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Environmental determinants of fish community structure in gravel pit lakes

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Abstract – Gravel pit lakes are increasingly common, and there is an urgent need to better understand the functioning of these artificial and disconnected ecosystems. However, our knowledge of the environmental determinants of fish community structure within these types of lakes remains poor. In this study, we quantified the taxonomic diversity, fish species and life-stage composition in 17 gravel pit lakes sampled in 2012 and 2013 located in south-west France to determine the potential role of environmental variables (i.e. lake morphology, productivity, water quality and human-use intensity) as drivers of fish community structure and composition. Our results demonstrated that fish community structure significantly differed between gravel pit lakes, and we notably found that lakes managed for angling hosted higher levels of taxonomic diversity. We also found that young and large lakes supported higher native species biomass and were dominated by native European perch (*Perca fluviatilis*). Older, smaller and more productive lakes, located closer to the main urban area, supported a higher biomass of non-native species such as largemouth bass (*Micropterus salmoides*). Native and non-native sport fishing species such as northern pike (*Esox lucius*), pikeperch (*Sander lucioperca*), common carp (*Cyprinus carpio*) and cyprinid prey species were positively associated with fishery management effort, suggesting that management practices play also a critical role in shaping fish species composition. Overall, our study demonstrated that fish community composition followed a predictable shift along environmental gradients associated with the maturation of gravel pit lakes and the associated human practices.

Key words: artificial ecosystems; community structure; species composition; gravel pit lakes; non-native species

Introduction

Freshwater ecosystems support a rich diversity of biological life and provide countless resources and services to human societies (Strayer & Dudgeon 2010). However, freshwater biodiversity and the associated ecosystem services have been strongly impacted in the last few decades by multiple pressures associated with the development of human populations (Darwall et al. 2011; Alofs et al. 2014). Habitat loss is, for instance, considered as one of the main drivers of the current freshwater biodiversity crisis (Dudgeon et al. 2005), and a large number of natural freshwater ecosystems have been subjected to pollution, dried-out or under the development of urban areas (Kozlowski & Bondallaz 2012). As a consequence, several aquatic organisms have been impacted and fish are currently recognised as one of the most widely threatened groups of freshwater organisms (Duncan & Lockwood 2001; Barletta et al. 2010; Pool et al. 2010). This is despite the fact that the estimated taxonomic diversity of fish species accounts for 30–50% of all the vertebrates (Geist 2011) and, importantly, that fish play a key functional role in fresh waters as changes in fish community structure (e.g. taxonomic composition, life-history characteristics, functional traits) can strongly affect ecosystem functioning (Nagdali & Gupta 2002; Mátyás et al. 2003; Jeppesen et al. 2010).

While many human activities are widely recognised as sources of degradation for natural ecosystems, humans can also create artificial freshwater ecosystems

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such as farm ponds, canals, reservoirs and gravel pit lakes (Santoul et al. 2004, 2009). These man-made habitats can represent important substitutes of the lost ecosystems for aquatic organisms (Santoul et al. 2004; Lenda et al. 2012). Once created and because they are usually located close to urban areas, gravel pit lakes are used for many purposes, including a myriad of recreational activities such as water sports and angling, creating important freshwater ecosystems that have recently attracted the scientific attention of biologists and ecologists (Santoul et al. 2009). Gravel pit lakes are usually small (1–100 hectares) and shallow (4–12 metres of maximum depth) (Kattner et al. 2000). However, one of their most intriguing features is that they are usually disconnected (except during exceptional flooding events) from other permanent aquatic systems, which is not the case of other artificial aquatic ecosystems such as reservoirs or canals that are located within riverine networks. Therefore, gravel pit lakes can be considered as '*islands within terrestrial seas*' (Hortal et al. 2014) and provide a unique opportunity to refine our understanding of the environmental determinants of freshwater fish community structure. Indeed, gravel pit lakes are usually filled by ground- and rainwater (Kattner et al. 2000), and the presence of strictly aquatic organisms such as fish primarily relies on the conjunction of mediated introductions (e.g. stocking for angling purposes) with environmental filters shaping fish communities.

Recently, Emmrich et al. (2014) demonstrated that fish communities in the littoral zone of gravel pit lakes do not differ from those in small natural lakes, providing a first empirical evidence that suggested some potential commonness in the functioning of their community. To date, however, there is still a gap in our understanding of the environmental determinants of fish community structure in gravel pit lakes. Empirical studies have long demonstrated the general importance of biotic, abiotic and spatial factors as determinants of fish community structure in natural ecosystems (reviewed in Jackson et al. 2001). Specifically, small- and large-scale abiotic drivers have been considered as the first environmental filters acting on fish community composition. For example, climate (e.g. temperature) can control species distribution at the regional scale, while chemical factors (e.g. oxygen and acidity) may play more important role in structuring local communities. Biotic interactions such as competition and predation can influence the occurrence of species and, to a greater extent, species abundance within a community (Jackson et al. 2001). In gravel pit lakes, one of the first filters acting on fish community is introduction history. Afterwards, the same ecological filters as in natural lakes can act (e.g. Jackson et al. 2001; Hortal et al. 2014), but their relative influence may vary in gravel pit lakes as these ecosystems mature. Therefore, one can expect that fish community composition in gravel pit lakes follow a predictable succession primarily driven by age and management practices that are likely to have stronger effects than in natural ecosystems.

The objectives of this study were to determine (i) how environmental characteristics are linked to fish community structure (i.e. taxonomic diversity, native and non-native species biomass) and (ii) the potential role of biotic, abiotic and spatial variables as potential drivers of fish community composition (i.e. species and life stages) in gravel pit lakes located in south-west France and distributed along a gradient of age and management practices. Specifically, we tested the following predictions. First, we predicted that fish community structure and composition differed between gravel pit lakes. Second, we predicted that differences in fish community structure and composition among gravel pit lakes were primarily driven by differences in environmental variables caused by their level of maturity and management practices.

Materials and methods

Study sites and fish sampling

In this study, 17 gravel pit lakes located in the central part of the Garonne floodplain (south-west of Toulouse, France) were monitored. To obtain a gradient of environmental conditions, we selected sites that were dredged between 1964 and 2007 (end-year of dredging) and managed under different practices and regulations regarding angling and accessibility (i.e. six lakes were under private management, while four and seven were managed under communal and federal fishing rights and practices, see details below) distributed across a heterogeneous landscape.

Fish communities were sampled using a combination of complementary approaches (i.e. gillnetting and electrofishing) from mid-September to mid-October. Sampling was performed using the same protocol in 2012 and 2013, with one lake being sampled per day. Two gillnets (length: 25 m, height: 3.1 m; mesh size: 20 and 50 mm respectively) were deployed in the pelagic area in the deepest zone of each lake. A set of gillnets (4–6 depending upon lake size; length: 20 m, height: 2.4 m; mesh size: 12, 20, 30, 60 mm) were distributed randomly within the lakes, perpendicular to the shore and representative of the different types of substrates and habitats in the littoral zone. In all lakes, gillnetting started in the morning (approx. 08:00 am). Importantly, netting duration was reduced to about 1 h (to approx. 09:00 am) to minimise fish mortality and to avoid excessive accumulation of fish in the nets (Erős et al. 2009). Electrofishing (Deka 7000; Deka, Marsberg, Germany) was performed using a point abundance sampling by electrofishing (PASE) approach from a small boat. PASE was selected to sample the shallow littoral habitat of the gravel pit lakes because it is a cost-effective and nondestructive method to sample different species and life stages in fish communities in lentic ecosystems (Persat & Copp 1990; Cucherousset et al. 2006). The specific procedure was conducted following Cucherousset et al. (2006). The sampling points were at least 25 m away from each other, and hand nets (5-mm mesh) were used to collect fish. Following the recommendation by Copp & Garner (1995) regarding the number of individual PASE locations, an average of 29.9 (±5.7 SD) and 29.5 (±5.3 SD) PASE locations were conducted in each lake in 2012 and 2013 respectively. All individuals sampled by gillnetting and electrofishing were identified to species and measured for fork length to the nearest mm. *Blicca bjoerkna* and *Abramis brama* were pooled together as bream spp. as earlier life-stages could not be discriminated in the field.

Fish community metrics

We first used total fish species richness, the number of non-native fish species and Shannon index (Shannon 1948) to characterise fish community structure in each lake. We also used the mass of each sampled individual estimated using length/weight relationship for each species to calculate several metrics of fish abundance: the biomass of native fish by gill netting (BPUENN, kg·net^{-1}), the biomass of non-native fish by gill netting (BPUENNON, kg·net^{-1}), the biomass of native fish by electrofishing (BPUEEN, kg·PASE^{-1}) and the biomass of non-native fish by electrofishing (BPUEENON, kg·PASE^{-1}). Then, the response of community composition to environmental variables was assessed by calculating the relative biomass of each life-stage of each species in each lake. This approach at the species life-stage level was selected because it can provide further understanding compared to taxonomic structure on population functioning (e.g. recruitment) and human activities (e.g. stocking). Therefore, each species was divided into different life-stages (i.e. young-of-the-year, juveniles and adults), and this was done through inspection of size (i.e. fork length) distribution in the studied populations and information about size at maturity. YOY were defined as the smaller group of individuals in the population size distribution with no or low overlap with the subsequent cohort, accounting for spawning period of each species in the study area (Keith et al. 2011). Adults were defined as the individuals with a fork length higher than reported size at maturity for each species (Keith et al. 2011; Froese & Pauly 2014). Juveniles were then defined as individuals smaller than size at maturity but larger than YOY. The same size limits were used to define the life stages of each species in all studied populations (further details available in Table S1). For four species (namely *Alburnus alburnus, Rhodeus amarus, Gambusia affinis and Gobio gobio*) that have an early age at reproduction, YOY and juveniles were pooled in the same life-stage.

Environmental variables

A set of 24 variables associated with the biotic and abiotic features of gravel pit lakes and human activities were selected based on their demonstrated importance in shaping fish community structures in freshwater ecosystems (e.g. Jackson et al. 2001; Mehner et al. 2005, 2007; Pool et al. 2010). These variables were grouped into four categories and described lake morphology, lake productivity, water quality and the intensity of human use (Table 1). These variables were collected using the following methodologies. Age of lakes (calculated as the difference between the last year of dredging and the sampling year) was provided by lake owners or local authorities. Shoreline development (SLD) was calculated using formula $\mathrm{SLD} = \mathrm{Pr}/(2\sqrt{\pi \mathrm{SA}})$ (Hutchinson 1957), where Pr was the perimeter of a lake and SA was the area of the lake. Pr, SA and other lake morphology variables, that is, distance to nearest river (DNR), distance to nearest gravel pits (DNG), ripisylve (Ri, percentage of area covered with trees within a 10-metre buffer around each lake) and island area (Ia, area of the island divided by the lake area) were calculated from aerial pictures and geographic information system (GIS) analyses. Mean depth (MD) and lake volume (Vl) were estimated using bathymetry analyses. Productivity and water quality variables were calculated based on the measurements (three replicates per lake) performed in each lake and for each year the month before and the month after fish sampling. Specifically, in each sampling time, chlorophyll *a* concentration (Chla) and turbidity (Tb) were measured using a portable fluorescence photometer (BBE-Moldaenke, Kiel, Germany), Secchi depth (Sec) was measured using a Secchi-disk, while pH and conductivity (Con) were measured using a portable multiparameter meter (WTW Multi 3400i, GmbH, Germany). Filtered and unfiltered water samples were collected, preserved in a cooler and subsequently frozen at the laboratory. Water samples were analysed for total phosphorus (TP), dissolved organic carbon (DOC) and dissolved nutrients (N-NH4 and P-PO4). The average value across sampling dates and

Table 1. Environmental variables [name, abbreviation, mean (±SD) and range] measured in the studied gravel pit lakes.

Name	Abbreviation	Mean (±SD)	Range
Morphology			
Age (years)	Age	23.3 (±12.0)	7–51
Mean depth (m)	MD	2.6 (±0.8)	1.2–4.2
Lake surface area (ha)	SA	12.33 (±7.02)	0.75–21.16
Lake volume ($m^3 \cdot 10^5$)	Vl	2.8 (±2.0)	0.2–7.4
Lake perimeter (m)	Pr	2044.9 (±1120.2)	425.2–4550.5
Distance to nearest river (m)	DNR	1461.8 (±584.8)	30–2460
Distance to nearest gravel pits (m)	DNG	300 (±649)	15–2285
Ripisylve (%)	Ri	42.0 (±24.0)	7.9–87.3
Island (%)	Ia	0.006 (±0.013)	0–0.05
Shore line development index	SLD	2.9 (±0.8)	2.1–5.0
Productivity			
Chlorophyll *a* ($mg \cdot l^{-1}$)	Chla	11.8 (±13.4)	0.9–58.8
Turbidity (FTUs)	Tb	6.5 (±5.4)	1.4–24.2
Secchi depth (cm)	Sec	153.9 (±81.7)	31.1–292.1
TP ($mg \cdot m^{-3}$)	TP	6.5 (±5.4)	7.2–122.2
Water quality			
pH	pH	8.2 (±0.4)	7.6–9.1
Conductivity ($\mu S \cdot cm^{-1}$)	Con	446.1 (±122.0)	258.6–700.8
N-NH4 ($\mu g \cdot l^{-1}$)	NNH4	105.5 (±59.3)	37.5–274.2
P-PO4 ($\mu g \cdot l^{-1}$)	PPO4	4.2 (±4.7)	2.0–28.2
DOC ($mg \cdot C \cdot l^{-1}$)	DOC	3.8 (±2.1)	1.6–8.6
Human-use intensity			
Fishing pressure ($angler \cdot km^{-1}$)	FP	0.56 (±0.82)	0–3.45
Fishing management	FM	NA	0, 1, 2
Distance to Toulouse (km)	DT	33.5 (±14.9)	16–61
Urbanisation (% in 5 km buffer)	UA	16.5 (±13.2)	5.0–47.3
Gravel pits exploitation (% in 5 km buffer)	GE	1.8 (±0.8)	0.1–3.5

replicates of each variable in each lake was used for subsequent analyses.

Human-use intensity variables were obtained as follows. Fishing management (FM) was used as an ordinal variable and was divided into three categories (0: private, 1: communal, 2: federal) that represented variable legal status and levels (from low to high) of public access and stocking practices in the lakes. Public access to private lakes is usually extremely restricted, while communal and federal lakes are accessible to the public. While historical records about stocking practices in the studied lakes were not available, owners and/or managers of lakes with private status usually never or rarely stocked fish, while lakes under federal management could be stocked up to several times every year. In the French legislation (Guevel 1997), lake owners and managers can stock fish species that are legally registered in the country except those listed as potential causing ecological damages (e.g. *Lepomis gibbosus*, *Ameiurus melas*). Fishing pressure (FP) was obtained by counting the number of anglers in each lake the month before and after fish sampling and calculated as the average number of anglers divided per lake perimeter. Distance to Toulouse (DT, the main urban area), urbanisation (UA, define as the percentage of urbanisation within a 5-km buffer around the centre of the lake) and gravel pit exploitation (GE, define as percentage of gravel pits area with a 5-km buffer around the centre of the lake) was calculated from aerial pictures and geographic information system (GIS) analyses.

Statistical analyses

Two-way ANOVAS were used to test for potential differences in fish community metrics between years and lakes and fish community variables. BPUEEN and BPUEENON were log-transformed prior to the analyses. We then performed a detrended correspondence analysis (DCA; Hill & Gauch, 1980) to examine both community structure (i.e. taxonomic diversity and biomass) and composition (i.e. species life-stage) and to determine whether redundancy analysis (RDA) or canonical correspondence analysis (CCA) would be the most appropriate model to describe the association between fish community and environmental variables (i.e. morphology, productivity, water quality and human-use intensity) using the lakes-years data set (N = 34). For community structure, the DCA ordination gradient was <3 SD (i.e. 1.71 SD) and revealed predominantly monotonic responses to environmental factors, thus suggesting that the linear model associated with RDA was more applicable (Ter Braak & Prentice, 1988). For community composition, the DCA ordination gradient (5.29 SD) revealed that unimodal responses predominated and suggested that CCA was the most appropriate method. Both RDA and CCA are direct gradient multivariate analyses, which can reveal the relationships among community structure, sites and environmental variables by a stepwise multiple regression (Ter Braak 1986). In the biplot, the importance of each environment characteristic was indicated by the length and angle of the vectors. Whether environment variables significantly explained fish data was subsequently tested using Monte Carlo permutation test with 999 permutations. A forward selection procedure with 999 permutations was also used to test the contributions of each environmental variable on all axes conjointly. All statistical analyses were conducted in R 2.14 (R Development Core Team 2011).

Table 2. Indices of fish community structure [name, abbreviation, mean (±SD) and range] in the studied gravel pit lakes. *P*-values are from two-way ANOVAS testing for differences between lakes and years. Significant *P*-values are in bold. BPUEEN and BPUEENON were log-transformed.

				Lake effect			Year effect		
Name	Abbreviation	Mean (±SD)	Range	Degrees of freedom	*F*	*P*-value	Degrees of freedom	*F*	*P*-value
Total species richness	SR	7.7 (±3.8)	2.0 to 15.0	16	20.380	**<0.001**	1	0.517	0.483
Non-native fish species richness	NonR	3.7 (±2.3)	0 to 8	16	17.730	**<0.001**	1	0.050	0.826
Shannon index	Snon	1.14 (±0.49)	0.07 to 1.90	16	10.480	**<0.001**	1	2.120	0.165
Biomass of native fish in gill nets (kg·net^{-1})	BPUENN	1.61 (±1.38)	0 to 4.67	16	7.554	**<0.001**	1	9.841	**0.006**
Biomass of non-native fish in gill nets (kg·net^{-1})	BPUENNON	1.94 (±3.94)	0 to 18.93	16	6.166	**<0.001**	1	3.873	0.067
Biomass of native fish by electrofishing (kg·PASE^{-1})	BPUEEN	1.41 (±0.59)	0 to 2.51	16	5.015	**0.001**	1	0.043	0.839
Biomass of non-native fish by electrofishing (kg·PASE^{-1})	BPUEENON	1.40 (±1.00)	−0.69 to 3.08	16	30.879	**<0.001**	1	6.146	**0.025**

Results

The studied lakes covered a large range of environmental conditions (Table 1). Surface area ranged from 0.75 to 21.16 ha (mean = 12.33 ± 7.02 SD) and mean depth ranged from 1.2 to 4.2 m (mean = 2.6 ± 0.8 SD). Productivity (e.g. chlorophyll *a* ranging from 0.9 to 58.8 mg·l^{-1}) and water quality (e.g. pH: ranging from 7.6 to 9.1) were also highly variable. Lakes were distributed along a large gradient of human-use intensity with the percentage of urbanisation ranging from 5.04 to 47.28% (mean = 16.55 ± 13.23 SD) and fishing pressure ranging from 0 to 3.45 angler·km^{-1} (mean = 0.56 ± 0.82 SD). Mean angling pressure was 0.12 (±0.34 SD), 0.75 (±1.16 SD) and 0.90 (±0.77 SD) angler·km^{-1} in lakes under private, communal and federal management respectively.

Fish community structure

In 2012 and 2013, a total of 25 fish species were sampled (13 native and 12 non-native species). Overall, mean total species richness was 7.7 (±3.8 SD), and mean non-native species richness was 3.7 (±2.3 SD). Non-native species were more abundant in term of biomass than native species as mean BPUENN was 1.61 (±1.38 SD) kg·net^{-1} and mean BPUENNON was 1.94 (±3.94 SD) kg·net^{-1}, while mean BPUEEN was 0.05 (±0.07 SD) kg·PASE^{-1} and mean BPUEENON was 0.12 (±0.22 SD) kg·PASE^{-1} (Table 2). Total species richness and non-native species richness did not differ significantly between 2012 and 2013 (two-way ANOVAS, $P = 0.483$ and $P = 0.826$ respectively), while they significantly differed between lakes (two-way ANOVAS, $P < 0.001$). Similarly, Shannon index did not differ significantly between years (two-way ANOVAS, $P = 0.165$) but was significantly different between lakes (two-way ANOVAS, $P < 0.001$). No significant difference in BPUENNON, BPUEEN were observed between 2012 and 2013 (two-way ANOVAS, $P = 0.067$ and $P = 0.839$ respectively), while BPUENN and BPUEENON were significantly different between the two sampling years (two-way ANOVAS, $P = 0.006$ and $P = 0.025$ respectively). BPUENN, BPUENNON, BPUEEN and BPUEENON were significantly different between lakes (two-way ANOVAS, $P < 0.001$, $P < 0.001$, $P = 0.001$ and $P < 0.001$ respectively).

Native species were numerically dominated by roach (*Rutilus rutilus*), European perch (*Perca fluviatilis*), rudd (*Scardinius erythrophthalmus*), tench (*Tinca tinca*) and bream spp., while non-native species were primarily represented by pumpkinseed (*Lepomis gibbosus*), common carp (*Cyprinus carpio*), largemouth bass (*Micropterus salmoides*), black bullhead (*Ameiurus melas*) and pikeperch (*Sander lucioperca*) (Table 3). These species occurred in more than 40% of the lakes and the three life stages of each species were found. In contrast, bleak (*Alburnus alburnus*), grass carp (*Ctenopharyngodon idella*), barbel (*Barbus barbus*), bitterling (*Rhodeus amarus*) and rainbow trout (*Oncorhynchus mykiss*) were found only at the adult life-stage (except bitterling with juvenile and adult) in a single lake (Table 3).

Environmental determinants of fish community structure

The RDA model testing the effects of environmental variables on fish community structure was significant ($P = 0.001$), and the first two axes explained 32.7% and 19.3% of the variation in fish community structure respectively. Among the 24 environmental variables tested, 16 had a significant effect ($P < 0.05$) on fish community structure (Fig. 1, Table S2). More specifically, the stepwise multiple regressions

Table 3. Common and scientific names, code, status (native or non-native) and occurrence of the fish species sampled in the studied gravel pit lakes in 2012 and 2013.

				Occurrence (%)	
Common name	Scientific name	Code	Status	2012	2013
Bleak	*Alburnus alburnus*	ala	Native	0	6
Silver carp	*Hypophthalmichthys molitrix*	hym	Non-native	6	12
Grass carp	*Ctenopharyngodon idella*	cti	Non-native	6	0
European eel	*Anguilla anguilla*	ana	Native	18	12
Barbel	*Barbus barbus*	bab	Native	0	6
Largemouth bass	*Micropterus salmoides*	mis	Non-native	41	53
Bitterling	*Rhodeus amarus*	rha	Native	6	0
Bream spp.	*Abramis brama* & *Blicca bjoerkna*	bre	Native	41	41
Northern pike	*Esox lucius*	esl	Native	24	29
Common carp	*Cyprinus carpio*	cyc	Non-native	65	59
Prussian carp	*Carassius gibelio*	cag	Non-native	24	35
Chub	*Squalius cephalus*	sqc	Native	6	18
Mosquitofish	*Gambusia affinis*	gaa	Non-native	29	35
Roach	*Rutilus rutilus*	rur	Native	88	94
Gudgeon	*Gobio gobio*	gog	Native	6	18
Ruffe	*Gymnocephalus cernua*	gyc	Non-native	12	18
Black bullhead	*Ameiurus melas*	amm	Non-native	47	41
European perch	*Perca fluviatilis*	pef	Native	76	76
Pumpkinseed	*Lepomis gibbosus*	leg	Non-native	65	65
Rudd	*Scardinius erythrophthalmus*	sce	Native	59	65
Pikeperch	*Sander lucioperca*	sal	Non-native	41	47
European catfish	*Silurus glanis*	sig	Non-native	6	6
Rainbow trout	*Oncorhynchus mykiss*	onm	Non-native	6	0
Tench	*Tinca tinca*	tit	Native	53	47

revealed that total species richness, non-native species richness and Shannon index were positively associated with fishing management, turbidity and urbanisation and negatively related to mean depth, distance to Toulouse and Secchi depth. The biomass of native species (BPUENN, BPUEEN) was positively associated with lake surface area, distance to nearest gravel pits, lake perimeter and shoreline development and negatively with distance to nearest river. In contrast, the biomass of non-native species (BPUENNON, BPUEENON) was positively associated with age, fishing management, chlorophyll *a* and dissolved organic carbon and negatively with lake volume, mean depth, Secchi depth and distance to Toulouse.

Environmental determinants of fish community composition

The CCA model testing the effects of environmental variables on species life-stage composition was significant ($P = 0.002$). The first two axes explained 25.8% of the variation (15.1% and 10.7% respectively). A total of 13 environmental variables had a significant effect ($P < 0.05$, Table S3) on life-stage composition (Fig. 2). All life stages of European perch, adult tench and YOY chub (*Squalius cephalus*) were positively associated with mean depth, lake volume, Secchi depth, distance to Toulouse and negatively with age, pH, urbanisation, conductivity and turbidity. In contrast, all life-stages of largemouth bass and YOY and juvenile pikeperch were positively associated with age, pH, urbanisation, conductivity and turbidity and negatively with mean depth, lake volume, Secchi depth and distance to Toulouse. Interestingly, popular sport fish species such as adult pikeperch, northern pike, common carp and the prey species such as YOY and juvenile roach and rudd were positively associated with fishing management.

Discussion

The present study investigates the environmental determinants of fish community structure and composition in gravel pit lakes, that is, artificial and disconnected aquatic ecosystems. Overall, the results supported our initial hypothesis that fish community structure and composition differed significantly between lakes and were linked to specific environmental drivers despite being located within a fairly restricted geographical area. Specifically, taxonomic metrics describing fish communities such as species richness, non-native species richness and Shannon index were strongly linked to fishing management with communal and federal lakes displaying a higher taxonomic diversity. In addition, these community metrics were associated with the distance and

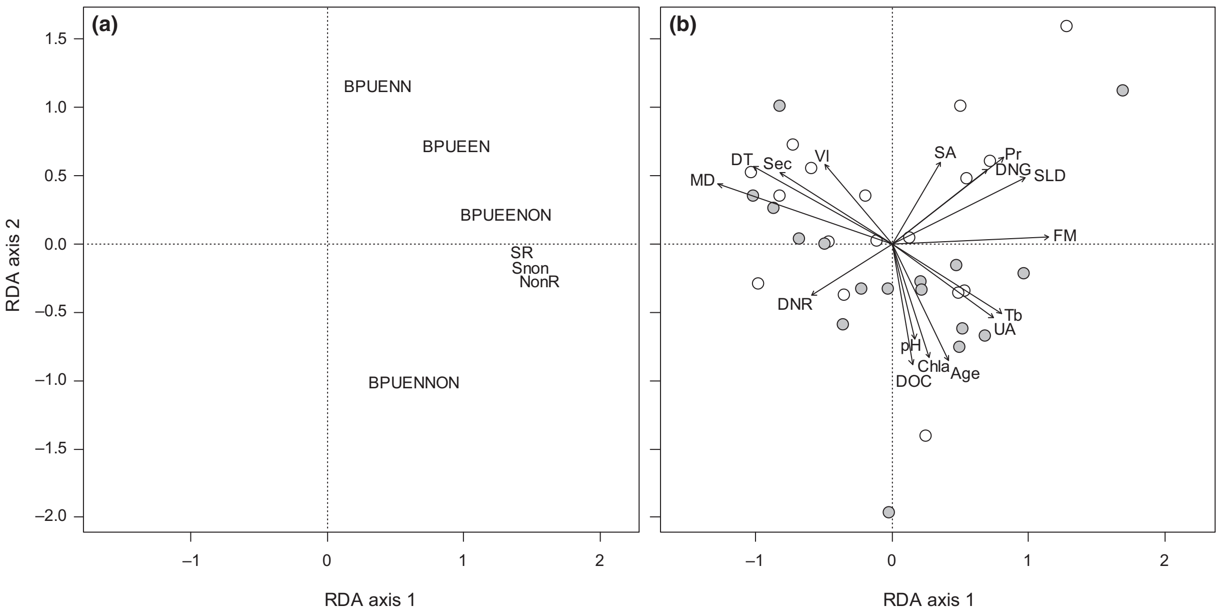

Fig. 1. Redundancy analysis of (a) the fish community diversity and (b) the environmental variables and lakes (white symbols: sampling lakes in 2012; grey symbols: sampling lakes in 2013). Arrows represent the vectors of the environmental variables. Only significant variables ($P < 0.05$) are depicted. Details about environmental and fish community variables are available in Tables 1 and 2 respectively.

proportion of urban areas. All together, these results support previous findings demonstrating that human activities such as angling and stocking can increase species richness in gravel pit lakes (Radomski & Goeman 1995), with lakes located nearby urban areas displaying higher species richness. Contrary to observations in natural lakes, we found that these taxonomic metrics were positively related to turbidity and negatively to mean depth and Secchi depth, with high taxonomic diversity in shallow and turbid lakes. We further demonstrated that biomass of native and non-native species was driven by different environmental factors. Specifically, large gravel pit lakes with high shoreline development index that were located the furthest from other lakes but closest to rivers had higher biomass of native species. Non-native species, especially medium-bodied life-stages, had higher biomass in mature and small lakes with high DOC and productivity, suggesting an accumulation of non-native species as lakes become older.

Previous studies indicated that predatory fish species could be a particularly important driver of community composition (Welborn et al. 1996). Similar to previous examples in natural lakes (e.g. Diehl 1988; Persson et al. 1991), our results demonstrated that European perch had higher biomass in young, deep, large gravel pit lakes with clear water. In these lakes, species composition was relatively simple with a very high proportion of European perch associated with a low proportion of few other native species. To date, there is still a general lack of understanding of why and how European perch is the pioneer and dominant fish species in newly created and disconnected habitats as dispersal movements of fish are mainly confined to local patterns among connected patches (Bie et al. 2012). Here, we hypothesise the existence of waterbird-mediated passive dispersal as a potential vector allowing the colonisation by fish such as European perch of newly created gravel pit lakes. However, molecular tools should be used to fully appreciate initial colonisation patterns and fish origins in gravel pit lakes. After colonisation, European perch can subsequently be a dominant predator and competitor over cyprinid species in lakes with low productivity (Persson et al. 1991). In addition, juvenile pikeperch and the three life-stages of largemouth bass displayed higher biomass in mature, highly turbid lakes with high pH. These results complement the findings of Rundberg (1977) and Brabrand & Faafeng (1993) indicating that pikeperch preferred nutrient-rich, turbid waters. However, they are in contradiction with previous findings showing that largemouth bass abundance was negatively related to water turbidity (Spencer & King 1984). This is likely because the range of turbidity in our lakes was below the values where largemouth bass abundance is lower (Brown et al. 2009). Almost all popular sport fish species (i.e. pikeperch, common carp, northern pike and prey species such as bream, roach and rudd) were strongly driven by fishery management in mesotrophic lakes, suggesting that species composition in gravel pit lakes are strongly affected by stocking practices. Although exhaustive information about stocking practices in the area were not available, reg-

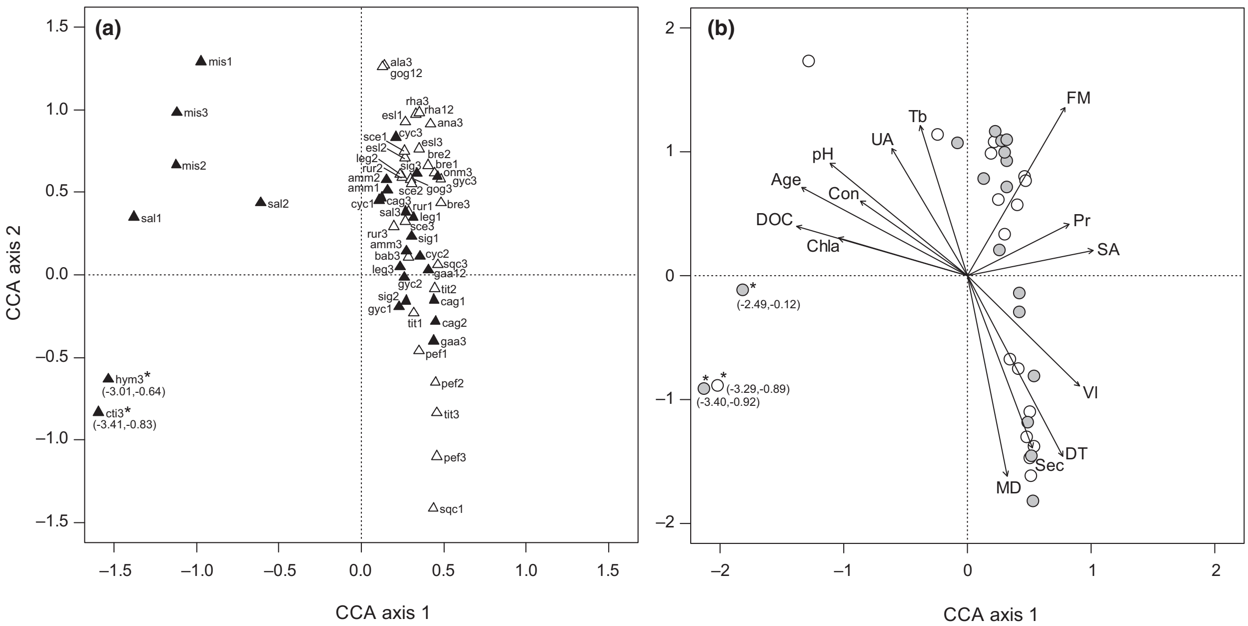

Fig. 2. Canonical correspondence analysis of (a) the relative biomass of each species life-stage (white triangles: native species; black triangles: non-native species) and (b) the environmental variables and lakes (white symbols: sampling lakes in 2012; grey symbols: sampling lakes in 2013). Arrows represent the vectors of the environmental variables and only significant variables ($P < 0.05$) are depicted. Species codes are detailed in Table 3. Codes of life-stages are (i) young-of-the-year, (ii) juveniles and (iii) adults. *denotes point outside of the panel with values reported in brackets. Details about environmental variables and fish species are available in Tables 1 and 3 respectively.

ular stocking might compensate the potential mortality of these sport species caused by angling, as suggested by the consistent occurrence of large-bodied individuals in highly managed lakes.

Empirical research have suggested the presence of predictable fish community succession along productivity and morphology (i.e. area and depth) gradients in natural temperate lakes (Persson et al. 1991; Mehner et al. 2005). In artificial ecosystems, our results demonstrated that fish community composition in gravel pit lakes followed a predictable shift as lakes become older, more productive and more managed: from an initial high biomass of pioneer species such as European perch that is slowly replaced by cyprinids (e.g. bream, roach and rudd) and subsequently by sport fishing species (e.g. northern pike, common carp and pikeperch) to fish community is mainly composed of non-native species (e.g. pumpkinseed, black bullhead, pikeperch and largemouth bass).

Overall, our results indicated that management practice is the main driver of taxonomic diversity, and it also plays a more critical role in shaping the fish species composition in gravel pit lakes. An increasing number of studies have used functional approaches to clarify the mechanistic influence of environmental variables in shaping fish composition (Hoeinghaus et al. 2007; Pool et al. 2010). We therefore argue that functional traits should be taken into account in future studies (McGill et al. 2006; Jung et al. 2010) to provide a better understanding of human-induced perturbations on fish communities (Mouillot et al. 2013) and that, by nature, gravel pit lakes provide a unique opportunity to test assembly rules in community ecology.

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References

Alofs, K.M., Liverpool, E.A., Taphorn, D.C., Bernard, C.R. & López-Fernández, H. 2014. Mind the (information) gap: the importance of exploration and discovery for assessing conservation priorities for freshwater fish. Diversity and Distributions 20: 107–113.

Barletta, M., Jaureguizar, A.J., Baigun, C., Fontoura, N.F., Agostinho, A.A., Almeida-Val, V.M.F., Val, A.L., Torres, R.A., Jimenes-Segura, L.F., Giarrizzo, T., Fabré, N.N., Batista, V.S., Lasso, C., Taphorn, D.C., Costa, M.F., Chaves, P.T., Vieira, J.P. & Corrêa, M.F. 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. Journal of Fish Biology 76: 2118–2176.

Bie, T., Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Gucht, K., Wichelen, J., Vyverman, W. & Declerck, S.A.J. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15: 740–747.

Brabrand, Å. & Faafeng, B. 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour. Oecologia 95: 38–46.

Brown, T.G., Runciman, B., Pollard, S. & Grant, A.D.A. 2009. Biological synopsis of largemouth bass (*Micropterus Salmoides*). Nanaimo: Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2884 v + 27 pp.

Copp, G. & Garner, P. 1995. Evaluating the microhabitat use of fresh-water fish larvae and juveniles with point abundance sampling by electrofishing. Folia Zoologica 44: 145–158.

Cucherousset, J., Paillisson, J.-M., Carpentier, A., Eybert, M.-C. & Olden, J.D. 2006. Habitat use of an artificial wetland by the invasive catfish *Ameiurus melas*. Ecology of Freshwater Fish 15: 589–596.

Darwall, W.R.T., Holland, R.A., Smith, K.G., Allen, D., Brooks, E.G.E., Katarya, V., Pollock, C.M., Shi, Y., Clausnitzer, V., Cumberlidge, N., Cuttelod, A., Dijkstra, K.-D.B., Diop, M.D., García, N., Seddon, M.B., Skelton, P.H., Snoeks, J., Tweddle, D. & Vié, J.-C. 2011. Implications of bias in conservation research and investment for freshwater species: conservation and freshwater species. Conservation Letters 4: 474–482.

Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53: 207.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163.

Duncan, J.R. & Lockwood, J.L. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. Biological Conservation 102: 97–105.

Emmrich, M., Schälicke, S., Hühn, D., Lewin, C. & Arlinghaus, R. 2014. No differences between littoral fish community structure of small natural and gravel pit lakes in the northern German lowlands. Limnologica – Ecology and Management of Inland Waters 46: 84–93.

Erős, T., Specziár, A. & Bíró, P. 2009. Assessing fish assemblages in reed habitats of a large shallow lake—A comparison between gillnetting and electric fishing. Fisheries Research 96: 70–76.

Froese, R. & Pauly, D. 2014. World wide web electronic publication. Available at: http://www.fishbase.org, version (last accessed 29/10/2014).

Geist, J. 2011. Integrative freshwater ecology and biodiversity conservation. Ecological Indicators 11: 1507–1516.

Guevel, B. 1997. La «loi pêche» (Code rural) et l'introduction des espèces piscicoles. Bulletin Français de la Pêche et de la Pisciculture. pp. 43–51.

Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

Hoeinghaus, D.J., Winemiller, K.O. & Birnbaum, J.S. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34: 324–338.

Hortal, J., Nabout, J.C., Calatayud, J., Carneiro, F.M., Padial, A., Santos, A.M.C., Siqueira, T., Bokma, F., Bini, L.M. & Ventura, M. 2014. Perspectives on the use of lakes and ponds as model systems for macroecological research. Journal of Limnology 73: 42–56.

Hutchinson, G.E. 1957. A treatise on limnology, Vol. 1. New York: Geography, Physics and Chemistry, Wiley. 1015 pp.

Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. 2001. What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 157–170.

Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S.A.J., Meester, L., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Conde-Porcuna, J.M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H.J., Liu, Z., Balayla, D. & Lazzaro, X. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia 646: 73–90.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. 2010. Intraspecific variability and trait-based community assembly. Journal of Ecology 98: 1134–1140.

Kattner, E., Schwarz, D. & Maier, G. 2000. Eutrophication of gravel pit lakes which are situated in close vicinity to the river Donau: water and nutrient transport. Limnologica – Ecology and Management of Inland Waters 30: 261–270.

Keith, P., Persat, H., Feunteun, E. & Allardi, J. 2011. Les poissons d'eau douce de France. Paris: Publication scientifique du Museum.

Kozlowski, G. & Bondallaz, L. 2012. Urban aquatic ecosystems: habitat loss and depletion of native macrophyte diversity during the 20th century in four Swiss cities. Urban Ecosystems 16: 543–551.

Lenda, M., Skórka, P., Moroń, D., Rosin, Z.M. & Tryjanowski, P. 2012. The importance of the gravel excavation industry for the conservation of grassland butterflies. Biological Conservation 148: 180–190.

Mátyás, K., Oldal, I., Korponai, J., Tátrai, I. & Paulovits, G. 2003. Indirect effect of different fish communities on nutrient chlorophyll relationship in shallow hypertrophic water quality reservoirs. Hydrobiologia 504: 231–239.

McGill, B., Enquist, B., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21: 178–185.

Mehner, T., Diekmann, M., Brämick, U. & Lemcke, R. 2005. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. Freshwater Biology 50: 70–85.

Mehner, T., Holmgren, K., Lauridsen, T.L., Jeppesen, E. & Diekmann, M. 2007. Lake depth and geographical position modify lake fish assemblages of the European "Central Plains" ecoregion. Freshwater Biology 52: 2285–2297.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28: 167–177.

Nagdali, S. & Gupta, P.K. 2002. Impact of mass mortality of a mosquito fish, *Gambusia affinison* the ecology of a fresh water eutrophic lake (Lake Naini Tal, India). Hydrobiologia 468: 45–51.

Persat, H. & Copp, G. 1990. Electric fishing and point abundance sampling for the ichthyology of large rivers. In: Cowx, I.G., ed. Developments in electric fishing. Cambridge: Cambridge University, pp 197–209.

Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S.F. 1991. Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structured interactions. Journal of Fish Biology 38: 281–293.

Pool, T.K., Olden, J.D., Whittier, J.B. & Paukert, C.P. 2010. Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. Canadian Journal of Fisheries and Aquatic Sciences 67: 1791–1807.

R Development Core Team, 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Avilable at: http://www.R-project.org/.

Radomski, P.J. & Goeman, T.J. 1995. The homogenizing of minnesota lake fish assemblages. Fisheries 20: 20–23.

Rundberg, H. 1977. Trends in harvests of pikeperch (*Stizostedion lucioperca*), eurasian perch (*Perca fluviatilis*), and northern pike (*Esox lucius*) and associated environmental changes in lakes Mälaren and Hjälmaren, 1914–74. Journal of the Fisheries Research Board of Canada 34: 1720–1724.

Santoul, F., Figuerola, J. & Green, A. 2004. Importance of gravel pits for the conservation of waterbirds in the Garonne river floodplain (southwest France). Biodiversity and Conservation 13: 1231–1243.

Santoul, F., Gaujard, A., Angélibert, S., Mastrorillo, S. & Céréghino, R. 2009. Gravel pits support waterbird diversity in an urban landscape. Hydrobiologia 634: 107–114.

Shannon, C.E. 1948. A mathematical theory of communication. Bell System Technical Journal 27: 379–423.

Spencer, C.N. & King, D.L. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. Canadian Journal of Fisheries and Aquatic Sciences 41: 1851–1855.

Strayer, D.L. & Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29: 344–358.

Ter Braak, C.J.F.T. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

Ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 271–317.

Welborn, G.A., Skelly, D.K. & Werner, E.E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337–363.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of the species (common name, scientific name and abbreviation) and body size limits (fork length in mm) used to define the different life stages.

Table S2. Results of the Monte Carlo permutation test for the redundancy analysis (RDA, $N = 999$ permutations) used to test the association between environmental variables and fish community structure. Significant *P*-values are in bold.

Table S3. Results of the Monte Carlo permutation test for the canonical correspondence analysis (CCA, $N = 999$ permutations) used to test the association between environmental variables and fish community composition. Significant *P*-values are in bold.