) and thus rejected the assumption of autocorrelation. Each lake-year was assumed an independent sample as we were not interested in specific lake-level effects, similar to Lewin et al. (2014).

All statistical analyses were performed in R version 3.6.1 (R Core Team, 2019). The PCR was conducted using the package *vegan* (Oksanen et al., 2019), Moran's I was calculated using the package *ape* (Paradis & Schliep, 2018), and the BRTs were modelled using the packages *gbm* (Greenwell et al., 2019) and *dismo* (Hijmans et al., 2017). BRT bootstrapping and visualization of the BRT results was conducted using modified commands of the *ggBRT* package (Jouffray et al., 2019).

Results

Lake environment and descriptive information on sampling outcomes

The gravel pit lakes were on average 7.1 ha in size with the smallest lake being 1 ha and the largest lake being 19.5 ha (Table 1). The SDF varied between 1.1 and 2.2 with an average of 1.5. Mean lake depth ranged between 1.7 and 11.9 m with an average of 4.4 m, and the shallow areas comprised between 8.6 and 67% of the total lake area. The TP concentration ranged between 9 and 183 $\mu\text{g l}^{-1}$ (average 30 $\mu\text{g l}^{-1}$),

and the Chl *a* concentration ranged between 2 and 59 $\mu\text{g l}^{-1}$ (average of 13 $\mu\text{g l}^{-1}$). The Secchi depth varied between 0.5 and 4.4 m (average 2.2 m) and the conductivity between 138 and 1004 $\mu\text{S cm}^{-1}$ (average 457 $\mu\text{S cm}^{-1}$).

Open littoral was the dominant shoreline structure with a share of 35.1% over all lakes and sampling events (Table 2). Reeds and wood were also common in the littoral zone with relative frequencies of 22.9% and 24.2%, respectively. Submerged macrophytes were only detected on 13.2% of the fished shoreline length, and deadwood represented the scarcest structure covering only 4.5% of the shorelines.

In total 65,261 individuals of 25 fish species were caught during 80 electrofishing surveys. The catch of all six fish species of interest summed up to a total of 53,853 fishes (Table 3). Small rudd (< 100 mm TL) was the most abundant species and size class with 25,293 individuals, while large pike (> 400 mm TL) were least abundant with 130 individuals, respectively. In eight gravel pit lakes, all six fish species were caught, while in three lakes only one or two of these species occurred (Table 4). Tench were caught in most of the lakes (90%), followed by perch (85%) and eel (80%). Pike and roach were each caught in 15 gravel pit lakes (75%), while rudd occurred least frequently (70%). Accordingly, the number of lake samples used in the models varied by species and size class with a minimum sample size (lake sampling events) of 31 for large roach and a maximum of 64 for small perch (Table 3).

Highest median CPUE values (number of fish per 50 m) were revealed for small perch with 4.8 (range 0.1–36.1) on lake level and 2.6 (range 0–123.8) on transect level (Table 3). The highest single species CPUE values were recorded for small rudd (lake level CPUE: 317.1; transect level CPUE: 779.1). Large pike were least abundant in the electrofishing catches with a median CPUE of 0.01 (range 0.01–0.56) on lake level and 0 (range 0–1.9) on transect level. In general, the species CPUEs for larger size classes were lower than for smaller size classes, except for stocked eel.

Importance of lake-level vs. transect-level variables

Aggregated lake- and transect- habitat variables both showed similar relative importance for most species

Table 2 Mean extents of fished shoreline structures and the sum of transects in which the specific shoreline structures were detected over the four sampling years

Lake	Mean extent (%) of fished shoreline structures					Sum of transects with the specific shoreline structure				
	Reeds	Wood	Deadwood	Submerged macrophytes	Open littoral	Reeds	Wood	Deadwood	Submerged macrophytes	Open littoral
Chodhemster Kolk	0.6	2.9	0.0	17.6	79.0	1	5	0	18	28
Collrunge	53.8	1.8	5.6	8.9	30.0	38	2	7	14	32
Donner Kiesgrube 3	2.3	54.7	8.1	26.8	8.0	3	16	6	14	5
Hopels	0.2	20.2	0.6	0.0	79.0	1	33	1	0	44
Kiesteich Brelingen	1.3	4.5	8.4	32.9	52.9	5	28	21	64	77
Kolshorner Teich	34.0	27.9	4.2	12.8	21.2	31	31	9	16	32
Linner See	8.0	33.4	9.7	12.0	36.9	20	82	29	35	89
Lohmoor	17.5	19.2	0.0	18.3	45.0	31	28	0	35	48
Meitzer See	66.9	13.3	8.0	0.2	11.6	74	47	15	2	48
Neumanns Kuhle	1.1	60.5	0.8	0.0	37.6	3	37	3	0	36
Pfütze	30.4	17.1	1.1	22.7	28.7	49	41	7	55	63
Ploekhorst	17.9	29.9	2.9	6.8	42.4	43	65	10	26	75
Saalsdorf	48.6	8.5	6.3	0.7	35.9	53	18	19	1	49
Schleptruper See	47.8	18.8	0.9	1.6	31.0	31	23	3	5	31
Stedorfer Baggersee	0.5	29.1	2.1	36.6	31.7	1	17	4	13	14
Steinwedeler Teich	25.1	34.3	1.9	12.1	26.6	54	68	9	38	69
Wahle	10.1	27.0	4.1	3.3	55.5	22	47	12	15	54
Weidekampsee	31.6	17.7	11.9	31.3	7.5	24	18	13	28	18
Wiesedermeer	22.6	23.0	1.5	20.1	32.9	28	25	3	18	32
Xella	37.1	41.1	12.5	0.0	9.3	22	24	6	0	19
Mean ± SD	22.9 ± 20.5	24.2 ± 15.7	4.5 ± 4	13.2 ± 12.1	35.1 ± 20.3	27 ± 21	33 ± 21	9 ± 8	20 ± 18	43 ± 23

Table 3 Size ranges and median sizes for all size classes of the six fish species

Species	Scientific name	Size class	Size range (mm)	Median size (mm)	Number of individuals	Lake samples	Lake CPUE (N 50 m ⁻¹)		Transect CPUE (N 50 m ⁻¹)	
							Median	Range	Median	Range
Eel	<i>Anguilla anguilla</i>	Small	78–300	230	1095	50	0.65	0.02–5.11	0.49	0.0–13.2
		Large	301–990	465	2472	57	1.63	0.05–6.78	0.99	0.0–21.2
Perch	<i>Perca fluviatilis</i>	Small	33–100	72	10,670	64	4.77	0.08–36.07	2.55	0.0–123.8
		Large	101–257	121	3412	63	1.48	0.03–20.77	0.81	0.0–45.5
Pike	<i>Esox lucius</i>	Small	88–200	126	439	38	0.31	0.03–2.8	0	0.0–6.3
		Medium	201–400	249	550	48	0.34	0.02–1.68	0	0.0–6.9
Roach	<i>Rutilus rutilus</i>	Large	401–970	551	130	42	0.1	0.02–0.56	0	0.0–1.9
		Small	31–100	64	5784	40	1.53	0.02–59.66	0	0.0–206.5
Rudd	<i>Scardinius erythrophthalmus</i>	Large	101–231	141	725	31	0.18	0.03–32.62	0	0.0–60.9
		Small	11–100	45	25,293	42	3.99	0.05–317.11	0.57	0.0–779.1
Tench	<i>Tinca tinca</i>	Large	101–385	114	1182	37	0.35	0.02–18.74	0	0.0–52.7
		Small	21–100	57	1616	43	0.46	0.03–11.79	0	0.0–44.7
		Large	101–450	143	485	57	0.15	0.02–4.29	0	0.0–8.7

Lake samples display the number of positive records for each species and size class from a total of 80 fishing events. Median and range of the CPUE (N 50 m⁻¹) were calculated for each year and are presented on lake level and transect level

Table 4 Information on caught fish species (Y = caught; N = not caught) for all sampled gravel pit lakes

Lake	Eel	Perch	Pike	Roach	Rudd	Tench
Chodhemster Kolk	Y	Y	Y	Y	N	Y
Collrunge	Y	Y	Y	Y	N	Y
Donner Kiesgrube 3	Y	Y	Y	Y	N	Y
Hopels	Y	N	N	Y	N	N
Kiesteich Brelingen	Y	Y	N	Y	Y	Y
Kolshorner Teich	Y	Y	Y	Y	Y	Y
Linner See	Y	Y	Y	Y	Y	Y
Lohmoor	N	N	N	N	Y	N
Meitzer See	N	Y	Y	Y	Y	Y
Neumanns Kuhle	Y	Y	Y	Y	Y	Y
Pfütze	N	Y	Y	N	N	Y
Plockhorst	Y	Y	Y	Y	N	Y
Saalsdorf	Y	Y	Y	Y	Y	Y
Schleptruper See	Y	Y	Y	N	Y	Y
Stedorfer Baggersee	Y	Y	Y	Y	Y	Y
Steinwedeler Teich	Y	Y	Y	Y	Y	Y
Wahle	Y	Y	N	N	Y	Y
Weidekampsee	Y	Y	Y	Y	Y	Y
Wiesedermeer	Y	Y	Y	Y	Y	Y
Xella	N	N	N	N	Y	Y
Σ	16	17	15	15	14	18
Frequency of occurrence (%)	0.8	0.85	0.75	0.75	0.7	0.9

Table 5 Summed relative importance (%) for all lake-level variables and all transect-level variables for all species and size classes; higher values in bold

Species	Scientific name	size class	Summed relative importance of lake-level variables (%)	Summed relative importance of transect-level variables (%)
Perch	<i>Perca fluviatilis</i>	Small	48.0	52.0
		Large	48.7	51.3
Roach	<i>Rutilus rutilus</i>	Small	46.7	53.3
		Large	81.6	18.4
Rudd	<i>Scardinius erythrophthalmus</i>	Small	47.9	52.1
		Large	55.5	44.5
Tench	<i>Tinca tinca</i>	Small	55.6	44.4
		Large	49.0	51.0
Eel	<i>Anguilla anguilla</i>	Small	70.4	29.6
		Large	61.8	38.2
Pike	<i>Esox lucius</i>	Small	53.2	46.8
		Medium	50.2	49.8
		Large	42.7	57.3

and size classes (Table 5), with few exceptions: The relative importance of lake- and transect-variables was 46.7% and 53.3%, respectively, for small roach, while

for large roach the lake-variables (81.6%) were much more influential for the littoral abundance than transect-variables (18.4%). This pattern was strongly

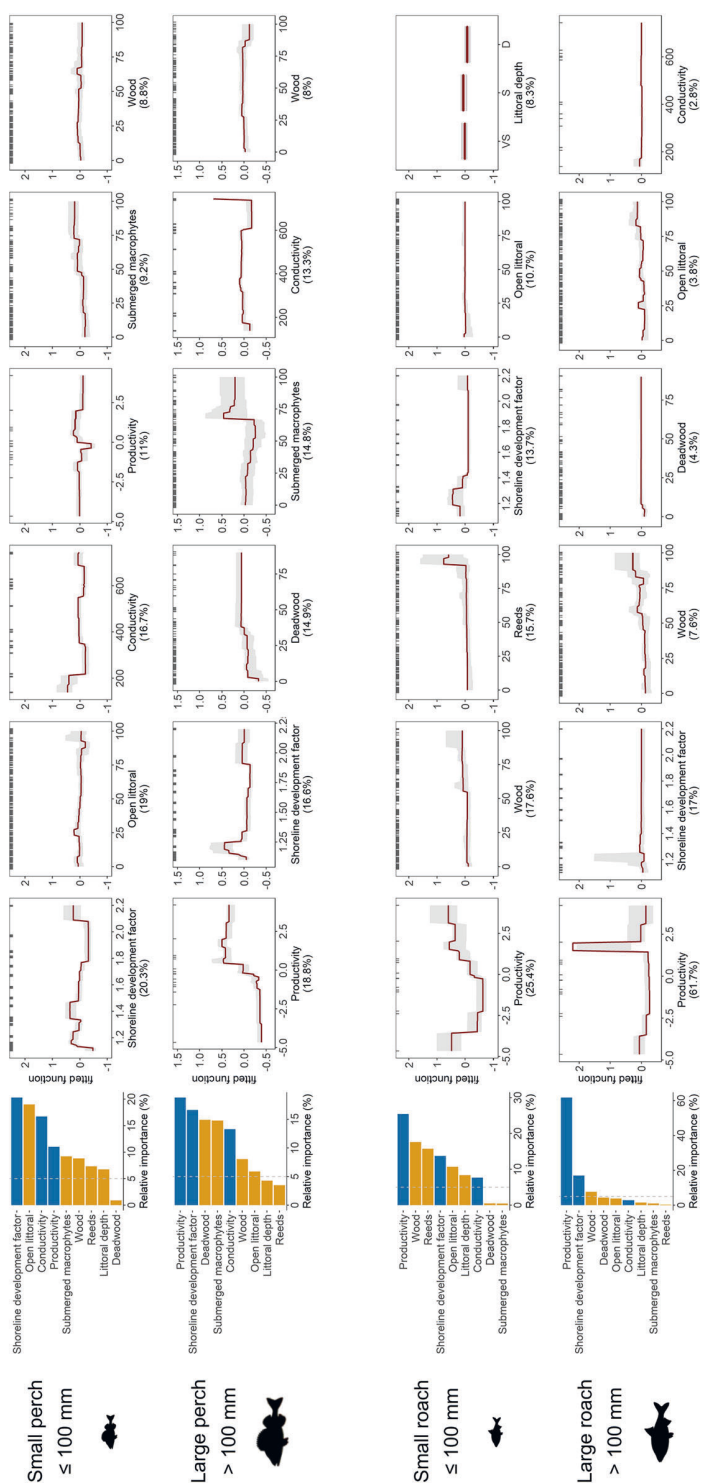


Fig. 2 Relative importance of lake-level variables (blue bars) and transect-level variables (yellow bars) for the abundances of small and large perch and roach. Partial dependence plots with 95% confidence intervals of the six most influential variables predicting the abundances are ordered by importance from left to right. Littoral depth contained the categories VS (very shallow; < 0.5 m); S (shallow; 0.5–1.0 m) and D (deep; 1.0–2.0 m). Ticks in each plot represent the distribution of the data

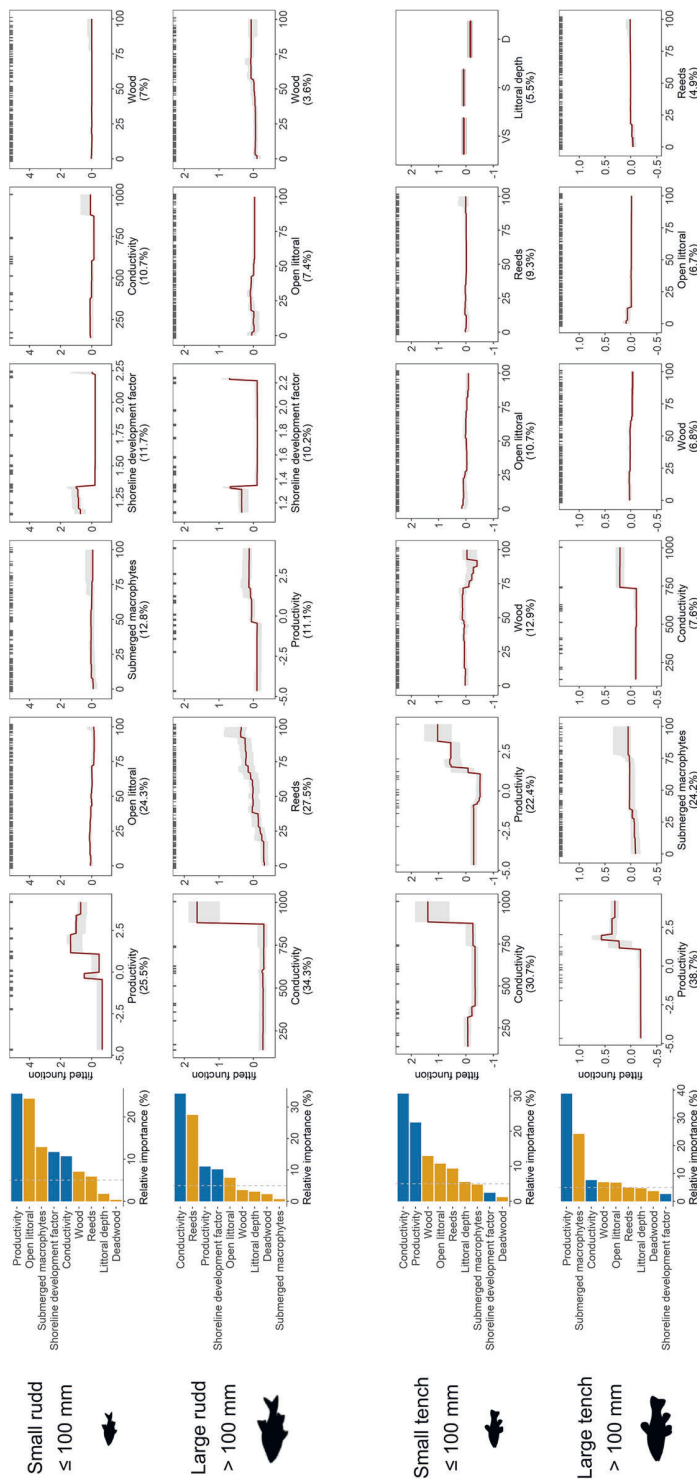


Fig. 3 Relative importance of lake-level variables (blue bars) and transect-level variables (yellow bars) for the abundances of small and large rudd and tench. Partial dependence plots with 95% confidence intervals of the six most influential variables predicting the abundances are ordered by importance from left to right. Littoral depth contained the categories VS (very shallow; < 0.5 m); S (shallow; 0.5–1.0 m) and D (deep; 1.0–2.0 m). Rugs in each plot represent the distribution of the data

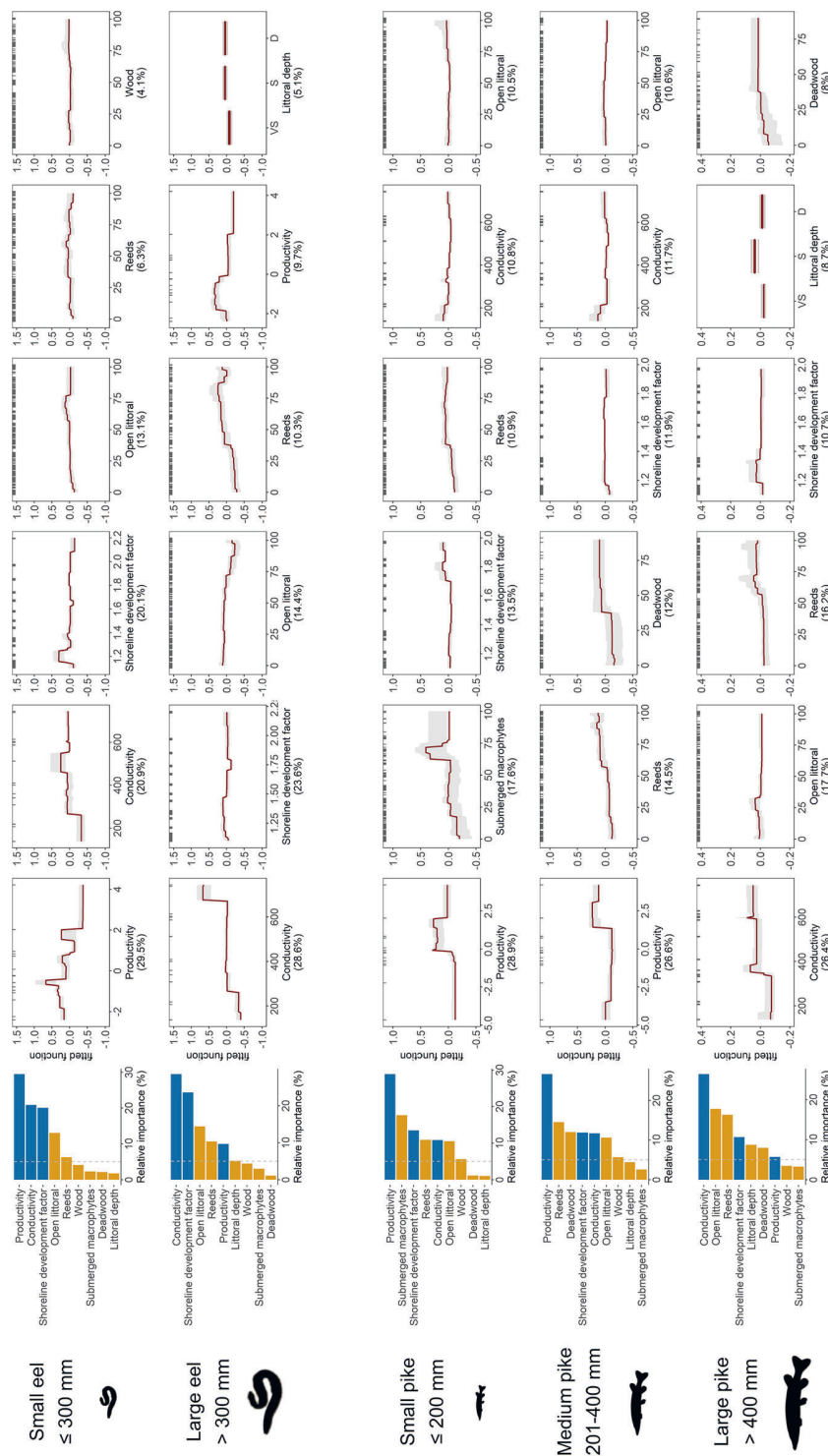


Fig. 4 Relative importance of lake-level variables (blue bars) and transect-level variables (yellow bars) for the abundances of small and large eels and small, medium and large pikes. Partial dependence plots with 95% confidence intervals of the six most influential variables predicting the abundances are ordered by importance from left to right. Littoral depth contained the categories VS (very shallow; < 0.5 m); S (shallow; 0.5–1.0 m) and D (deep; 1.0–2.0 m). Rugs in each plot represent the distribution of the data

driven by the high relevance of lake productivity (61.7%; Fig. 2) for large roach. For stocked eel, the relative importance of lake-variables also exceeded those of transect-variables with 70.4% for small eels and 61.8% for large eels. For pike the relative importance of the transect-variables compared to lake-level variables increased with size classes (small: 46.8%; medium: 49.8% and large: 57.3%), and the importance of lake-level variables decreased accordingly (small: 53.2%; medium: 50.2% and large: 42.7%).

Lake-level effects

In each of the species and size classes, one of the lake-level variables had the highest relative importance in affecting fish abundance (Figs. 2, 3 and 4). In all cases, except for small perch, productivity or conductivity most strongly explained the observed abundances. The abundance of small perch was best explained by the SDF, a variable measured on lake-level, but describing the quantity of littoral habitat (Fig. 2). With the exception of large rudd, productivity was of high relative importance for the three cyprinid species roach (small: 25.4%; large: 61.7%), rudd (small: 25.5%) and tench (small: 22.4%; large: 38.7%). In all cases, abundances of these three species increased at higher productivity levels. Productivity was also of highest relative importance for large perch (18.8%), small pike (28.9%) and medium sized pike (26.6%). For large perch and medium-sized pike increasing productivity led to increases in abundance, while abundances of small pike and also small perch peaked at an intermediate level of productivity.

Conductivity positively affected CPUE and appeared of high relative importance for abundances of eel (small: 20.9%; large: 28.6%), small tench (30.7%), large rudd (34.3%), and large pike (26.4%). A relatively high importance of conductivity was also detected for perch (small: 16.7%; large: 13.3%), but without a clear positive or negative effect on the fish catches.

The SDF was of high relative importance for the abundance of all size classes of perch (small: 20.3%; large: 16.6%), roach (small: 13.7%; large: 17%), eel (small: 20.1%; large: 23.6%), and pike (small: 13.5%; medium 11.9%; large: 10.7%); however, no clear direction of the effect was detected (Figs. 2, 3 and 4).

Importance of specific littoral habitats

Relative importance, effect size and direction of effects of the different habitat structures varied for fish species and size classes. At transect level open littoral best described the abundance of small perch (19%), small rudd (24.3%), eel of both size classes (small: 13.1%, large: 14.4%) and large pike (17.7%). Increasing shares of unstructured, open littoral correlated with decreasing abundances of all species, except small eel. Wood was the most important habitat variable for explaining the abundance of small tench (12.9%), small and large roach (17.6% and 7.6%). High shares of over 50% wood in the littoral zone were positively related to the abundance of small and large roach, while abundances of small tench decreased at over 70% wood within a transect. A high relative importance of deadwood was found for explaining the abundance of large perch (14.9%) and medium sized pike (12%). Shares of 40% deadwood on the shoreline had the largest effects, but the number of transects with high deadwood abundances was low (Figs. 2 and 4). Reeds were found an important habitat variable for the abundance of small roach (15.7%), large eel (10.3%), large rudd (27.5%), as well as all size classes of pike (small: 10.9%, medium: 14.5% and large: 16.2%). Except for small roach, reeds influenced the fish abundances positively. Finally, submerged macrophytes were found highly important for the abundance of large perch (14.8%) and small pike (17.6%). Littoral depth had the highest relative importance for explaining the abundances of small roach (8.3%) and large pike (8.7%). In both cases highest abundances were detected in shallow water.

Non-linearities and threshold effects

There were several non-linear responses of fish abundance to habitat features and lake-level variables. In particular, non-linear relationships among a variable and fish abundance were detected for productivity impacts on tench of both size classes (Fig. 3). Abundances of large perch also increased with productivity in a non-linear pattern, with a threshold value that was smaller than the one for tench.

Non-linear pattern and threshold effects were also detected for habitat variables measured at transect level. For large perch and small pike, abundances peaked at an intermediate submerged macrophytes cover of approximately 70% and declined thereafter

(Figs. 2 and 4). By contrast, deadwood was an important shoreline structure for medium sized pike and large perch reaching highest abundances at about 40% of deadwood, while even larger amounts did not further affect the abundances. For medium and large pike, abundances strongly increased in reed-dominated transects at a threshold of at least 50% reed cover.

Discussion

General findings

We studied the influence of specific shoreline structures on littoral fish species by comparing the importance of littoral habitats to those of environmental lake-level variables on species-specific abundances. In support of H1, the importance of littoral habitats was found to be species- and size-specific, and in some cases (e.g. both size classes of perch), the transect variables better explained the abundances than the lake-level environmental variables. This finding shows that the littoral fish abundance was strongly influenced by the littoral environment in gravel pit lakes. We further hypothesized a positive effect of specific littoral structures especially on the abundances of small fishes (H2), which was confirmed only for small and medium sized pike. Furthermore, we found non-linear patterns with species- and size-class specific threshold effects for certain shoreline structures on fish abundance (H3), in particular vegetation, woody structures and the extent of fully unstructured habitats. Littoral depth played only a minor role for fish abundances in gravel pit lakes, indicating that in our study lakes the habitat types were dominant factors affecting transect-level fish abundance.

Lake-level vs. transect-level impacts on fish abundance

Our results revealed a high importance of both, lake environment and shoreline habitats, for the local abundance of most species and size-classes. Lake-level environmental variables, such as morphology and nutrient level, are known to be important drivers of lake fish communities and abundances (Persson et al., 1991; Jeppesen et al., 2000; de Leeuw et al., 2003; Mehner et al., 2005; Lewin et al., 2014).

However, in our work the combined effect of all littoral variables was of similar or sometimes even higher importance than that of the pooled lake environment for driving local fish abundance in gravel pit lakes. Littoral structures are known to be crucial for the lifecycle of certain lentic fish species (e.g. pike; Casselman & Lewis, 1996; Nilsson et al., 2014) and hence changes in the shoreline habitat strongly affect fishes on species and community levels as well as abundance (Whitfield, 1986; Sass et al., 2006, 2012; Helmus & Sass, 2008; Ziegler et al., 2017). Using a similar methodological approach to ours, Lewin et al. (2014) found substantially higher importance of lake-level variables compared to the littoral characteristics in natural German lakes (compare Table S3). Our results are different, by revealing a higher relative importance of littoral variables compared to lake-level variables in gravel pit lakes. Compared to natural lakes, man-made gravel pit lakes are often characterized by steep slopes and higher littoral depth (Gee, 1978; Emmrich et al., 2014) and thus the distribution of submerged macrophytes and reeds is often more limited (Duarte & Kalf, 1986). The amount of deadwood is also lower in gravel pit lakes than in natural lakes, due to their young age (Robichon, unpublished data). Because of these deficits in littoral structures, their relative increases may have a stronger impact in gravel pit lakes compared to natural lakes with natural shorelines studied by Lewin et al. (2014). Nevertheless, the littoral fish community structure does not differ between gravel pit lakes and natural lakes as found in previous work in the same study region (Emmrich et al., 2014).

Lake-level environmental effects

We found lake productivity as an important, but not outstanding factor influencing littoral fish abundances in small gravel pit lakes. The relevance of the lake's trophic state for fish abundance is well established in the fish ecological literature: productivity and carrying capacity for fish biomass are strongly related to nutrient levels (Hanson & Leggett, 1982; Downing et al., 1990). Abundances of cyprinid species peak in eutrophic to polytrophic lakes, because these species benefit from increasing algal biomass and related zooplankton as food source (Persson et al., 1991; Jeppesen et al., 2000; de Leeuw et al., 2003; Mehner et al., 2005). Our study mostly included oligotrophic to

mesotrophic lakes and this might have downplayed the relevance of trophic state as key lake environmental factor, relative to Lewin et al. (2014). Nevertheless and in line with literature, we also saw a strong relevance of our productivity index for abundances of cyprinids, particularly roach and tench, in the littoral zone. Abundances of pike and perch have previously found to peak at a meso- to slightly eutrophic state and decrease afterwards (Persson et al., 1991; Jeppesen et al., 2000; de Leeuw et al., 2003; Mehner et al., 2005; Lewin et al., 2014). Similarly, Haugen & Vøllestad (2018) reported highest pike abundance at intermediate phosphorus concentrations of $15 \mu\text{g l}^{-1}$ in shallow lakes, likely because of the loss of macrophytes with increasing trophic state. We detected only small perch and small pike abundances to peak at intermediate productivity levels, while medium sized pike and large pike benefited from higher productivity levels, suggesting that the trophic states we observed were not limiting to the abundance of pike. Relatedly, Jeppesen et al. (2000) failed to find inverse relationships of productivity and abundance of pike in shallow lakes in Denmark, and Haugen & Vøllestad (2018) reported no decline of pike abundance with nutrient levels in deep lakes, indicating that pike can tolerate a wide range of productivities and might even benefit from increasing trophic state through higher prey availability (Nilsson et al., 2009). Overall, our lakes did not consistently cover the full productivity gradient from oligotrophic to polytrophic states and, thus, we might not have covered the threshold of decreasing abundances with elevated trophic state.

We found SDF to be of major importance for perch abundances. The SDF broadly describes the availability of littoral habitats. The littoral zone displays an important habitat for fishes, especially in deep lakes, by providing food (Hampton et al., 2011) and shelter from predators (Beauchamp et al., 1994; Stoll et al., 2008). Perch, the dominating fish species in mesotrophic natural lakes (Persson et al., 1991; Mehner et al., 2005) and gravel pit lakes (Matern et al., 2019), highly rely on the littoral zone during their ontogeny (Amundsen et al., 2003). Furthermore, SDF is an important factor determining growth of perch as revealed for some of our study lakes (Höhne et al., 2020). Hence, our findings are in accordance with perch literature and show the SDF as good surrogate to explain not only growth (Höhne et al., 2020), but also abundance of perch.

Conductivity was identified as important lake-level variable especially for the catch of large pike, rudd and eel, but also of small tench. Generally, the catches of all species and size classes were positively related to conductivity. Conductivity is known to influence the size of the electric field created through the electrofishing device, with larger efficient field sizes at higher conductivity (Bohlin et al., 1989; Zalewski & Cowx, 1990) and hence increased catches. However, at low conductivity catches of larger individuals were disproportionately lower and probably the abundances were also underestimated in low conductivity lakes.

Effect of littoral structures at the transect level

We found a strong positive effect of specific littoral structures on abundances of small and medium sized pike. The observed abundances of small pike peaked in highly, but not completely macrophyte-dominated transects, which is in agreement with previous studies (Grimm, 1989; Casselman & Lewis, 1996). While low or entirely unvegetated habitats were avoided due to increased risk of cannibalism (Grimm & Klinge, 1996; Skov et al., 2003; Skov & Koed, 2004), too dense habitat structures might limit foraging success (Savino & Stein, 1989; Eklöv, 1997), explaining the detected patterns. Abundances of medium sized pike increased in less complex reeds and deadwood, which corresponds with previously reported raising independence from vegetation cover with increasing body size in this species (Chapman & Mackay, 1984; Rosell & MacOs-car, 2002; Kobler et al., 2008, 2009).

The expected highest abundances of large fish in medium-structured habitats were only observed for large perch. Perch are superior competitors to roach in medium structured littoral habitats (Persson & Eklöv, 1995), however, highly complex and dense aquatic vegetation negatively influences foraging efficiency of percids (Savino & Stein, 1982; Diehl, 1988; Gotceitas & Colgan, 1989) and, thus, abundances (Brosse & Lek, 2002). Our results suggest that similarly to pike, large perch benefit from intermediate macrophytes coverage.

Submerged macrophytes were also highly relevant for large tench and this pattern was rather linear. Tench select for densely vegetated habitats of floating and submerged macrophytes, as well as reeds (Perrow et al., 1996; Gallardo et al., 2006; Lewin et al., 2014). Hence, highest tench abundances can be expected in

habitats with highest structural complexity, which is in agreement with our results.

A further positive linear effect was detected for littoral reed stands on large rudd abundances. Aquatic vegetation has always been stated as typical rudd habitats (Eklöv & Hamrin, 1989), but Lewin et al. (2014) already revealed a higher relevance of reed habitats compared to submerged macrophytes for rudd abundance. Our results confirm this finding for rudd larger 100 mm.

Open littoral was found to negatively affect the abundance of small rudd and large eels. Lewin et al. (2014) found similar eel abundances in structured and unstructured habitats, but did not investigate size effects. River studies on *Anguilla* species showed an increased importance of riparian cover for eels larger 300 mm, while smaller individuals selected for diverse sediments as shelter habitat (Jellyman et al., 2002; Glova et al., 2010). Hence, the absence of littoral cover negatively affects the abundances of larger eels, while small eel abundances might be more influenced by the diversity of the sediment, a variable not measured here. Furthermore, our findings indicate a general dependence of small rudd and large eel on littoral habitat complexity, but not specifically on a distinct habitat type.

Importance of littoral water depth was generally low throughout all species and size classes compared to littoral structures. Generally, shallow water zones are often stated as habitat for fishes because they warm quicker and offer refuge from larger bodied predators (e. g. Paterson & Whitfield, 2000), and Brosse et al. (1999) detected a higher species-specific importance of littoral depth. However, Brosse et al. (1999) conducted electrofishing from June to mid-September, while our sampling was conducted from end of August to mid-October. Hence, littoral depth might be particularly important for larval fishes, and the importance of littoral depth decreases with increasing fish size.

Special case of stocked eel

Pattern and variances in eel catches were best explained by lake-level rather than transect-level variables. Lewin et al. (2014) already detected a high importance of the lake-level variables “trophic index” and “mean lake depth” on eel abundances in shallow lakes. In shallow lakes eel abundances and growth rates are usually highest at high trophic levels

(Anwand, 1982; Lewin et al., 2014). In comparison to that, in deep lakes shoreline development factor and shoreline structure become more important for eel (Lewin et al., 2014). However, eel populations in unconnected gravel pit lakes completely rely on stocking through recreational-fisheries management (Emmrich et al., 2014; Matern et al., 2019), which can positively impact their abundances if the environment offers suitable conditions (Simon & Dörner, 2014; Arlinghaus et al., 2015). Our analysis did not consider stocking effects on lake-level and, therefore, does neither allow for an accurate interpretation of the lake variable effects nor for a comparison of lake environment vs. littoral habitat effects as these results may be biased by individual stocking actions per lake. Nevertheless, the comparison of the different shoreline structures and their specific effects on the eel abundances remain valid.

Study limitations and future research needs

In our study, all data were collected by electrofishing, which is known for being size and species-selective and exhibiting lower efficiency in deep water and open habitats. However, it is still the most broadly applicable standard method for fish sampling in littoral habitats (Mueller et al., 2017). We analysed conductivity effects to account for lake-specific catchability. Nevertheless, the abundances of large fish in general and of all fish in the unstructured, open littoral habitats might have been underestimated. However, even if absolutely underestimated, at higher stock densities relatively more large fish get captured and also more fish in the less structured habitats should have been caught, such that the relative differences among habitats should broadly hold.

In our study, we exclusively used data from daytime electrofishing samplings in autumn (end of August until mid-October). Littoral habitat utilization of fishes differs between day and night (Copp, 2010; Říha et al., 2015) and between seasons (Kobler et al., 2008; Nakayama et al., 2018; Westrelin et al., 2018). Hence, fish samplings over all seasons and both times of the day might reveal other patterns than we presented here. Future research focusing on these aspects would complete the knowledge of the littoral zone to verify its importance for the fish abundance in gravel pit lakes. As a final limitation, we have to mention that we did not fully randomly select study

lakes such that our inferences are confined to the environmental gradients characteristic of our study lakes. However, in the study region, similar to many other cases in central Europe, most gravel pit lakes are mesotrophic (Emmrich et al., 2014; Zhao et al., 2016; Søndergaard et al., 2018) and match the environmental characteristics of our study lakes. Therefore, our results remain transferable to most gravel pit lakes in Europe and might also hold for natural lakes of similar ecological conditions.

Conclusions and implications

Our results suggest that the availability and characteristics of littoral habitats are highly relevant and shape the abundance of littoral fish in gravel pit lakes, and in certain cases (e.g. perch of both size classes) their importance can even exceed those of environmental lake-level effects. We further demonstrated that fish-habitat associations are dependent on the species, size-class and the type of littoral habitat, often revealing non-linearities and threshold effects. Hence, we recommend that fisheries managers should not only rely on stocking and harvest regulations, but also consider habitat enhancement in the littoral zone of lakes as a suitable means to manage fish abundance in lakes (Sass et al., 2017). Generally, increasing amounts of littoral structure lead to increasing fish abundances for most species, with exceptions of small pike and large perch, which benefit from intermediate coverage of submerged macrophytes. We can conclude that diverse shoreline structures and the availability of various habitat types support a diverse fish community (e.g. Werner et al., 1977; Dustin & Vondracek, 2017) and elevate fish abundance in gravel pit lakes. These results are likely to hold for natural water bodies with degraded shorelines as well.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations Our fish sampling complied with fisheries law in Lower Saxony, Germany and included permissions for electrofishing.

Conflict of interest The authors have no conflict of interest.

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Paper V

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Seasonal and diurnal patterns of littoral microhabitat use by fish in gravel pit lakes, with special reference to supplemented deadwood brush piles.

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Seasonal and diurnal patterns of littoral microhabitat use by fish in gravel pit lakes, with special reference to supplemented deadwood brush piles

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Abstract The habitat quality of the littoral zone is of key importance for almost all lentic fish species. In anthropogenically created gravel pit lakes, the littoral zone is often structurally homogenized with limited fish habitats. We supplemented deadwood brush piles in the littoral zone of eight gravel pit lakes and investigated the diurnal and seasonal use of this and other typical microhabitats by six dominant fish species. Shoreline habitats were sampled using point abundance electrofishing during day and night in all four seasons, and patterns of fish abundance were compared amongst unstructured littoral habitats, emerged macrophytes and brush piles. We caught a total of 14,458 specimens from 15 species in the gravel pit lakes. Complex shoreline structures were used by all

fish species that we examined, especially during day-time, whilst the use of unstructured habitats was highest during night. The newly added brush piles constituted suitable microhabitats for selected fish species, perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and pike (*Esox lucius*), particularly during winter. Supplemented deadwood provides suitable fish habitat in gravel pit lakes and may to some degree compensate for the loss of submerged macrophytes in winter by offering refuge and foraging habitat for selected fish species.

Keywords Fish distribution · Deadwood · Habitat enhancement · Fisheries management · Point abundance electrofishing · Quarry lake

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Introduction

Multiple threats (e.g. habitat loss, pollution) negatively affect freshwater ecosystems (Arlinghaus et al., 2002; Collen et al., 2014; Reid et al., 2019), resulting in a pertinent biodiversity crisis (Dudgeon et al., 2006; Reid et al., 2019). Conservation and restoration of freshwater ecosystems are key policy goals (Geist, 2011; Geist & Hawkins, 2016; Tickner et al., 2020). In this context, human-created water bodies, such as ponds or quarry lakes, can contribute to biodiversity conservation (Seelen et al., 2021, 2022).

Artificial water bodies created by past mining activities, predominantly to quarry sand and gravel but also peat, clay, and chalk, are common water bodies globally (Blaen et al., 2016; Søndergaard et al., 2018; Nikolaus et al., 2021; Seelen et al., 2021, 2022). In 2019, over 26,000 active excavation sites existed in 24 European countries alone, with Germany being one of the leading sand and gravel producers (European Aggregates Association, 2019). In the Federal State of Lower Saxony (North-Western Germany) more than 37,000 drainable ponds and non-drainable sand and gravel pit lakes (<20 ha size) currently exist, representing the vast majority (70%) of all stagnant waterbodies (Nikolaus et al., 2020). At such staggering numbers, pit and other quarry lakes are important supplementary habitats for colonization by aquatic species and may serve as areas for biodiversity conservation (Chester & Robson, 2013; Emmrich et al., 2014; Hill et al., 2015; Damjanović et al., 2018; Oertli, 2018; Søndergaard et al., 2018; Vucic et al., 2019; Reyne et al., 2020; Nikolaus et al., 2021). Moreover, many artificial lakes, especially small ones between 1 and 20 ha, are intensively used for leisure activities and therefore, improving habitat quality for fishes and other wildlife may also enhance recreational quality and ecosystem services, specifically recreational fisheries (Meyerhoff et al., 2019; Seelen et al., 2022; Kaemingk et al., 2022).

The morphology of gravel pit lakes typically differs from natural lakes. For example, gravel pit lakes are on average deeper and have steeper depth gradients than natural lakes (Emmrich et al., 2014; Molléma & Antonellini, 2016; Søndergaard et al., 2018), which results in a reduced littoral zone-to-lake area ratio (Gasith, 1991). Littoral zones play an outstanding ecological role in lake ecosystems (Winfield, 2004; Moss, 2008) and offer important habitats for

numerous lake fish species (Hall & Werner, 1977; Crowder & Cooper, 1982; Savino & Stein, 1982; Eklöv, 1997). Many freshwater fish use the littoral zone during particular or all ontogenetic life stages (Grimm & Klinge, 1996; Sammons & Bettoli, 1999; Schulze et al., 2006; Brosse et al., 2007).

Littoral habitat use by fish varies between day and night and amongst seasons caused by factors, such as spawning (Winfield, 2004; Chapman et al., 2011), predation (Lucas & Baras, 2001; Skov et al., 2013), foraging (Thorpe, 1974; Okun & Mehner, 2002), light and turbidity (Utne-Palm, 2002; Pekcan-Hekim & Lappalainen, 2006; Pekcan-Hekim et al., 2010). The habitat use of the littoral zone by fishes, specifically, smaller-bodied individuals, is crucially affected by the availability of microhabitat structures and shallow water zones, which serve as refuge from predation (Tonn & Magnuson, 1982; Hatzenbeler et al., 2000) especially in clear water conditions (Miner & Stein, 1996; Abrahams & Kattenfeld, 1997). Of key importance for many freshwater species is submerged vegetation, which serves as spawning habitat for phytophilic species such as tench (*Tinca tinca* (Linnaeus, 1758)) or pike (*Esox lucius* Linnaeus, 1758) and generally as refuge and foraging habitat for many other species subject to predation risk (Savino & Stein, 1989; Bry, 1996; Lewin et al., 2004; Järvalt et al., 2005). The greatest fish species diversity and abundance in the littoral zone of lakes can be observed during the summer months when most fish species have spawned and the larval and juvenile fishes use the warm and productive littoral zone for foraging and as refuge habitat (Hall & Werner, 1977; Fischer & Eckmann, 1997a; Hatzenbeler et al., 2000). However, the use of the littoral zone is species and size specific with some species like pike being present in the littoral zone during the entire year (Rossier, 1995; Hatzenbeler et al., 2000; Brosse et al., 2007; Kobler et al., 2008; Westrelin et al., 2021), whilst others—such as perch—are moving to deeper overwintering habitats as the temperature declines (Imbrock et al., 1996; Vehanen & Lahti, 2003; Westerberg & Sjöberg, 2015).

Abundant underwater vegetation can be a key microhabitat structure that adds resilience to lake ecosystems (Hilt et al., 2006; Scheffer & Jeppesen, 2007). However, cover and biovolume of aquatic vegetation decay when temperature and light intensity decrease in winter (Barko et al., 1982), resulting in

a decline of available habitats for structure-dependent fish species (Grimm & Klinge, 1996). Most fish species prefer shallow littoral zones to avoid predation, especially during their early-life stages (Ruiz et al., 1993; Paterson & Whitfield, 2000) and may even overwinter in sheltered habitats in the littoral zone to reduce both their metabolic costs and risk of predation (Jacobsen et al., 2004; Shuter et al., 2012; McMeans et al., 2020). However, studies of habitat use by fish in winter are generally rare (Eklöv, 1997; Hatzembeler et al., 2000; Jepsen & Berg, 2002; Brosse et al., 2007; Skov et al., 2008, 2013; Brönmark et al., 2010), which has been described as a general void of winter ecology in freshwater studies (Shuter et al., 2012).

Small individuals are particularly susceptible to predation (Mittelbach & Persson, 1998; Gaeta et al., 2018). To avoid predation they are dependent on either turbid conditions that interfere with the success of visual predators (Cook & Bergersen, 1988; Abrahams & Kattenfeld, 1997), shallow zones that limit access to larger-bodied predators (Ruiz et al., 1993; Paterson & Whitfield, 2000) or availability of structurally complex habitats like dense macrophyte stands, which reduce predator success rates, especially in clear waterbodies (Anderson, 1984; Diehl, 1988; Savino & Stein, 1989; Chick & McIvor, 1994; Rossier et al., 1996). In addition to submerged and emerged macrophytes, deadwood structures are important components of littoral zones that enhance the habitat quality for selected species of fish and other aquatic organisms (O'Connor, 1991; Everett & Ruiz, 1993; Lewin et al., 2004; Naimann & Latterell, 2005; Newbrey et al., 2005; Sass et al., 2006; Czarnecka, 2016). Analyses of species-specific use of specific littoral habitat structures repeatedly showed that juvenile pike, tench and rudd (*Scardinius erythrophthalmus* (Linnaeus, 1758)) strongly associate with emerged and submerged macrophytes, whereas perch (*Perca fluviatilis* Linnaeus, 1758), roach (*Rutilus rutilus* (Linnaeus, 1758)) and adult pike have also been reported to regularly use and sometimes prefer woody habitats (Casselmann & Lewis, 1996; Lewin et al., 2014; Matern et al., 2021). These findings were obtained from daytime samples, but pronounced diurnal migrations of fish between littoral and pelagic habitats are well documented in lakes (Hall et al., 1979; Bohl, 1980; Gliwicz & Jachner, 1992; Haertel & Eckmann, 2002; Jüza et al., 2014; Nakayama

et al., 2018). Larger fish migrate to the banks at night for foraging (Schulz & Berg, 1987; Kubečka, 1993; Wolter & Freyhof, 2004; Říha et al., 2011, 2015), whilst smaller fish often express reverse movements from the structured littoral to the open water column to predate on plankton when visually active predators are less able to hunt (Bohl, 1980; Gliwicz & Jachner, 1992; Gliwicz et al., 2006; Říha et al., 2015). The horizontal diurnal migration of small fish is typically explained by a trade-off between predator avoidance during daytime and resource availability in the form of pelagic dwelling zooplankton during low light conditions at dawn/dusk or during night (Bohl, 1980; Gliwicz & Jachner, 1992; Gliwicz et al., 2006; Říha et al., 2015). For example, Lewin et al. (2004) observed pronounced diel patterns of selection for shallow woody habitats in juvenile fish, specifically roach and perch, in a large German lake. However, much less is known about altered habitat choice of fish after structural enhancement as part of lake restorations and amongst seasons, especially during winter.

Human use and increasing development of lake shorelines have frequently led to a reduction in extent and quality of natural littoral structures (Ostendorp et al., 1995; Christensen et al., 1996; Chhor et al., 2020). Especially, the supply of coarse woody debris (CWD) in lakes is inversely related to human use intensity of lake shorelines and near-lake housing or other infrastructure (e.g. pier) development (Christensen et al., 1996; Jennings et al., 2003; Marburg et al., 2006). For example, research on CWD abundance in young gravel pit lakes with low amounts of large riparian trees, the main source for CWD in natural lakes (Marburg et al., 2006), revealed a lack of complex woody structures compared to natural lakes, which was explained by clean-up actions by recreational anglers removing wood (Matern et al., unpublished data). In gravel pit lakes low quantities of CWD together with limited littoral areas and potentially lower macrophyte abundance due to unstable sandy substrates (Emmrich et al., 2014; Vucic et al., 2019) can reduce the overall structural quality of littoral zones. Therefore, introductions of brush piles as structural habitat enhancement (Cowx & Gerdeaux, 2004; Hickley et al., 2004; Nagayama & Nakamura, 2010; Arlinghaus et al., 2016) may be a promising tool for improving the ecological state of gravel pit shore zones. In Danish lakes research on brush pile

installation revealed that these structures may serve as habitats for selected species, such as pike (Skov & Berg, 1999).

The objective of the present study was to identify spatio-temporal patterns of littoral microhabitat use by fish in eight German gravel pit lakes, less than two years after their enhancement with deadwood brush piles. We tested the following hypotheses: I) structured habitats and specifically brush piles are a suitable habitat for various fish species in gravel pit lakes, especially in clear water conditions; II) the use of brush piles is length specific with large individuals preferring brush piles compared to typical young fish habitats (e.g. densely structured macrophytes or shallow water zones); III) use of littoral structures is higher during day compared to night when the use of open habitats increases and IV) microhabitat use of long-lasting brush piles increases in winter when the structural complexity of aquatic vascular plants decay. To test these hypotheses, eight gravel pit lakes

that previously received littoral structure enhancement with deadwood brush piles, covering 20% of the shoreline length, were repeatedly electrofished during day and night over all four seasons of the year. This is the first study covering all seasons, day and night, using random point abundance sampling by electrofishing (PASE) in multiple lakes, because most previous studies were focused on individual lakes (e.g. Lewin et al., 2004) or covered only the daytime period (Fischer & Eckmann, 1997a; Brosse et al., 2007).

Methods

Study sites and brush pile implementation

We sampled eight gravel pit lakes (Fig. 1) located in the Federal State of Lower Saxony, North-Western Germany (Matern et al., 2019). All lakes were part

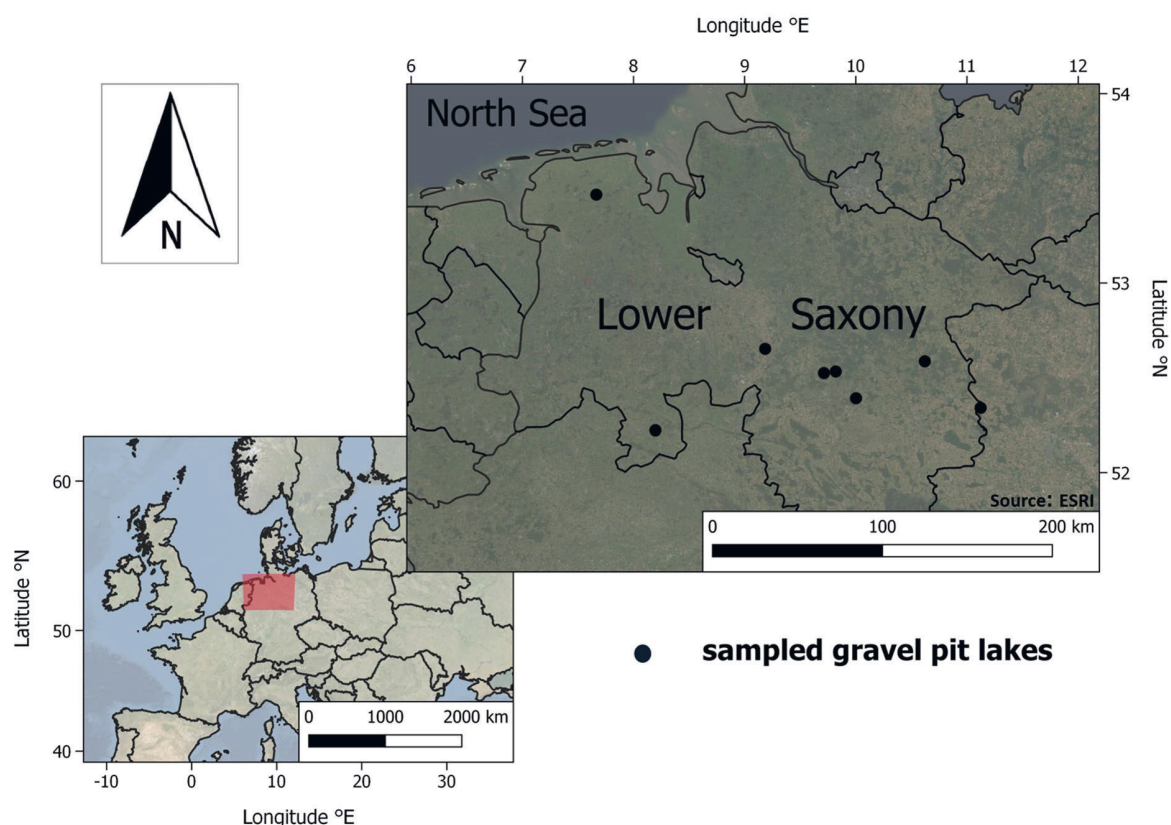


Fig. 1 Location of the eight gravel pit lakes supplemented with brush piles and investigated for microhabitat use by fishes

of the research project BAGGERSEE (www.baggersee-forschung.de), which investigated the effects of littoral habitat enhancements on fish communities in German gravel pit lakes (Radinger et al., in press). Each lake was enhanced with brush piles between December 2017 and March 2018 (Fig. S1). The brush piles consisted of deadwood in standardized circular bundles each 3 m long and 0.8 m in diameter. The deadwood bundles consisted predominantly of thin branches with mean diameter of 0.5–5.0 cm and included in maximum 2–3 branches with > 15 cm diameter (the overall range in branch diameter was 0.5–21 cm) originating from different, native wood species, mainly European hornbeam (*Carpinus betulus* L.), birch (*Betula* spp.) and alder (*Alnus glutinosa* (L.) Gaertn.). Branches were bundled and tied together with plant-based decomposable sisal ropes

using a harvester machine (Pinox 828 forwarder and harvester unit, Pinox Oy, Finland). The bundles (each 300 kg) were transported attached to boats and released in preselected areas manipulating 20% of the lake's shorelines. The brush piles were placed orthogonally to the shoreline in depths of one to three metres and weighed down using decomposable jute bags filled with gravel. All piles were placed within seven metres maximum distance to shore. In total, 800 brush piles were implemented to cover 20% of the littoral zone in each lake. Accordingly, the number of brush piles per lake varied between 30 in the smallest lake and 190 in the lake with the longest shoreline (Table 1).

Table 1 Morphological, physical, and chemical parameters (mean \pm SD) of the sampling lakes (TP=total phosphorous) and number of deadwood brush piles added, always covering 20% of lake's shoreline

Characteristic	Lake								
	Collrunge	Donner Kiesgrube 3	Kiesteich Brelingen	Kolshorner Teich	Linner See	Meitzer See	Saalsdorf	Weidekampsee	Mean \pm SD
Begin excavation	1970	1977	1980	1965	1969	1980	1969	1991	1975 \pm 8.5
End excavation	1982	2000	1999	1980	2000	2006	1995	1991	1994 \pm 9
Area (ha)	4.3	1.3	8.4	4.2	17.7	19.5	9	2.8	8.4 \pm 6.8
Shoreline length (m)	838	417	2271	1095	2752	2028	1414	964	1472 \pm 802
Mean depth (m)	4	3.3	3.2	6.4	5.1	11.9	5.3	2.3	5.18 \pm 3
Maximum depth (m)	8.6	5.2	8.7	16.1	11.2	23.5	9.2	4.3	11.6 \pm 7.2
Percentage littoral area (%)	21.9	30.9	43.1	21.9	19.2	8.6	16.9	58.3	27.6 \pm 16
Number of brush piles	62	30	136	74	190	142	96	70	100 \pm 52
Mean conductivity ($\mu\text{S cm}^{-1}$)	216.2 \pm 3.2	592.5 \pm 9.2	335.7 \pm 15.7	577.4 \pm 3.7	338.7 \pm 13.2	642.5 \pm 5.9	628.4 \pm 22.8	389.5 \pm 34.6	465.1 \pm 163.6
Mean Chlorophyll a ($\mu\text{g l}^{-1}$)	10.1 \pm 10.1	10.5 \pm 6.9	4.8 \pm 1.8	4.5 \pm 3.5	9.1 \pm 5	1.6 \pm 0.1	12.8 \pm 3.2	7 \pm 7.3	7.6 \pm 3.7
Secchi depth (m)	2.9 \pm 1	1.9 \pm 0.5	1.7 \pm 0.6	4.4 \pm 1	2.6 \pm 1.1	3.9 \pm 0.7	1.4 \pm 0.5	3.1 \pm 0.8	2.7 \pm 1.1
Mean TP ($\mu\text{g l}^{-1}$)	21.5 \pm 21	27.2 \pm 16.6	17.2 \pm 6.6	15.2 \pm 8.6	19.4 \pm 12	8.5 \pm 5.4	29.5 \pm 15.8	10.7 \pm 3.9	18.7 \pm 7.4
Spring TP ($\mu\text{g l}^{-1}$)	7	21	17	5	14	5	31	14	14 \pm 9
Summer TP ($\mu\text{g l}^{-1}$)	52	20	16	16	12	16	21	6	15.3 \pm 4.7

Fish sampling

Fish abundance at the microhabitat level was assessed using PASE (Copp & Peñáz, 1988; Copp, 2010) during day and night and in four seasons: autumn (18 October 2018–27 October 2018), winter (10 January 2019–20 January 2019), spring (20 May 2019–31 May 2019) and summer (21 July 2019–01 August 2019). PASE was conducted from a boat using a generator-powered electrofishing aggregate (8 kW; 150–300 V/300–600 V; EFKO 171 Fischfanggeräte GmbH Leutkirch, www.efko-gmbh.de) with a 4-m-long copper cathode and netted ring anode (ring diameter=0.45 m, mesh size=6 mm). Sampling was performed by rapidly immersing the activated anode for ten seconds close to the specific microhabitat. In complex structures such as brush piles, dense submerged and emerged macrophytes, electronic flux between the poles was halted three times to provoke the anodic reaction of fish.

The distance between point samples was kept large enough (at least 5 m) to generate independent samples (Copp, 2010). PASE started after sunrise for daytime fishing and after complete darkness for nighttime fishing. In each lake, day and night fishing were conducted within 24 h. Sampling locations for night fishing were randomly preselected during the day, marked by buoys and left out in day fishing to ensure that different points were always fished to avoid bias by repeated sampling. Sampling points were equally distributed along each lake's shoreline cardinal direction. All dominant microhabitat structures in the littoral zone of the study lakes were sampled at random. At each point captured fish were determined to species level, counted, measured (total length, TL to the nearest mm) and released. The number per unit effort (NPUE) was calculated for each fish species as individuals per sampling point to enable comparisons of relative abundance within different structures, seasons and daytime.

Microhabitat assessment

The microhabitats in the littoral zone of the study lakes were categorized into six predefined habitat types: (1) open littoral, unvegetated littoral areas with no or low structural complexity, (2) supplemented deadwood, introduced deadwood brush piles, (3) natural deadwood, aggregation of snags, branches or

submerged trees, (4) overhanging trees (overhanging branches of shoreline vegetation), often immersed into the waterbody, (5) emerged macrophytes, mainly common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) stands, cattail (*Typha* spp.) and water mint (*Mentha aquatica* L.) and (6) submerged macrophytes, dominated by *Elodea* spp., *Myriophyllum* spp. and *Stratiotes aloides* L.

Abiotic data

We calculated lake-specific mean and maximum depth, total area and depth strata (CEN, 2015) percentages from contour maps (see Matern et al., (2019) for further details). Shoreline length was calculated using QGIS (QGIS Development Team, 2019). At every fishing event, Secchi depth was measured to cover lake turbidity. Conductivity was measured at the surface using a Multi 350i sensor, 164 device (WTW GmbH™, Weilheim, Germany). Total phosphorous (TP) was measured following the molybdenum blue method (Murphy & Riley, 1962; ISO, 2004). Water samples for phosphorous analyses were taken at the surface in the middle of the lake during each fishing event and mean values were estimated from all four samplings to generate robust results for mean annual concentrations.

Statistics

Three microhabitats, natural wood, overhanging trees and submerged macrophytes had to be excluded from further analyses, because of insufficient sample sizes (Table S1). Therefore, we only analysed the three most abundant littoral microhabitats (open littoral, deadwood brush piles and emerged macrophytes) using generalized linear mixed models (GLMM). We defined five model structures a priori. First, we modelled the species-specific NPUE as function of the interaction between the categorical explanatory variables of season (categorical, levels: spring, summer, autumn, winter) and microhabitat (categorical, levels: open littoral, deadwood brush piles, emerged macrophytes) and a random intercept for "lake" (categorical, eight levels) to identify season-specific differences in fish abundance amongst the microhabitats.

- (1) Number of Individuals per point (NPUE) ~ Season * Microhabitat + (1|Lake)

Second, to identify possible patterns of turbidity on the microhabitat use of fishes, species NPUE was modelled as a function of an interaction term of microhabitat and mean Secchi depth (continuous variable):

- (2) Number of Individuals per point (NPUE) ~ Mean Secchi depth*Microhabitat + (1|Lake)

Third, to identify potential diurnal effects within each season, we modelled species-specific NPUE as function of interactions between daytime (categorical, two levels: day, night) and microhabitat, including lake as a random intercept to account for the dependency of data through multiple measurements within each lake.

- (3) Number of Individuals per point (NPUE) ~ Daytime*Microhabitat + (1|Lake)

To identify length differences amongst the three microhabitats amongst seasons, GLMM models were ran in species subsets with fish length (continuous; total length in mm) as numerical-dependent variable against a function of the categorical variable microhabitat and lake as a random effect.

- (4) Fish length (mm) ~ Microhabitat + (1|Lake)

Fifth, to identify diurnal effects on fish size distribution in each of the sampled microhabitats amongst the seasons, fish length was modelled against an interaction of daytime and microhabitat and lake as a random effect.

- (5) Fish length (mm) ~ Daytime*Microhabitat + (1|Lake)

In total, for each of the six dominant species eel (*Anguilla anguilla* (Linnaeus, 1758)), perch, pike, roach, rudd and tench one model for patterns amongst seasons, one model for turbidity effects on microhabitat use, four models to identify diurnal patterns within each season, one model for size-specific patterns of microhabitat use amongst seasons and one model for diurnal size-specific patterns amongst microhabitats use were run. Species-specific models were run with data subsets, including only lakes with species occurrence.

GLMM models with negative binomial (NB) distribution with a log link function were estimated using the glmmTMB package (Brooks et al., 2017) and a dispersion parameter allowed for greater variances compared to the mean (Zeileis et al., 2008). The model residuals were tested for overdispersion and heteroscedasticity using the DHARMA package (Hartig, 2020). To account for heteroscedasticity, the dispersion parameter was adjusted using a log link function (Brooks et al., 2017). Zero-inflation was tested using the zero-inflation test implemented in the DHARMA package (Hartig, 2020). In two cases (season*microhabitat interaction model for perch and roach) overdispersion was detected after using a negative binomial distribution. However, as GLMMs are generally robust against violations of assumptions (Schielzeth et al., 2020) and for comparability the model structure was kept.

Pairwise comparisons amongst interactions of estimated marginal means using the emmeans package (Lenth et al., 2018) were applied as post hoc tests, using Tukey (HSD) p-value adjustment (Abdi & Williams, 2010). This procedure allowed direct comparisons amongst contrasts of the respective model to identify differences expressed by incidence rate ratios (IRR) in microhabitat-specific abundance and fish length across season and daytime. The IRR is a comparison of measured rates (e.g. the rate of abundance) between two groups, where an IRR value of one indicates the same rate in both groups, an IRR of 0.5 indicates half the rate in the second group compared to the first, and an IRR of two indicates double the rate in the second group compared to the first. All statistical analyses were performed in R version 3.6.1 (R Core Team, 2021).

Results

Lake environment

All gravel pit lakes were relatively young (mean age \pm SD = 42.9 ± 7.96 years, range: 27–53 years; Table 1). The lakes covered a size range from 1.3 to 19.5 ha (mean \pm SD = 8.4 ± 6.84 ha), and the shoreline length ranged from 417 to 2752 m with a mean \pm SD of 1472.4 ± 802.2 m. Mean lake depth was 5.2 ± 3 m (range = 2.3 to 11.9 m). On average, the sampled lakes were characterized by a mean littoral share (Lake

stratum to a depth of 3 m) of $27.6 \pm 16\%$. Conductivity (mean \pm SD) ranged from $216.2 \pm 3.2 \mu\text{S cm}^{-1}$ in Collrunge to $642.5 \pm 5.9 \mu\text{S cm}^{-1}$ in Meitzer See. The mean Secchi depth estimated for all sampling lakes amongst the sampling seasons was 2.7 ± 1.1 m, the highest mean Secchi depth of 3.9 ± 0.7 m was measured in Meitzer See, whereas the lowest mean Secchi depth was found in Saalsdorf (1.4 ± 0.5 m). Total phosphorous concentrations \pm SD varied between $8.5 \pm 5.4 \mu\text{g l}^{-1}$ in Meitzer See and $29.5 \pm 15.8 \mu\text{g l}^{-1}$ in Saalsdorf (Table 1). Accordingly, the lakes we sampled were small and mesotrophic with steep depth gradients from the shore. All lakes were actively managed and exploited by recreational fisheries.

Fish sampling, species composition and general habitat preferences

In total, 4097 points were fished with an almost equal effort distribution amongst seasons ($N_{\text{spring}} = 1020$; 25%, $N_{\text{summer}} = 1158$; 28%, $N_{\text{autumn}} = 943$; 23%, $N_{\text{winter}} = 976$; 24%) and between day and night ($N_{\text{day}} = 2083$; 51%, $N_{\text{night}} = 2014$; 49%; Table S1). Brush piles ($N = 1206$; 29%), open littoral ($N = 1091$; 27%) and emerged macrophytes ($N = 843$; 21%) were the most common structures found in the sampling lakes and thus, predominantly sampled through our

random sampling design (Table S1). Overhanging trees ($N = 349$; 8%), natural deadwood ($N = 323$; 8%) and submerged macrophytes ($N = 285$; 7%) were scarce and thus, much less sampled, which ultimately did not allow further analyses.

A total of 14,458 specimens from 15 fish species were caught in the eight lakes. Perch and roach were the only species occurring in all eight lakes, whereas eel, pike and tench were each missing in one lake (Tables 2, Fig. S2). Rudd and bream occurred in four and five sampling lakes, respectively, whilst most other species were detected in only one lake (Table 2). Across all lakes, the most abundant species was perch with 8268 sampled fish (57% of the total catch), followed by 2728 roach (19% of the total catch). Perch was dominant in almost all microhabitats, except emerged macrophytes, where cyprinid species (rudd and roach) contributed most to the total catch (Fig. S2). Eel was caught in all microhabitats in low numbers. Pike was mainly caught in submerged and emerged macrophytes, but in overall low abundance (Fig. S2). Tench abundance was highest in the open littoral, under overhanging trees, and in artificial deadwood habitats (Fig. S2).

Table 2 Total catch, frequency of occurrence (proportion of lakes containing a species) and mean NPUE \pm SD per species

Common name	Scientific name	Total N	Presence (n/8)	Mean NPUE \pm SD
European perch	<i>Perca fluviatilis</i> L., 1758	8268	8/8	2.06 ± 0.8
Roach	<i>Rutilus rutilus</i> (L., 1758)	2727	8/8	0.7 ± 0.8
Rudd	<i>Scardinius erythrophthalmus</i> (L., 1758)	1803	4/8	0.7 ± 1.1
Tench	<i>Tinca tinca</i> (L., 1758)	449	7/8	0.11 ± 0.1
European eel	<i>Anguilla anguilla</i> (L., 1758)	438	7/8	0.25 ± 0.3
Northern pike	<i>Esox lucius</i> L., 1758	265	7/8	0.07 ± 0.05
Bream	<i>Abramis brama</i> (L., 1758)	215	5/8	0.09 ± 0.09
Prussian carp	<i>Carassius gibelio</i> (Bloch, 1782)	205	1/8	0.38
Common carp	<i>Cyprinus carpio</i> L., 1758	30	5/8	0.01 ± 0.003
European catfish	<i>Silurus glanis</i> L., 1758	22	1/8	0.04
Ruffe	<i>Gymnocephalus cernua</i> (L., 1758)	15	2/8	0.01 ± 0.01
Pikeperch	<i>Sander lucioperca</i> (L., 1758)	9	1/8	0.02
Cyprinid hybrid	<i>Scardinius x Abramis</i>	9	3/8	<0.01
Rainbow trout	<i>Oncorhynchus mykiss</i> (Walbaum, 1792)	1	1/8	<0.01
Goldfish	<i>Carassius auratus</i> (L., 1758)	1	1/8	<0.01
Gudgeon	<i>Gobio gobio</i> (L., 1758)	1	1/8	<0.01

Microhabitat-specific size differences amongst the seasons

Generally, with eel as an exception, predominantly smaller individuals of each species were caught. The mean total length ($mean_{TL}$) of fishes differed amongst the microhabitats and amongst the seasons. Overall, the size of eel caught in brush pile habitats was significantly larger ($mean_{TL} \pm SD = 445.9 \pm 142.2$ mm) compared to both other microhabitats (open littoral— $mean_{TL} \pm SD = 281.1 \pm 136.4$ mm/emerged macrophytes— $mean_{TL} \pm SD = 359.2 \pm 140.3$ mm). In spring, summer and autumn, eel within the well-structured habitats were significantly larger than in

the open littoral (Fig. 2, Tables 3, Table S3). Only in winter, when eel catches were generally low, no size difference was detected amongst eels in the different habitats (Fig. 2, Table 3, Table S3). Within all seasons perch caught in brush piles ($mean_{TL} \pm SD = 92.5 \pm 30.1$ mm) and emerged macrophytes ($mean_{TL} \pm SD = 93.1 \pm 36.1$ mm) were significantly larger than in the open littoral ($mean_{TL} \pm SD = 85.2 \pm 27$ mm) (Fig. 2, Table 3, Table S3). In summer perch caught in brush piles were significantly larger than in the two other microhabitats (Fig. 2, Table 3, Table S3). Overall, the length of pike caught in brush piles ($mean_{TL} \pm SD = 323.8 \pm 127.4$ mm) was on average larger than compared to both

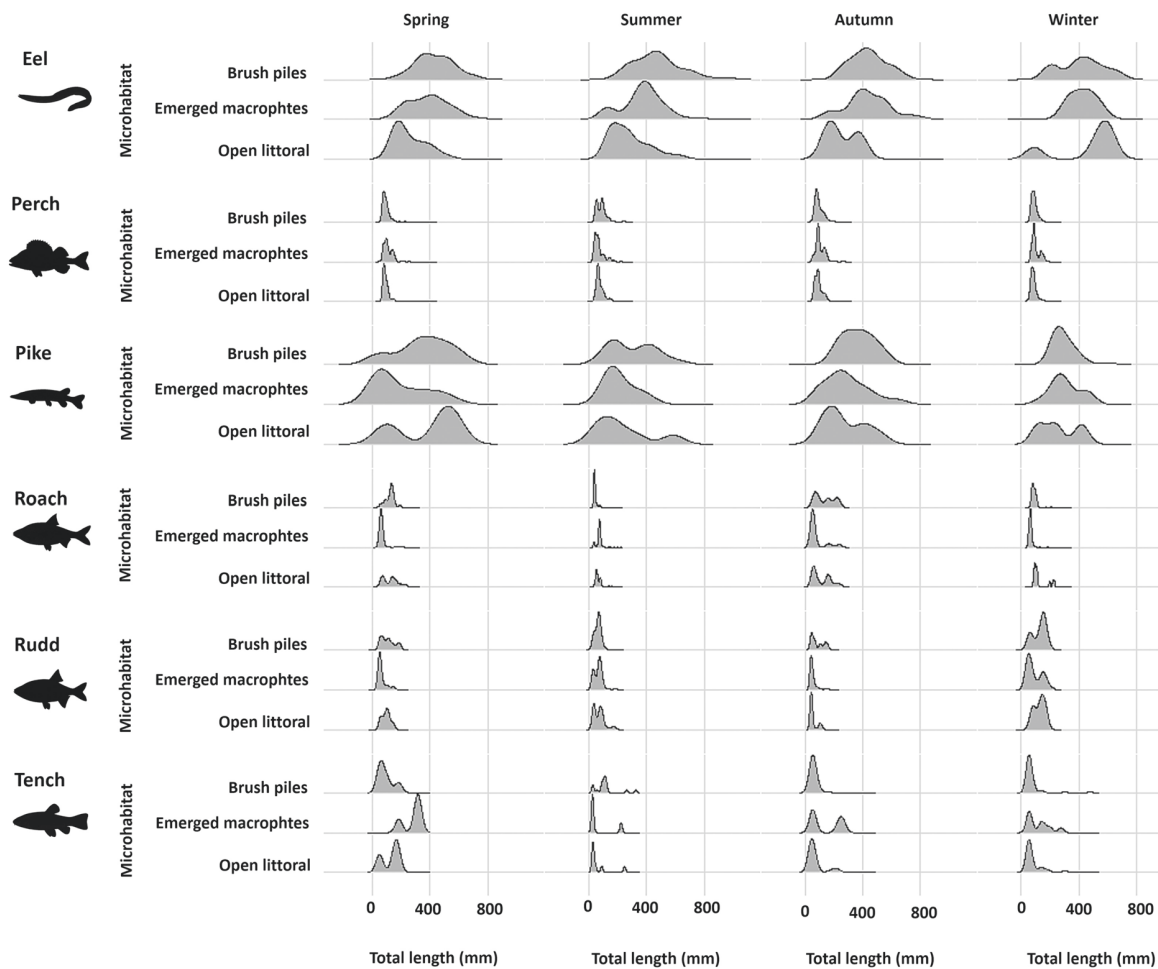


Fig. 2 Season- and species-specific density distribution of fish size (total length in mm) amongst the three most dominant microhabitats averaged amongst daytimes

Table 3 Total number of individuals, mean size \pm SD and size range (minimum and maximum total length in mm) of fish species caught in the three dominant microhabitats

Species	Microhabitat	Total No. of individuals	Total length (mm)			
			Mean	SD	Min	Max
Eel	Open littoral	78	281.1	136.4	90	639
	Emerged macrophytes	146	395.2	140.3	100	795
	Brush piles	133	445.9	142.2	152	967
Perch	Open littoral	2340	85.2	27	11	272
	Emerged macrophytes	1182	93.1	36.6	27	274
	Brush piles	3145	92.5	30.1	34	303
Pike	Open littoral	26	266.7	173.9	52	591
	Emerged macrophytes	118	257.9	146.4	47	665
	Brush piles	76	323.8	127.4	50	630
Roach	Open littoral	567	92.1	51.2	35	290
	Emerged macrophytes	813	68.7	25.3	27	252
	Brush piles	1109	63.4	38.6	20	330
Rudd	Open littoral	159	74.2	34.9	25	182
	Emerged macrophytes	1053	64.2	34.2	17	216
	Brush piles	412	86.7	43.2	9	201
Tench	Open littoral	94	74.6	58.2	26	302
	Emerged macrophytes	28	140.3	104.7	25	322
	Brush piles	248	68.9	49.9	27	476

other habitats microhabitats (open littoral— $\text{mean}_{\text{TL}} \pm \text{SD} = 266.7 \pm 173.9$ mm/emerged macrophytes— $\text{mean}_{\text{TL}} \pm \text{SD} = 257.2 \pm 146.4$ mm); however, this difference was not statistically significant (Fig. 2, Tables 3, Table S3). Mean_{TL} of pike did not differ significantly amongst the seasons (Fig. 2; Table 3, Table S3). Overall the roach individuals caught in the unstructured littoral ($\text{mean}_{\text{TL}} \pm \text{SD} = 92.1 \pm 51.2$ mm) were significantly larger compared to both structured microhabitats (brush piles— $\text{mean}_{\text{TL}} \pm \text{SD} = 63.4 \pm 38.6$ mm/emerged macrophytes— $\text{mean}_{\text{TL}} \pm \text{SD} = 68.7 \pm 25.3$ mm) (Fig. 2, Tables 3, Table S3). This pattern was observed in spring, summer and winter. Comparison amongst structured habitats revealed that in spring and winter the size of roach caught within brush piles was significantly larger compared to individuals caught in emerged macrophytes (Fig. 2; Tables 3, Table S3). In all seasons, length of rudd caught in brush piles ($\text{mean}_{\text{TL}} \pm \text{SD} = 86.7 \pm 43.2$ mm) and the open littoral ($\text{mean}_{\text{TL}} \pm \text{SD} = 74.2 \pm 34.9$ mm) was significantly larger than in the emerged macrophytes ($\text{mean}_{\text{TL}} \pm \text{SD} = 64.2 \pm 34.2$ mm), whereas there was no difference in length of rudd within

brush piles and the open littoral (Fig. 2; Tables 3, Table S3). Only in autumn rudd caught in emerged macrophytes and the open littoral were significantly smaller than rudd caught in brush piles (Fig. 2; Tables 3, Table S3). Amongst all season, sizes of tench caught in emerged macrophytes ($\text{mean}_{\text{TL}} \pm \text{SD} = 140.3 \pm 104.7$ mm) were significantly larger compared to the other main microhabitats (brush piles— $\text{mean}_{\text{TL}} \pm \text{SD} = 68.9 \pm 49.9$ mm/open littoral— $\text{mean}_{\text{TL}} \pm \text{SD} = 74.6 \pm 58.2$ mm) (Fig. 2; Tables 3, Table S3). In autumn, tench caught in brush piles and emerged macrophytes were significantly larger than tench caught in the open littoral (Fig. 2, Tables 3, Table S3).

Diurnal size differences of fish within the microhabitats

Diurnal size differences in each microhabitat amongst the seasons were found for roach, rudd and eel, whereas no significant diurnal size differences were observed for perch, pike and tench (Table 4). Eel and rudd caught in brush piles and the open littoral did not differ in size amongst day and night catches, but

Table 4 Pairwise comparisons, averaged over seasons, of microhabitat-specific fish length amongst day and night catches and microhabitat-specific mean total length \pm SD (in mm). GLMM using estimated marginal means and Tukey HSD p-value adjustment. Values present the incidence rate ratio (IRR) indicating lower size of fish caught during daytime compared to nighttime at IRR < 1

Bold characters indicate significant differences ($p < 0.05$)

Species	Microhabitat	IRR	p value	Total length in mm			
				Day		Night	
				Mean	SD	Mean	SD
Eel	Open littoral	0.81	0.12	254.0	116.0	311.0	148.7
	Emerged macrophyte	0.86	0.03	373.7	159.4	410.6	121.5
	Brush piles	1.04	0.96	459.8	128.1	430.6	153.9
Perch	Open littoral	1.04	0.31	86.9	29.0	85.2	27.8
	Emerged macrophyte	0.97	0.57	89.1	31.7	94.8	38.4
	Brush piles	1.01	0.98	90.7	27.0	93.9	32.1
Pike	Open littoral	0.77	0.93	265.0	170.9	267.1	170.4
	Emerged macrophyte	1.12	0.69	283.0	143.5	223.8	141.9
	Brush piles	1.06	0.98	318.5	113.9	328.1	135.8
Roach	Open littoral	0.80	<.001	65.7	29.0	96.7	52.7
	Emerged macrophyte	0.84	<.001	65.1	15.6	108.3	57.9
	Brush piles	0.93	0.14	56.0	29.0	103.7	55.7
Rudd	Open littoral	0.87	0.94	65.5	24.9	74.7	35.3
	Emerged macrophyte	0.85	<.001	60.4	26.9	70.8	43.3
	Brush piles	1.06	0.81	90.4	47.7	83.7	38.6
Tench	Open littoral	1.07	0.94	74.7	55.4	74.5	60.4
	Emerged macrophyte	0.93	0.99	133.2	81.1	145.6	116.2
	Brush piles	1.08	0.51	76.4	65.0	61.9	27.0

significantly larger individuals were detected during night in emerged macrophytes compared to daytime catches (Table 4). For roach individuals caught during night in the open littoral but also in emerged macrophytes were significantly larger compared to individuals detected during daytime (Table 4).

Seasonal variance in fish distributions amongst littoral microhabitats and effects of turbidity

Abundance patterns of the investigated species within microhabitats varied amongst seasons (Fig. 3; Table S4). In the open littoral winter catches were significantly lower for all fish species, except tench, compared to the other three seasons (Fig. 3; Table S4). In brush piles, relative abundances of perch and pike were highest in winter, and relative abundance of roach was elevated in winter compared to autumn and spring, but highest in summer (Fig. 3; Table S4). No significant differences in catches were detected between the structurally complex habitats emerged macrophytes and brush piles, although in the latter pike and roach catches tended

to be higher in winter (Fig. 4; Table S5). Compared to the other two microhabitats, in brush piles perch catches in winter and tench catches in autumn were significantly greater (Fig. 4; Table S5). In emerged macrophytes, relative abundance of eel, pike and rudd were higher compared to open littoral and brush piles in all seasons (Fig. 4; Table S5).

Amongst the seasons two main effects of turbidity on species-specific fish catches were observed. Increasing water clarity generally had a positive effect on catches of eel and pike for all microhabitats (Table S6). By contrast, catches of perch, roach, rudd and tench decreased with increasing water clarity (Table S6). Interacting effects of turbidity and specific microhabitats were observed for some species (e.g. in perch with significantly decreasing predicted catches in emerged macrophytes in clearer water when compared to brush piles), whilst no effect was detected for other species (e.g. tench) (Fig. S3; Table S7).

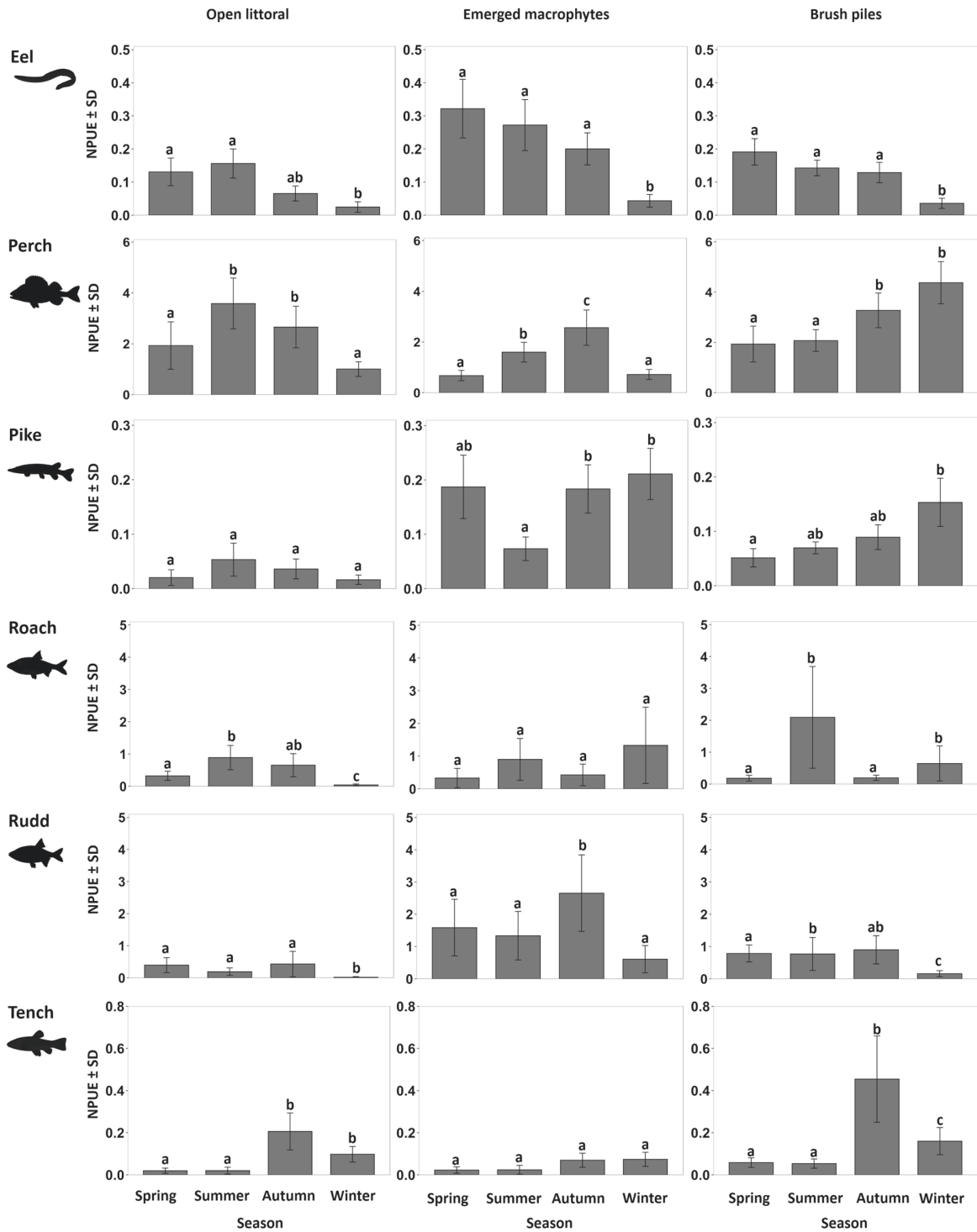


Fig. 3 Seasonal- and microhabitat-specific mean NPUE \pm SD of the six dominant fish species pooled for lakes and daytime. Different letters indicate significant differences amongst the seasons within each microhabitat

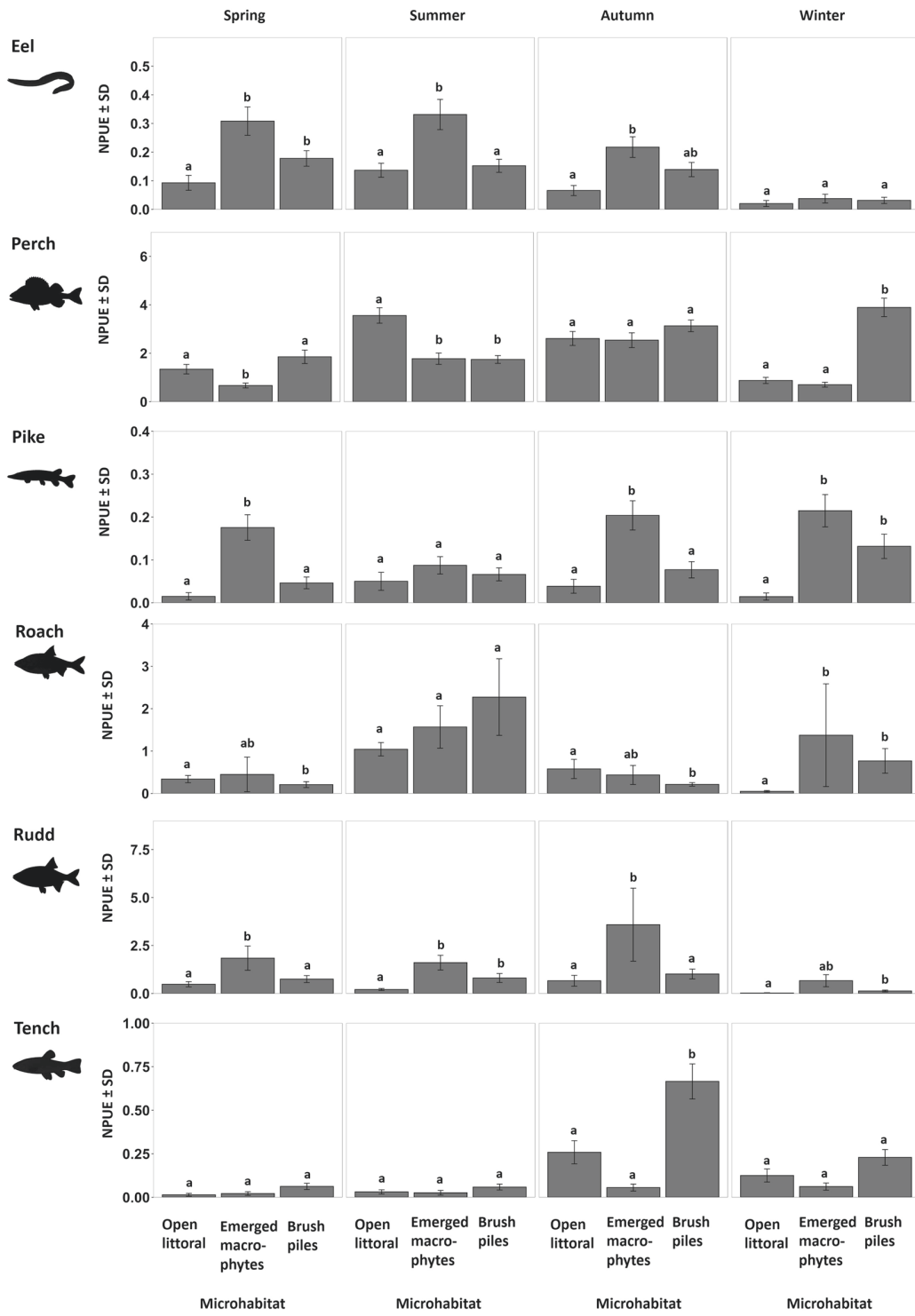


Fig. 4 Season-specific mean NPUE ± SD of the six dominant fish species within the three main microhabitats pooled for lakes and daytime. Different letters indicate significant differences amongst the microhabitats within each season

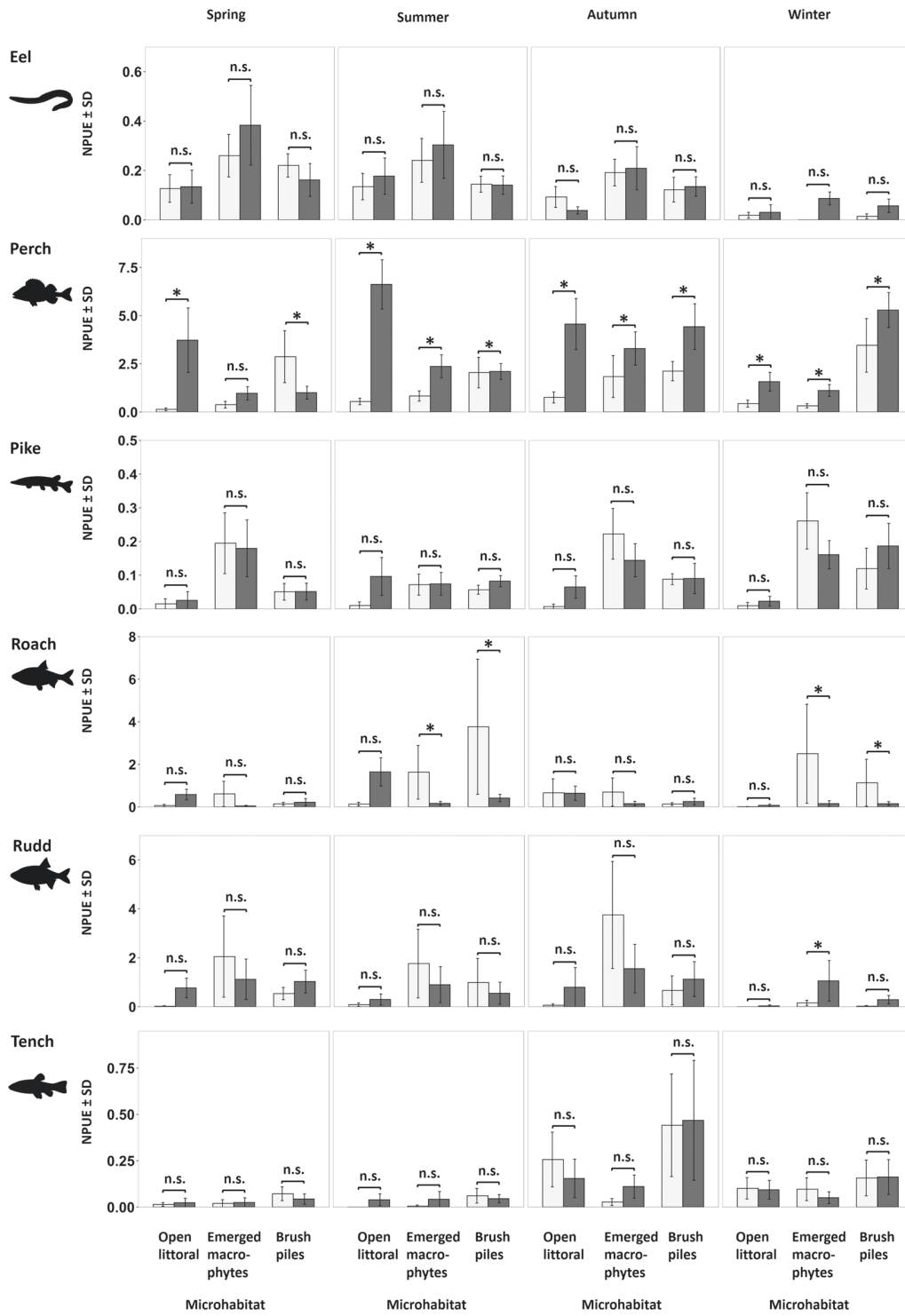


Fig. 5 Seasonal and diurnal mean NPUE ± SD of the six dominant fish species within the three main microhabitats. White and black represent catches during day and night, respectively; significant differences are indicated by asterisks

Diurnal variances in fish distribution amongst littoral microhabitats

Relative abundance as revealed by PASE was usually higher at night compared to daytime, which was especially evident in the open littoral (Fig. 5; Table S8). Diurnal differences in microhabitat catch rates, however, differed according to species (Fig. 5; Table S8). In all microhabitats perch NPUE was always significantly higher during nighttime, except for brush piles in spring (Fig. 5; Table S8). By contrast, relative abundance of roach in the two structurally complex habitats was higher during daytime, especially in summer and winter (Fig. 5; Table S8). No significant differences between day and night samples were found for eel, pike, tench and rudd (Fig. 5; Table S8). In emerged macrophytes, relative abundance of rudd was only significantly higher at night compared to daytime during winter (Fig. 5; Table S8).

Discussion

We studied the spatio—temporal patterns in microhabitat use of fish in eight gravel pit lakes. Our findings provide partial support for our first hypothesis as perch, roach, eel and tench were caught in high proportions in the supplemented deadwood brush piles, particularly during the colder months of the year, but differences to the other littoral habitats were only significant for perch in winter and tench in autumn. Furthermore, we did not observe effects of turbidity on microhabitat use when the unstructured microhabitat was compared to the well-structured microhabitats. Only catches of eel and pike increased with increasing water clarity, whilst catches of the other species decreased with water clarity. Our second hypothesis that larger individual fish prefer brush pile habitats was only supported for eel and perch where we caught larger individuals amongst all seasons in the brush pile habitats. By contrast, amongst seasons smaller cyprinid specimens (roach and rudd) were found in the well-structured brush pile and emerged macrophyte habitats, whereas larger individuals were caught in the open littoral. Our third hypothesis was not supported as we did not detect increased use of structured habitats during the day compared to night for any of the species studied; rather we found species-specific differences in diurnal use of littoral

structures. For example, during the day roach abundance was higher in structured habitats compared to unstructured habitats in summer and winter, whilst perch abundance was generally higher during the night in all sampled habitats, with two exceptions in brush piles in spring and summer. In addition to active habitat use, results might also be affected by light-dependent catchability of the electrofishing unit (see below). Supporting our fourth hypothesis, we detected significantly greater species-specific abundance in brush piles compared to unstructured littoral areas in winter. In addition, perch abundance was greater in brush piles than in emerged macrophytes, indicating the relevance of this microhabitat for perch specifically.

Use of littoral structures and implemented brush piles

We focused on six species (eel, perch, pike, roach, rudd, tench) typically occurring in gravel pit lakes and other temperate European lakes (Emmrich et al., 2014; Matern et al., 2019, 2022). All of these species were found to use the newly added brush piles throughout the year, and in some cases (e.g. perch), we detected elevated abundances of fish in brush piles compared to other structures. Also, structured habitat was often hosting larger fish abundances (e.g. eel, pike and rudd) compared to the unstructured open littoral. In particular, eel was strongly associated with structured habitats, mainly emerged macrophytes, supporting previous studies on the habitat choice of this species (Laffaille et al., 2001; Ovidio et al., 2013; Lewin et al., 2014; Matern et al., 2021). Abundances of perch and roach were also strongly associated with structurally complex habitats, including artificially implemented deadwood in some seasons, which was expected based on previous work investigating microhabitats in a natural lake and corresponding natural occurrences of deadwood (Lewin et al., 2004).

Vegetated microhabitats are known to be a key-structured habitat in most lakes and indeed, submerged and emerged macrophyte stands have been identified as key habitat structures for pike (Grimm & Backx, 1990; Eklöv, 1997; Kobler et al., 2008; Matern et al., 2021), rudd (Eklöv & Hamrin, 1989; Lewin et al., 2014; Matern et al., 2021) and tench (Perrow et al., 1996; Lewin et al., 2014). Similarly, in our work, we found emerged macrophytes highly

important, especially for rudd, whereas tench and pike were also associated with woody habitats in autumn and winter. In gravel pit lakes, previous research at meso-habitat scales already showed that pike abundance was not associated with the extent of submerged macrophytes, but was positively related to the degree of deadwood habitat (Matern et al., 2021). Accordingly and in line with literature (e.g. Skov & Berg, 1999) supplemented deadwood brush piles offered suitable habitats for pike and other typical lake fish species.

Structurally complex habitats, however, are known to be less important for predation-prone fishes with increasing turbidity, as the hunting success for visual hunting predators is impeded (Cook & Bergersen, 1988; Abrahams & Kattenfeld, 1997; Utne-Palm, 2002; Snickars et al., 2004). Hence, even though the turbidity gradient amongst the lakes was rather small and eutrophic turbid lakes were not included in our study, turbid conditions should have positively impacted the catch rates in the unstructured littoral and in contrast lowered the catches in the structurally complex habitats (Miner & Stein, 1996; Abrahams & Kattenfeld, 1997). Indeed, we found turbidity to positively impact catch rates of perch, roach, rudd and tench in all microhabitats, but did not detect significant differences in fish abundance when the unstructured microhabitat was compared with the structurally complex microhabitats amongst different turbidity levels (Fig. S3, Table S7). The generally positive effect of turbidity on fish abundance was likely related to increased productivity in turbid lakes (Persson et al., 1991; Olin et al., 2002) and/or a generally higher catch efficiency due to lower escape distances of fishes (Korman & Yard, 2017). In contrast to this pattern, abundances of eel and pike increased with decreasing turbidity; however, water clarity affected the abundance in structured and unstructured habitats in the same manner as indicated by a lack of clear interaction effects amongst turbidity and habitat type. As visually hunting predators (Casselman & Lewis, 1996), pike are more effective predators in clearwater conditions where they mostly rely on submerged structures, especially macrophytes (Jacobson & Engström-Ost, 2018). Hence pike abundances and pike recruitment are described to peak in lakes of intermediate trophic state (which are often quite clear) (Haugen & Vøllestad, 2018), likely explaining the positive effect of increased water clarity on

pike abundances in our study. In isolated gravel pit lakes eel abundances depend on stocking (Emmrich et al., 2014; Matern et al., 2021), hence in our sampling lakes eel catches are best explained by stocking intensity, suggesting that clearer waterbodies by chance had higher stocking rates or lower exploitation rates post stocking. Generally, we did not observe the expected shifts in habitat use intensity according to varying turbidity states, most likely because of a relatively narrow turbidity gradient across the mesotrophic sampling lakes.

Size-specific use of littoral microhabitats

We found species-specific variation of fish size distribution in the different studied littoral microhabitats. Amongst the seasons, significantly larger individuals of eel and perch were found in brush piles and emerged macrophytes, but also larger pike were more frequently caught in the brush piles. By contrast, the average size of the cyprinids roach and rudd caught in the structured habitats was lower compared to open habitats. Whereas, juvenile roach and rudd are known to be strongly associated with dense structures such as reed stands where they seek shelter from predation during daytime (Kennedy & Fitzmaurice, 1974; Bohl, 1980; Gliwicz et al., 2006; Nakayama et al., 2018), larger individuals especially of roach are less reliable on structural complexity and are known for inshore movements during night (Wolter & Freyhof, 2004; Říha et al., 2015), which likely explains the greater fish size in the open littoral in the dark. Another reason could simply be reduced fleeing reactions of the larger roach during the night. Tench of all size classes as a cryptic species (e.g. Weatherley, 1959) are known to favour well-structured littoral habitats (Perrow et al., 1996; Herrero et al., 2003; Moreno et al., 2003). Similar to findings reported by Perrow et al. (1996), we found large tench individuals in emerged macrophytes stands, whereas rather small individuals of tench were caught in brush piles (where smaller individuals might have found shelter in the crevices beneath the branches) and in the open littoral (where small tench might have found shelter in benthic coarse organic debris (e.g. accumulations of fallen leaves)). The ability of smaller individuals to hide in a vast variety of coarse substrates (e.g. Fischer & Eckmann, 1997b; Christoffersen et al., 2018; Nilsson et al., 2020; Steendam et al., 2020) likely explains

why the mean size of eel in the open unstructured littoral was significantly lower compared to individuals caught in the more complex structures, especially in brush piles. In contrast to juveniles, larger eels are known to depend on more complex shelter such as woody structures (e.g. roots) especially during daytime (Baras et al., 1998; Ovidio et al., 2013). Larger individuals of perch and pike were also found in the complex habitats compared to the open littoral, which especially holds true for larger perch individuals in brush piles, which are known to be associated with woody habitats in lakes (e. g. Westrelin et al., 2018; Matern et al., 2021). The brush pile habitats offer accumulations of small sized prey fish such as roach and well-suited hunting conditions for predatory species that rely on structure–open water interfaces where they are able to ambush their prey (Eklöv & Diehl, 1994; Casselman & Lewis, 1996; Eklöv, 1997). Hence, different size classes of typical species in gravel pit lakes benefit from structurally complex microhabitats, with larger individuals especially of predatory species benefitting from improved hunting conditions and smaller specimens, especially of cyprinid species, finding shelter within these habitats.

Diurnal variation in littoral use

In line with other studies, species-specific abundance revealed by electrofishing at night was substantially greater than during daytime (Dumont & Dennis, 1997; Pierce et al., 2001; Ross et al., 2016). This finding was particularly evident in the unstructured littoral microhabitat and might either represent active habitat choice [e.g. foraging in profitable patches of zooplankton or benthos at lower predation risk due to diurnal horizontal migration (Lewin et al., 2004; Gliwicz et al., 2006)] or reflect improved catchability at night (Alabaster & Stott, 1978; Paragamian, 1989). However, the result of greater abundance at night was not general across all six species investigated. Specifically, diurnal differences were identified for perch and roach, moving from the structured habitats to the open littoral at night (Bohl, 1980; Copp & Jurajda, 1993; Lewin et al., 2004; Gliwicz et al., 2006). Juvenile perch are reported to leave their groups and be more broadly distributed in open habitats during nighttime (Copp & Jurajda, 1993; Wang & Eckmann, 1994; Haertel & Eckmann, 2002). Additionally, perch in mesotrophic lakes have been reported to move

from the pelagic to the littoral where they remain during night (Jacobsen et al., 2015; Nakayama et al., 2018). Our work thus agrees with previous reports on species-specific diurnal behaviours.

Pattern of diurnal horizontal migrations have been observed for roach and can be explained by higher predation risk during daytime, but also greater zooplankton availability in the open habitats during nighttime (Gliwicz & Jachner, 1992; Okun & Mehner, 2002, 2005; Lewin et al., 2004; Gliwicz et al., 2006; Schulze et al., 2006). Hence, some fish leave the safe-structured habitats during night and swim into open water areas when predation pressure by visually hunting predators (e.g. perch or pike) is reduced (Pitcher & Turner, 1986). This behaviour likely contributed to the observed higher roach abundance during night in the unstructured littoral and higher abundances during daytime in well-structured habitats in summer and winter. In addition, inshore movements by larger individuals (e.g. Říha et al., 2015) during nighttime, as observed in our study, might have caused greater catches in the littoral zone during the night. By contrast, catches of eel, pike, rudd and tench remained generally unaffected by time of day as these species strongly depend on various littoral structures throughout the entire day (Lewin et al., 2014; Matern et al., 2021), rendering diel habitat shifts less relevant and less pronounced compared to perch and roach. Most likely, also elevated catchability in open water during low visibility conditions likely contributed to the roach patterns revealed in our work.

Seasonal variation in littoral use

We detected differences in habitat use intensity amongst seasons, most clearly expressed during winter, when many species were rather structure oriented and far less frequently observed in the unstructured habitats. The use intensities of perch, roach and pike in the structured habitats were especially high during winter. The underlying mechanisms might have differed according to species, but can generally be explained by a seasonal habitat shift into sheltered structures as survival strategy to lower predation risk at reduced foraging and metabolic costs in winter (Shuter et al., 2012). Following the decay of submerged macrophyte stands, structural oriented fish (e.g. pike) are forced to use other available structures during the colder phases of the year (e.g. Grimm

& Klinge, 1996; Baade & Fredrich, 1998). Pike as structure-dependent sit-and-wait predator (Grimm & Klinge, 1996) might have found better cover conditions and prey availability around the constantly present woody habitats (e.g. Skov & Berg, 1999). Roach and perch were also found in increasing numbers in the brush pile microhabitats during the colder phases of the year, most likely to reduce their predation risk, which was not only higher due to the presence of pike foraging during winter (Diana & Mackay, 1978) but potentially also due to the higher occurrence of winter migrating piscivorous birds (Orpwood et al., 2010; Lemmens et al., 2016), primarily cormorants (*Phalacrocorax carbo* (Linnaeus, 1758)), frequently observed on the sampling lakes. As lower temperatures affect the physiology of poikilothermic fish leading to limitation of maximum swimming speed and general activity (e.g. Claireaux et al., 2006), probabilities of evading attacks by piscivores are reduced at low water temperature. Hence, remaining in the persistent structurally complex deadwood structures likely reduced the predation risk and predation-related stress during winter (e.g. Jacobsen et al., 2004). Only eel abundance was low within artificial deadwood structures during winter, likely because of avoidance of shallow zones and dormancy behaviour expressed by low activity rates when temperatures decrease (Walsh et al., 1983; Westerberg & Sjöberg, 2015).

Fish aggregations in seasonally robust structures, such as woody structures, as a response to changing conditions in winter observed here are in agreement with previous research, which showed that fish using supplemented woody habitats had reduced predation risk and higher survival chance (Russell et al., 2008; Orpwood et al., 2010; Lemmens et al., 2016). However, when both predator (e.g. perch) and prey share the same habitat during winter, it can create an ecological trap for the prey (Robertson & Hutto, 2006). Hence, an increase of long-lasting complex deadwood structures in gravel pit lakes, that otherwise lack structural complexity, certainly increases the availability of shelter to predation-prone fish, potentially leading to an increased winter survival and generally better conditioned fish. Alternatively, aggregations of piscivorous fish together with their prey might lead to higher predation rates, reversing the positive outcomes of shelter for the prey fish. Answering the latter question, however, needs

before-after-control-impact study designs. Our work only examined the habitat use and distribution of fish and did not study how artificial brush piles might have affected total abundance of fish.

Limitations

We used electrofishing to identify fish distributional patterns, which has different efficiencies according to species and size classes (Dolan & Miranda, 2003; Menezes et al., 2013; Rümmler, 2015). Hence, certain species and size classes might be underrepresented in the present dataset; however, our results are based on intraspecific comparisons across habitat types and should, thus, not be affected by gear selectivity. Additionally, electrofishing is less effective in deeper and unstructured habitats (Bohlin et al., 1989), which could have resulted in lower and, hence, biased catches in open water habitat. Specifically, daytime catches might be underestimated when fish detect the approaching boat and escape earlier, whilst at night escape distance is less (e.g. Paragamian, 1989). However, electrofishing is widely used and results are robust concerning species diversity and abundance, especially when applied in complex habitats where other methods are not applicable (Jurajda et al., 2009; Copp, 2010; Mueller et al., 2017). Further studies of microhabitat use in deeper littoral areas of especially cautious, larger fish that were underrepresented here might use scuba diving (e.g. Brosse et al., 2001) or camera-based observations (Ellender et al., 2012) to avoid this sampling bias.

Longevity of brush pile structures and effects on water quality

Decomposition rates of our brush piles and thus longevity of management measures remain unknown. Hardwood as used in our study is known to decompose slower in aquatic compared to terrestrial environments (Bilby et al., 1999) and mass loss can be very slow (France et al., 1997). As a consequence, brush piles made from hardwood can potentially last for decades under water (Bilby et al., 1999). In agreement with this assumption we did not observe visible reductions of brush piles within the first years after application. Leaching of nutrients from the deadwood was not measured, but no changes in pH values and nutrient compositions were observed on the lake level

before and after brush pile addition (Arlinghaus et al., in press), indicating no significant changes in water chemistry as a consequence of deadwood addition to mesotrophic lakes.

Conclusion and implications

The present study showed the generally high relevance of structurally heterogeneous microhabitats for common fish species in the littoral zones of gravel pit lakes throughout all seasons. The efficiency of deadwood brush piles immediately after supplementation was indicated by its attraction of selected fish species, especially during the colder phase of the year. Hence, habitat enhancement by adding deadwood structures increases the overall habitat availability for structurally oriented fish and might lead to higher fish abundance of some species, especially in artificial water bodies (Radinger et al., in press). It is recommended that fisheries managers consider deadwood applications, especially in shallow areas, to support fish populations by improving the structural complexity of littoral zones rather than solely relying on stocking or harvest regulations (e.g. Sass et al., 2017). Authorities could support such deadwood applications by keeping bureaucratic hurdles low. However, this study identified spatio-temporal dynamics, i.e. effects of deadwood provision on fish distribution rather than fish productivity or abundance. Further research is needed to differentiate distributional effects of habitat placement from additive effects on abundance. Alternatives to deadwood implementations, such as creation of shallow water zones where underwater vegetation can develop, should also be investigated in terms of effects on habitat use and abundance, because deadwood installation in deeper water might also serve as an ecological trap for prey fish by attracting both predators and prey. By contrast, shallow water zones might be less accessible to larger predators and thus more effective in raising fish abundance than deadwood placements (Radinger et al., in press).

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The fish sampling complied with Lower Saxonian fisheries law and included permission for electrofishing (# 34.2–65434–IV, # 34.2–65434–II). The authors have no conflict of interest.

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