Selecting fish-based metrics responding to human pressures in French natural lakes and reservoirs: towards the development of a fish-based index (FBI) for French lakes

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Running headline: Response of fish-based metrics to human pressures in French lakes.

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ABSTRACT (**Word count:** 149 words)

1. Fish-based indices of biotic integrity (IBI) have been developed for many lotic systems but remain scarce for lakes. The goal of the present study was to assess the responses of lentic fish assemblages to anthropogenic pressures when environmental variability was controlled for, and to compare them between French natural lakes and reservoirs.

2. Environmental features, catchment-scale anthropogenic descriptors and fish data were collected from 30 natural lakes and 59 reservoirs throughout France.

3. Functional fish metrics were regressed against both anthropogenic variables and the natural environmental conditions.

 Our results show that fish assemblages are appropriate ecological indicators for both natural and artificial lakes. They underline the necessity to control for the environment when

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developing indices at broad geographical scales. The relevant metrics differ between natural lakes and for reservoirs, which challenges the attempts to use natural systems as references to assess the ecological potential of artificial ones.

Six keywords: functional metric • fish assemblage • natural lake and reservoir • index of biotic integrity • European Water Framework Directive• bioassessment

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Introduction

Frey (1977) and then Karr and Dudley (1981) defined the concept of ecological integrity of freshwater ecosystems as their ability to support and maintain "a balanced, integrated, adaptive community of organisms having a species composition diversity and functional organization comparable to that of the natural habitat of the region." Since this publication, fish assemblages have become accepted as reflecting the "overall integrity of biological communities" and as "excellent indicators of the environmental quality of aquatic ecosystems" (Fausch et al. 1990).

Following Karr's studies on Midwestern U.S. streams, many other multimetric fish-based indices of biotic integrity (IBIs) have been developed for the running waters of North and Central America, and Europe (Hughes & Oberdorff 1999; Miller et al. 1988; Roset et al. 2007; Simon & Lyons 1995).

Conversely, the development of IBIs for lakes remains scarce (Appelberg et al. 2000; Drake & Pereira 2002). The main difficulty hampering this development was heterogeneity in fish sampling (Jackson & Harvey 1997). Even scarcer are the attempts to assess the quality of reservoirs using fish assemblages (but see Hickman and McDonough 1996; Jennings et al. 1995), despite their importance for water resource managers (Jennings et al. 1995). One reason put forward was that reservoirs are artificial systems that lack natural reference sites to assess the deviation from unaffected natural conditions (Hickman & McDonough 1996; Jennings et al. 1995).

In Europe, the implementation of the European Water Framework Directive (WFD) (European Community 2000) requires the use of fish-based tools to assess the ecological status of all lentic water bodies, i.e., natural lakes and reservoirs, over 50 ha. The first multi-metric index for lake fish was developed in Sweden (Appelberg et al. 2000; Holmgren et al. 2007). However, completed fish-based indices still remain rare and concern almost solely natural lakes. Moreover, they generally focus on specific types of environments (e.g., mountain or wetland lakes) and they are often based on taxonomic metrics, which are poorly transferable due to limited fish species distribution areas. In this context, the development of methods for monitoring the biological responses of fish assemblages to natural and anthropogenic factors is essential and remains to be improved. This is particularly true in some countries (e.g., France, Spain, Portugal, the Czech Republic) where most lakes are manmade.

Reservoirs are frequently considered as an intermediate between rivers and lakes (Gelwick & Matthews 1990; Irz et al. 2006; Wetzel 1990): however, biological cross-ecosystem studies are currently not common (Pace 1991). Nevertheless, reservoirs satisfy some of the definition criteria of lakes (Politou et al. 1993), because most of the major processes (e.g., internal mixing, nutrient uptake, predator–prey interactions) occur in both natural lakes and reservoirs (Thornton 1990). Currently, the question of whether a common fish-based index could be used for both lentic ecosystems has been raised.

Therefore, the goals of this study were (i) to test if some candidate metrics, including functional metrics, are correlated to anthropogenic pressure gradients when the environment is controlled for in each type of lentic ecosystem and (ii) to compare the selected metrics between natural lakes and reservoirs.

Study Sites

Throughout this article we refer to lakes of natural origin as natural lakes and to man-made lentic systems as reservoirs; the generic term 'lakes' is used for both types. Only freshwater lakes are included in the present study.

Anthropogenic pressure indices were computed using 40 natural lakes and 106 reservoirs located throughout France. Fish data were collected from 30 natural lakes and 59 reservoirs among these 146 lakes (Figure 1). The lake data set represented a wide range of each environmental condition (Table 1), but as demonstrated in previous works on French lakes (Argillier et al. 2002b; Irz et al. 2004a; Irz et al. 2002), sites with altitudes over 1500 meters above sea level had to be excluded from these analyses because they shelter only introduced fish species. ***Scheduled locations of Figure 1 and Table 1.***

Material and methods

Environmental parameters. – Five large-scale environmental parameters related to lake and drainage basin morphology, and known to affect the distribution patterns of fish assemblages, were considered (Table 1). The lake area (A_L) is a strong predictor of fish richness (Barbour & Brown 1974; Eadie & Keast 1984); the drainage basin area (A_{DB}) is an indicator of habitat diversity upstream of lake and of inflows into lakes (Irz et al. 2004b); the maximum depth (D_{max}) acts both directly on fish habitat availability by determining the importance of the lake littoral zone (Argillier et al. 2002c) and indirectly on the lake water dissolved oxygen level

(Hondzo & Stefan 1996); the lake shoreline development factor (*SLDF*) (Eadie & Keast 1984) accounts for an indicator of habitat diversity into lakes; and the volume development (V_d) (Håkanson 1981) gives information on the lake basin shape and therefore on the size of the lake littoral zone. The AURELHY climate model (Benichou & Le Breton 1987) was used to compute January and July mean air temperatures, because air temperatures are known to control the distribution of fish species (Daufresne & Boet 2007; Irz et al. 2007b; Mason et al. 2008) by affecting the metabolism (Gillet 1991) and the growth of juveniles (Jensen 1990; Staggs & Otis 1996) (SumT; DiffT; see Table 1). The hydrological model developed by Pella et al. (2006) was used to evaluate the lake yearly inflow in order to calculate residence time (RT). A geologic index (GI) displaying the percentage of the catchment area as calcareous, based on 1/50,000 geological maps (BRGM: http://www.brgm.fr/cartegeol.jsp), was computed on the whole lake catchment area. This GI enables us to understand lake catchment chemistry, which is an important factor affecting fish abundance (Shaw et al. 2004). Finally, the water level maximum amplitude (WL) was considered as an additional hydrological parameter, due to its detrimental effect on fish feeding conditions, sheltering and reproduction (Bragg et al. 2003; Winfield 2004).

Anthropogenic pressures. – Anthropogenic pressures were assessed for the overall French lake data set (*n* = 146) using seven variables derived from features of the lakes' catchments (Table 2). Land cover percentages allow evaluation of the agricultural and urban land use (Drake & Pereira 2002). Population density relates to the watershed dynamic, especially chemical discharges into lakes (see Pitt et al. 1995). The network density of roads and railways reflects fragmentation (Forman & Alexander 1998; Jones et al. 2000). The soil surface nitrogen balance and phosphorus balance were simulated using the NOPOLU System 2 model (PÖYRY) (LeGall, *personal communication*). These are the differences between the total quantity of nutrients entering the soil and the quantity leaving it annually. The nitrogen balance was kept as a pressure variable, but the phosphorus balance was adjusted according to the recommendation of Coale (2000). As particulate phosphorus is not very mobile (Carpenter et al. 1998), Coale proposed to multiply the phosphorus balance by the mean value of the lake's watershed soil erosion after log transformation (log(x+1)). This watershed soil erosion was estimated with a model developed by the French National Institute for Agricultural Research (INRA – Ifen – Gis Sol, 2000 –

http://eusoils.jrc.ec.europa.eu/ESDB_Archive/serae/grimm/erosion/inra/europe/analysis/maps_and_listings/web_erosion/index.html). This model is based on soil slumping, erodibility, topography, land cover, rainfalls and dominant cultivated land cover.

We assume that these seven variables derived from GIS data reflected the anthropogenic pressures undergone by lakes at the catchment scale. The population density and agricultural land cover were log-transformed (log(x+1)) and the percentage of the urbanised catchment area was transformed to arcsine√(X). The other four anthropogenic variables were kept raw.

In order to reduce dimensionality, a standardised principal component analysis (PCA) was performed on each group of anthropogenic variables (Table 2). On the one hand, we carried out a PCA on urban variables, and lake coordinates on the first principal component were considered a synthetic urban pressure variable (PU). The same was done on agricultural variables in order to create a synthetic agricultural pressure variable (PA). ***Scheduled location of Table 2.***

Fish sampling procedures. − Fish data for the 89 French lakes were collected between 2005 and 2009 using a standardised method (C.E.N. 2005). A stratified random sampling scheme was implemented during summer (June–October, surface water temperature over 15°C). The sampled lakes were divided into depth strata and randomly located samplings were performed within each depth stratum. Both pelagic and benthic multi-mesh gillnets made out of uncolored nylon were used. Benthic nets were 30 m long and 1.5 m deep and composed of 12 different mesh sizes (the panel for each mesh size was 2.5 m long) ranging between 5 mm to 55 mm following geometry series, with an approximately 1.25 ratio between mesh sizes. The pelagic nets were 27.5 m long and 6 m high and had the same mesh sizes without the 5 mm mesh size. The number of nets increased with lake depth and area. Nets were set around 7 p.m. for approximately 12 h. Fish were identified to species and counted. The method provides the number of fish that were caught and the biomass for each one. We then calculated a whole-lake estimate for species relative abundances (RA), expressed as the ratio of the number of individuals belonging to a fish species to the total number of individuals in the lake; catch per unit effort (CPUE), and biomass (in grams) per unit effort (BPUE) (including both the benthic and the pelagic nets), respectively expressed as the overall number of individuals or biomass captured divided by the unit-of-effort (i.e., nets' surfaces multiplied

by the sampling duration). Finally, this method provided fish data that were comparable over time within a lake and between lakes.

Candidate metrics. – Altogether, 42 species were caught in these 89 lakes (Table 3). **Scheduled location of Table 3.**

Ten biological traits (Table 4) derived from functional guilds were used: two from tolerance guilds (overall tolerant (OTol) and overall intolerant (OIntol)), three from reproductive guilds (lithophilic species (Lith), strict lithophilic species (StLith), and strict phytophilic species (StPhyto)), and five from trophic guilds (omnivorous (Omni), invertivorous (Invert), planktivorous (Plankt), herbivorous (Herb) and piscivorous species (Pisc)). The 42 fish species caught were assigned to these attributes (Appendix 1), based on previous grey or published literature, online resources (Froese & Pauly 2009 – http://www.fishbase.org/; Pont et al. 2006) or expert judgments (H. Persat, O. Schlumberger & N. Poulet, *personal communications*). In addition, native species (Nat) were distinguished using Keith & Allardi's (2001) classification. **Scheduled location of Table 4.**

A set of candidate metrics was derived from species richness and faunal composition as in other lake and stream IBIs (Drake & Pereira 2002; Holmgren et al. 2007; Karr et al. 1986; Minns et al. 1994; Schulz et al. 1999). These metrics (Table 5) were expressed as (i) number of species sharing a trait (Sp_*trait*), (ii) number of species sharing a trait divided by the total number of species in the lake (%Sp_*trait*), (iii) number of individuals sharing a trait caught by unit effort (Nb_*trait*), (iv) number of individuals sharing a trait divided by the total number of individuals in the lake (%Nb_*trait*), (v) biomass of individuals sharing a trait caught by unit effort (B_*trait*) or (vi) biomass of individuals sharing a trait divided by the total biomass of individuals in the lake (%B_*trait*). The total species richness (RS) metric was calculated, and three diversity indices based on fish abundances in each sampled site – i.e., Shannon's index (SWI) (Shannon & Weaver 1949), Simpson's index (SI) (Simpson 1949) and evenness index (EI) (Hill 1973) – were also considered, as well as BPUE, CPUE and the average biomass (AB) calculated for each lake sampled as the ratio of BPUE to CPUE (Table 5). **Scheduled location of Table 5.**

All functional fish traits considered here are shared by at least three species. Moreover, as in other studies (Irz et al. 2007a; Jennings et al. 1995; Pont et al. 2007), introduced species

were not excluded from the metrics calculations because they may play an important functional role in lake ecosystems.

This set of metrics reflects complementary aspects of assemblage richness and functioning.

Statistical analysis. – For environmental variables, to retrieve less skewed distributions, the residence time, catchment area, lake area and maximum depth were log-transformed. For biological variables, classic monotonic transformations were used to meet the requirements of the linear model (normality, linearity, homoscedasticity): count (abundance, richness) and biomass metrics were log-transformed, proportion metrics were arcsine-square-root-transformed, whereas diversity indices were kept untransformed. These metrics were then scaled and the variation partitioning of each metric was performed using constrained redundancy analysis (Legendre & Legendre 1998). Here, with a single response variable, redundancy analysis consists in a multiple linear regression on the principal components of predictors with orthogonal residuals. The three sets of predictors involved are: the ten environmental predictors, the agricultural pressure index (PA) and the urban pressure index (PU). A permutation test based on residuals after partial RDA was used to assess the significance of the parts of variance explained solely by PA and solely by PU.

Each metric significantly explained by at least one of the two pressure indices was then regressed using a stepwise "both sides" selection of predictors based on Bayesian information criterion (BIC) from the complete model:

$$\text{Metric} \sim (A_L + A_{DB} + D_{max} + SLDF + V_d + SumT + DiffT + RT + GI + WL) + PA + PU \quad (1)$$

The pressure effect of a given pressure on a metric was considered only if: (i) the adjusted R-squared of the resulting model was higher than 0.2; (ii) the coefficient of that pressure in the resulting model was significantly different from zero; and (iii) the pressure was also included in the best model selected on the basis of the root mean square error (RMSE) using a leave-one-out cross-validation procedure (LOO).

All statistical analyses were performed using R statistical software (R.2.9.1) as well as 'vegan', 'pls', and 'caret' R packages (Ihaka & Gentleman 1996; R Development Core Team 2008).

Results

Study sites and environmental parameters. – In the present study, natural lakes are located either in mountain areas (e.g., the Alps, the Massif Central) or next to the coast (Figure 1). On the contrary, reservoirs are roughly randomly spread throughout France. The mean values of most environmental parameters are quite similar between natural lakes and reservoirs, although natural lakes have larger residence time (692 days vs. 137 days) (Student *t*-test with Welch correction, t = 2.16, *P* < 0.05) (Table 1), lower *SLDF* (with Welch correction, t = -6.83, *P* < 0.001), smaller catchment areas (t = -3.29, *P* < 0.001) and lower water level fluctuations (t = -7.53, *P* < 0.001) than reservoirs.

Differences between lake types are clearer with respect to anthropogenic pressures (Table 2). Apart from network densities and urbanised areas, all anthropogenic pressures displayed higher mean values for artificial lakes than for natural ones. For natural lakes, the negative nutrient balances indicate a deficit of nutrients in the soil surface of the catchment, whereas their highly positive values for reservoirs show a nutrient accumulation. In addition, all agricultural variables reached higher maximum values for reservoirs than for natural lakes – more than twice as much. For example, reservoirs have higher maximum values of agriculture land cover areas (8,783.4 km^2 vs. 790.6 km^2) and nutrient balances (877.1 t(N) vs. 432.3 t(N), and 2,523.1 t(P) vs. 849.2 t(P)) than natural lakes. In summary, reservoirs undergo much more agricultural pressure than natural lakes do.

Fish sampling and candidate metrics. – Lakes and reservoirs are very similar in terms of common and rare species (Table 3). Indeed, 68% of the fish species occur in both types of ecosystems. In both natural lakes and reservoirs, *Perca fluviatilis* (Linnaeus, 1758), *Rutilus, rutilus* (L., 1758) and *Scardinius erythrophthalmus* (L., 1758) were widespread (more than two-thirds of the sampling sites) and had a high mean relative abundance (>5% in at least one of two types). In addition, fish species with low occupancy (<10% of the sampling sites) and poor average relative abundance (<1% in at least one of the system types) were nearly the same as well (Table 3). On the contrary we observed clear differences (≥ 25% in frequency) between lake types concerning *Abramis brama* (L., 1758), *Alburnus alburnus* (L., 1758), *Blicca bjoerkna* (L., 1758), *Gymnocephalus cernuus* (L., 1758), *Sander lucioperca* (L., 1758) and *Coregonus lavaretus* (L., 1758) (Table 3). All of them, except the last one were more frequent in reservoirs than in natural lakes.

Most of the functional fish-based metrics also indicated similarities between lake types (Student *t*-test, with Welch correction if needed, see Table 5).

Overall, 11 out of 73 candidate fish metrics displayed a significant response to anthropogenic pressures (Table 6). None of the metrics based on the lithophilic, strict lithophilic, intolerance, and invertivorous traits displayed a significant response. Moreover, anthropogenic impacts do not appear significant on species richness or on diversity indices. In addition, none of the candidate metrics indicated a significant anthropogenic impact on both natural lakes and reservoirs. ***Scheduled location of Table 6.***

Three metrics displayed a significant response to anthropogenic pressures in natural lakes (Table 6). %B_OTol increases with urbanisation stress (30% of the variance explained). Nb_StPhyto and %B_Plankt seem to be good indicators of agricultural impacts (Table 6) (20% and 17% of variance, respectively, explained exclusively by agricultural pressure).

For the reservoirs, eight metrics were selected, including BPUE (Table 6). Five of them relate to assemblage trophic structure and two to tolerance guild metrics (Sp_OTol and B_OTol). The only type of pressure significantly contributing to the model was PA (Table 6). Apart from the percentage of piscivorous species, the other seven metrics displayed a positive response to the agricultural pressure when the environment was controlled for. The metric %Sp_Pisc showed the strongest response with 17% of its variance attributed to PA. B_Herb and %Sp_Plankt came next with 13% and 12%, respectively.

All linear models included at least one significant coefficient for environmental variables (unpublished results). This highlights the importance of accounting for the environmental patterns of variability when studying the response of fish-based metrics to anthropogenic pressures at broad spatial scales. For the natural lakes, this is particularly true for the %B_Plankt and %B_OTol (Table 6), with 28%, and 27%, respectively, of their variance attributed to environmental variables. For reservoirs, this mostly concerns B_OTol and BPUE, with 38%, and 37%, respectively, of their variance explained by environmental variables.

Discussion

The data set processed here can be considered representative of the diversity of lakes at the national scale (excluding lakes above 1500 m). Although natural lakes and reservoirs both meet the generic definition of lakes (Politou et al. 1993), they clearly differ in terms of

morphological characteristics, functioning (e.g., water level fluctuation (Table 1)) and anthropogenic pressures (Cooke et al. 1993; Thornton 1990). Reservoirs undergo much more agricultural pressures than natural lakes do certainly because the storage of water in artificial lakes favors the development of irrigation.

Assessing lake conditions through fish assemblages

The present study provides evidence that fish assemblages are good potential indicators of urban and agricultural impacts on lakes. Eleven metrics (among the initial set of 73) responded to the lake catchment pressures when the environment was controlled for.

Most of the selected metrics responded to agricultural pressures. This prevailing effect of agriculture versus urban land use can be explained by the differences in intensity of these two pressures. The mean percentage of agricultural land cover in catchments exceeds by one order of magnitude that of urban land use (Table 2). The buiding of treatment plants for domestic and industrial sewage certainly contributed to mitigate the impact of urban land use on freshwater ecosystems. Conversely, agriculture is still a major user of fertilisers and pesticides, and it contributes to soil erosion. In this context the prominent effect of agriculture on freshwater assemblages is not really surprising, even though the processes involved remain unclear. Direct impacts (e.g., by toxicity) are certainly less important than those explained by habitat alteration or eutrophication. Finally, there is also more variability in agricultural than in urban land cover (synthesized by higher SD, see Table 2), which may explain a clearer response of fish-based metrics. Moreover, in the present study, the urbanisation of catchments was very low compared to that in other studies (Drake & Pereira 2002; Whittier 1999). In addition, the lack of significance might also be due to the fact that these relationships between metrics and pressures are actually non-linear, which was not considered here. Metrics might indeed be, for example, sensitive to a given pressure above a certain threshold.

Regarding natural lakes only three metrics displayed a significant response to anthropogenic pressures (Table 6). This is less than for reservoirs, which may be explained by the above-mentioned differences in the agricultural pressure between natural lakes and reservoirs. Furthermore, we have to acknowledge that the number of natural lakes included in the present study and the variability between these lakes (i.e. coastal to mountain lakes) may limit the possibility of identifying certain relevant metrics. Nevertheless, considering the low number (less than 70) of French natural lakes over 50 ha, this exercise will remain difficult at

a national scale, whatever the sampling method used. At the European level, similar tests would be more powerful.

Finally, it is obvious that fish management practices can influence fish species composition and abundance (Argillier et al. 2002a). However, in this study, fish species were considered self-sustaining. Indeed, all species are not stocked and when they are, according to our knowledge of local management practices, this is infrequent. Furthermore, even if none of the lakes studied was concerned with commercial fishing, we cannot exclude bias in our metric calculations (i.e., metrics related to the abundance of piscivores and salmonids) due to intensive recreational angling.

Fish-based metric responses on both lentic ecosystems

For planktivorous species, for example, agriculture has a significant effect on %B_Plankt for natural lakes and on %Sp_Plankt for reservoirs (Table 6), but no metric revealed a common response to a pressure on both natural lakes and reservoirs.

The selected fish-based metrics

Only fish-related metrics based on tolerance, reproduction, and trophic guilds were retained in this study. The tolerance-related metrics seemed to display clear responses to anthropogenic pressures both on reservoirs and natural lakes. Most IBIs developed on rivers (Oberdorff et al. 2002; Pont et al. 2006), reservoirs (Karr & Dionne 1991; McDonough & Hickman 1999) or natural lakes (Belpaire et al. 2000; Drake & Pereira 2002) use some measure of the relative dominance of tolerant species to assess moderate to high levels of degradation (Simon & Lyons 1995). Nevertheless, as discussed previously, the metric units of the selected tolerance-related metrics were different between natural lakes and reservoirs. Moreover, it is apparent that 5 of 11 intolerant species are salmonids (see Appendix 1) and they likely occupy mainly the coldwater lakes located above 1500 m that were excluded from our analyses. In spite of the absence of response of intolerant species-based metrics, most of our results confirm the value of tolerant-related metrics.

Apart from the proportion of piscivorous species, all other trophic-based metrics displayed significantly positive relationships with agricultural pressure, among both types of lakes. All six trophic-based metrics selected in this study responded similarly to those found in other IBI adaptation studies (Appelberg et al. 2000; Drake & Pereira 2002; Jennings et al. 1995; Karr &

Dionne 1991). In contrast to temperate stream ecosystems, it is acknowledged that lentic ecosystems are considered more stable from an environmental point of view, thereby promoting intra-assemblage interactions (e.g., competition, predation) and giving rise to trophically structured assemblages (Hugueny & Paugy 1995; Ibañez et al. 2009; Oberdorff et al. 1998). Hence, studying the response of the trophic composition metrics to anthropogenic pressures in lentic ecosystems was useful, while nutrient loadings induced by agricultural land use could probably modify the equilibrium between the different trophic levels (Carpenter et al. 1985; Vitousek et al. 1997).

Among the metric based on reproductive guilds, Nb_StPhyto was the only one that showed a significant response to agricultural pressure; this was observed only for natural lakes (Table 6).

Candidate metrics displaying no response

Species richness was not correlated to catchment-scale anthropogenic pressures. This is congruent with previous results (Irz et al. 2007a). Various responses were reported for this metric. It can increase due to eutrophication (Dodson et al. 2000; Mittelbach et al. 2001) or species introduction (Irz et al. 2004a), but decrease due to the extirpation of habitat-sensitive taxa (Corbacho & Sanchez 2001).

The three diversity indices were not either correlated to anthropogenic factors. These indices have rarely been used in fish index development, probably because they are highly correlated with each other and because the information they provide is difficult to interpret (Holmgren et al. 2007). In addition, zoogeographic factors (e.g., post-glacial dispersal, hydrographic regions, and pH) relevant for explaining species richness and diversity indices have not been considered in this analysis (Griffiths 1997; Irz et al. 2004a).

Despite a strong negative relationship between the native related metrics and anthropogenic pressures observed in other studies (e.g., Jennings et al. 1999), this association was not detected. However, the species driving this relation in the French data set were in the majority *Rutilus rutilus* (L., 1758), *Perca fluviatilis* (L., 1758), *Blicca bjoerkna* (L., 1758) and *Abramis brama* (L., 1758). These species are overall tolerant as regards degraded lake conditions. Hence, the selection of a fish species able to respond, depending on the biological trait that is studied, in both directions to degraded lake conditions explains why the response of those candidate metrics could be concealed in our study. The same explanation can be

advanced to account for the absence of relationships between agricultural or urban pressure and fish-based metrics related to lithophilic, strict lithophilic, and invertivorous species.

In addition, the near absence of reproduction-related metric responses highlighted by this study may be the result of the poor relevance or the deficiency of the lake descriptors considered. It is commonly accepted that both local and large-scale processes influence local fish assemblages in lakes (Irz et al. 2007; Petesse et al. 2007). In this study, only large-scale pressures were considered and more relevant descriptors of habitat and hydromorphological alteration have to be collected; further studies will then be required to better understand the influence of regional versus local anthropogenic pressures on fish assemblages (Irz et al. 2007a).

Finally, the relationship between intolerant species-related metrics and anthropogenic pressures can be concealed, as reported by Irz et al. (2007a), because "a species could be considered as intolerant in some regions where it is restricted to some particular type of environment, and tolerant in another region where it is widespread." However, in this study we can note that, apart from *Gobio gobio* (L., 1758), all other fish species driving that relation had either low occupancy (<3% of the sampling sites) or poor average relative abundance (<1% in at least one of both types). Consequently, intolerant species-related metrics displayed a very narrow range of variance, thus explaining their lack of response to anthropogenic pressures.

Additional work is needed, and as suggested by Berrebi-dit-Thomas et al. (1998) and Whittier et al. (2007), metrics based on biological traits that are the expression of specialized attributes (e.g., invertivores, lithophilic) should be calculated without considering overall tolerant fish species. Indeed, this modification may prevent the sensitivity of a specific biological parameter from being concealed due to the heterogeneity of the fish species contributing to the calculation of the fish-based metric.

Multiple testing

No corrections were made for multiple testing. We are aware of the increasing risk of false positive. However, there is much true dependence between the metrics tested since they are based on guild composed by partly the same species and for a given guild six metrics are based on the same species but measured differently. In short, because of this dependence, the

true number of effective testing must be largely fewer than the number of metrics considered (Cheverud 2001). Nevertheless, much attention must be paid to the levels of significance.

Conclusion

The present study indicates that fish assemblages are appropriate ecological indicators for both natural and artificial lakes. Our results underline the necessity to control for the environment when developing FBIs at broad geographical scales. They also prove that the relevant metrics differ between natural lakes and for reservoirs. This challenges the attempts to use natural systems as references to assess the ecological potential of artificial ones.

Acknowledgements

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Figure captions

Figure 1: Location of the 89 study sites in the French hydrographic network. ◊ Natural lakes ♦ Reservoirs

Tables

Table 1: Environmental parameter mean values, and extreme values of the 89 study sites.

Parameter	Reservoirs (n=59)		Natural lakes (n=30)	
	Mean	Range	Mean	Range
Geologic Index (GI) (% of the drainage basin as calcareous)	0.26	0~1	0.38	0~1
Residence Time (RT) (day)	137.09	0.11~922.80	692.08	5~5095
Water level maximal amplitude (WL)[a]	1.53	0~2	0.45	0~2
Catchment area (A_{DB}) (km^2)	662.23	8.42~10533.34	152.80	1.25~1033.34
Lake area (A_L) (ha)	251.00	44~2272	781.00	13~5768
Maximum depth (D_{max}) (m)	23.87	2~100	23.13	2~110
Shoreline development factor (SLDF)[b]	3.34	1.01~9.20	1.62	1.01~3.80
T°C mean Jan + T°C mean Jul (SumT)	23.86	15.49~31.27	20.44	13.18~31.51
T°C mean Jul - T°C mean Jan (DiffT)	15.97	10.43~19.42	17.19	13.48~19.91
Volume development (V_d)[c]	1.21	0.37~2.96	1.42	0.30~2.66

[b]3 classes: 0 (no variation), 1 (≤3m), 2(>3m)

[b]Calculated as: perimeter / ($\sqrt{4\pi \times \text{surface}}$).

[c]Calculated as: 3 × Lake volume / (Maximum depth × Lake area).

Table 2: Description of the anthropogenic variables included in the analysis; and principal component analysis (PCA) carried out on the watershed pressure variables. Table entries are the variable correlations with the first principal component on each of the two PCAs, one carried out on agricultural variables only (PA) and another carried out on urban variables only (PU). Those loading most heavily on each PC are in bold.

		All lakes (n = 146)		Reservoirs (n=59)		Naturals (n=30)	
		PA	PU	Mean	Range	Mean	Range
Variable	*Inertia*	63%	72%				
% catchment agricultural		**0.84**	-	51.41	0 ~ 93.80	24.30	0 ~ 87.50
Agriculture land cover area (km^2)		0.65	-	427.06	0 ~ 8783.40	54.35	0 ~ 790.60
Nitrogen balance (t)		0.79	-	122.19	-598.20 ~ 877.10	-40.44	-346.80 ~ 432.30
Phosphorus balance (t) * erodibility coefficient		**0.88**	-	421.71	-156.60 ~ 2523.10	-12.95	-389.10 ~ 849.20
% catchment urban		-	**0.90**	3.95	0 ~ 55	3.40	0 ~ 15.30
Population density in catchment (people/km^2)		-	**0.86**	65.33	4.10 ~ 1006.50	40.02	3.70 ~ 260.50
Transportation network density		-	0.78	2.17	0 ~ 10.30	2.09	0 ~ 11.30

Table 3: Occurrence rates of the 42 fish species in natural lakes and reservoirs. Rates over 75% are in bold.

Common name	Species	Frequency Reservoirs (%)	Frequency Naturals (%)	Average Relative Abundance Reservoirs (%)	Average Relative Abundance Naturals (%)
Bream	*Abramis brama*	**76.67**	51.61	9.25	4.87
Sterlet	*Acipenser ruthenus*	1.67	0.00	0.00	0.00
Spirlin	*Alburnoides bipunctatus*	0.00	3.23	0.00	0.02
Bleak	*Alburnus alburnus*	53.33	29.03	2.05	2.25
Brown Bullhead	*Ameiurus melas*	28.33	29.03	7.13	1.18
European eel	*Anguilla anguilla*	1.67	3.23	0.01	0.00
Stone Loach	*Barbatula barbatula*	5.00	6.45	0.22	0.10
Barbel	*Barbus barbus*	6.67	0.00	0.04	0.00
White Bream	*Blicca bjoerkna*	66.67	22.58	8.05	3.46
Goldfish	*Carassius auratus auratus*	8.33	0.00	0.01	0.00
Crucian Carp	*Carassius carassius*	11.67	9.68	0.03	0.10
Common Whitefish	*Coregonus lavaretus*	3.33	32.26	0.03	1.61
Bullhead	*Cottus gobio*	1.67	6.45	0.02	0.04
Common Carp	*Cyprinus carpio*	38.33	19.35	0.23	0.03
Northern Pike	*Esox lucius*	58.33	67.74	0.35	0.27
Mosquitofish	*Gambusia affinis*	1.67	0.00	0.01	0.00
Gudgeon	*Gobio gobio*	15.00	32.26	2.07	1.07
Ruffe	*Gymnocephalus cernuus*	63.33	38.71	6.08	3.17
Silver carp	*Hypophthalmichthys molitrix*	1.67	0.00	0.01	0.00
Pumpkinseed	*Lepomis gibbosus*	30.00	32.26	0.19	0.23
Belica	*Leucaspius delineatus*	3.33	3.23	0.00	0.25
Ide	*Leuciscus idus*	1.67	0.00	0.00	0.00
Common Dace	*Leuciscus leuciscus*	3.33	9.68	0.03	0.03
Golden grey mullet	*Liza aurata*	1.67	0.00	0.00	0.00
Thinlip Mullet	*Liza ramada*	1.67	0.00	0.12	0.00
Burbot	*Lota lota*	0.00	3.23	0.00	0.00
Rainbow Trout	*Oncorhynchus mykiss*	10.00	9.68	0.83	0.42
European Perch	*Perca fluviatilis*	**93.33**	**93.55**	21.95	28.72
Eurasian Minnow	*Phoxinus phoxinus*	5.00	3.23	0.41	1.81
Bitterling	*Rhodeus amarus*	3.33	0.00	0.03	0.00
Roach	*Rutilus rutilus*	**91.67**	**96.77**	31.31	38.85
Freshwater Blenny	*Salaria fluviatilis*	0.00	3.23	0.00	0.01
Brown Trout	*Salmo trutta fario*	15.00	16.13	1.13	0.65
Charr	*Salvelinus alpinus*	0.00	9.68	0.00	0.78
Lake Trout	*Salvelinus namaycush*	0.00	3.23	0.00	0.04
Pike Perch	*Sander lucioperca*	**78.33**	41.94	4.41	1.83
Rudd	*Scardinius erythrophthalmus*	**81.67**	70.97	3.39	5.88
Wels Catfish	*Silurus glanis*	21.67	9.68	0.05	0.01
European Chub	*Squalius cephalus*	21.67	38.71	0.44	1.06
Western vairone	*Telestes souffia*	0.00	3.23	0.00	0.79
Grayling	*Thymallus thymallus*	1.67	0.00	0.02	0.00
Tench	*Tinca tinca*	25.00	35.48	0.09	0.45

Table 4: Proposed guild classification for French lake fishes

Guilds		Definitions
Tolerance guild (Karr et al. 1986)	Overall Tolerants	Species sensitive to any common impact related to altered flow regime, nutrient regime, habitat structure and water chemistry. Loss of intolerant species is a response to degradation, whereas the number of tolerant species will tend to increase with disturbance.
	Overall Intolerants	
Reproduction guild (Balon 1975; Dycus & Meinert 1994)	Lithophilic	Can reproduce on unsilted mineral substrates whose larvae are photophobic.
	Strict Lithophilic	Need mineral substrates to reproduce.
	Strict Phytophilic	Need plant substrates to reproduce and whose larvae are not photophobic.
Trophic guild (Bruslé & Quignard 2001; Dycus & Meinert 1994; Goldstein & Simon 1999; Pont et al. 2006)	Omnivores	Feed on both animal and vegetal items (more than 25% plant material and more than 25% animal material).
	Invertivores	Feed at least partially on invertebrates/insects (more than 75% macro-invertebrates in the diet).
	Planktivores	Feed mainly on zooplankton and/or phytoplankton (more than 75% of plankton in the diet).
	Herbivores	Feed on plant items (more than 75% of plant material in the diet).
	Piscivores	Feed on fish at least partially when adults (more than 75% fish in the diet).

Table 5: Mean values (standard deviation) of the fish-based metrics and *p*-values of Student *t*-test (with Welch correction if needed) obtained from the functional traits between natural lakes and reservoirs; $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

Functional traits	Reservoirs (*n*=59)					Naturals (*n*=30)				
	CPUE	Proportion in number of individuals	BPUE	Proportion in biomass of individuals	Species Richness	CPUE	Proportion in number of individuals	BPUE	Proportion in biomass of individuals	Species Richness
Overall Species Richness	-	-	-	-	9.50 (2.60)	-	-	-	-	8.40 (2.50)
Shannon index	-	-	-	-	1.29 (0.32)*	-	-	-	-	1.15 (0.21)*
Simpson index	-	-	-	-	0.63 (0.13)	-	-	-	-	0.58 (0.10)
Evenness index	-	-	-	-	0.59 (0.13)	-	-	-	-	0.56 (0.11)
Natives	0.08 (0.09)	0.66 (0.32)	3.30 (2.70)	0.62 (0.30)	5.70 (2.40)	0.06 (0.10)	0.78 (0.35)	2.40 (2.20)	0.74 (0.29)	5.70 (2.60)
Intolerants	0.00 (0.00)	0.01 (0.07)	0.04 (0.20)*	0.02 (0.09)**	0.30 (0.60)*	0.00 (0.01)	0.04 (0.08)	0.2 (0.30)*	0.09 (0.15)**	0.80 (1.10)*
Tolerants	0.09 (0.09)	0.80 (0.23)	3.90 (2.70)**	0.74 (0.20)*	5.40 (1.90)**	0.08 (0.11)	0.80 (0.21)	2.40 (2.10)**	0.64 (0.20)*	4.20 (1.70)**
Lithophilic	0.09 (0.09)	0.88 (0.19)	4.20 (2.60)**	0.83 (0.17)	6.60 (2.00)	0.08 (0.12)	0.91 (0.14)	2.60 (2.00)**	0.79 (0.23)	6.20 (2.20)
Strict lithophilic	0.00 (0.02)	0.10 (0.19)	0.50 (0.80)	0.11 (0.19)	1.10 (1.00)	0.00 (0.01)	0.08 (0.17)	0.30 (0.40)	0.13 (0.20)	1.70 (1.50)
Strict phytophilic	0.02 (0.04)	0.12 (0.19)	0.90 (1.10)	0.16 (0.16)	2.80 (1.30)*	0.01 (0.02)	0.08 (0.14)	0.80 (1.60)	0.21 (0.23)	2.20 (1.20)*
Omnivores	0.05 (0.05)	0.47 (0.22)	2.90 (2.10)*	0.55 (0.19)	3.90 (1.50)*	0.06 (0.10)	0.54 (0.26)	2.00 (1.70)*	0.51 (0.21)	3.20 (1.20)*
Invertivores	0.10 (0.09)	0.95 (0.05)**	4.40 (2.70)*	0.86 (0.10)	8.10 (2.30)	0.09 (0.12)	0.98 (0.03)**	3.10 (2.30)*	0.90 (0.11)	7.30 (2.20)
Planktivores	0.06 (0.07)	0.55 (0.26)	3.40 (2.60)*	0.62 (0.20)	5.00 (1.90)*	0.06 (0.11)	0.57 (0.26)	2.20 (1.90)*	0.58 (0.20)	4.20 (1.60)*
Herbivores	0.03 (0.04)	0.34 (0.22)	1.30 (0.90)	0.28 (0.17)	1.60 (0.80)	0.04 (0.07)	0.41 (0.21)	0.90 (0.80)	0.27 (0.13)	1.80 (0.90)
Piscivores	0.04 (0.06)	0.36 (0.25)	1.60 (1.20)	0.35 (0.19)	3.60 (1.20)	0.03 (0.04)	0.36 (0.24)	1.30 (1.00)	0.44 (0.21)	3.60 (1.20)

Table 6: Regression of fish metrics versus the environmental and anthropogenic variables. Table entries are the regression coefficient model, R square adjusted, coefficient significance level, and variance partitioning; *var env* is the percentage of the total variation attributable to pure environmental effects, *var PA* to pure agricultural pressure effects, *var PU* to pure urban pressure effects, and *unexpl* variation unexplained by the model. For abbreviations see section "Candidate metrics".

		PA	PU	R^2-adjusted	var env	var PA	var PU	unexpl
Reservoirs	BPUE	0.09*	-	0.56	0.37	0.03*	<0.00	0.40
n = 59	Sp_OTol	0.20**	-	0.39	0.18	0.07*	0.00	0.59
	B_OTol	0.20***	-	0.68	0.38	0.06**	0.01	0.33
	Sp_Omni	0.20***	-	0.25	0.01	0.10*	0.02	0.79
	Sp_Plankt	0.20***	-	0.34	0.10	0.10*	0.01	0.70
	%Sp_Plankt	0.06***	-	0.21	<0.00	0.12**	<0.00	0.85
	B_Herb	0.20***	-	0.33	0.14	0.13**	0.02	0.71
	%Sp_Pisc	-0.08***	-	0.28	0.06	0.17**	<0.00	0.73
Natural lakes	%B_OTol	-	0.20***	0.43	0.27	<0.00	0.30**	0.51
n = 30	Nb_StPhyto	0.03***	-	0.66	0.23	0.20**	0.01	0.39
	%B_Plankt	0.20*	-	0.42	0.28	0.17*	<0.00	0.65

*significant at 0.05 level; **significant at 0.01 level; ***significant at 0.001 level

Appendix 1: Assignment of the 42 fish species into reproductive, trophic, and tolerance guilds used to derive assemblage traits.

Species	Overall Intolerant species	Overall Tolerant species	Lithophilic	Strict Lithophilic	Strict Phytophilic	Omnivores Generalist	Invertivores	Planktivores	Herbivores	Piscivores
Abramis brama	0	1	1	0	0	1	1	1	0	0
Acipenser ruthenus	0	0	1	1	0	0	1	0	0	0
Alburnoides bipunctatus	1	0	1	1	0	0	1	1	0	0
Alburnus alburnus	0	1	1	0	0	1	1	1	0	0
Ameiurus melas	0	1	1	1	0	0	1	0	0	1
Anguilla anguilla	0	1	0	0	0	0	1	0	0	1
Barbatula barbatula	0	0	1	0	0	0	1	0	0	0
Barbus barbus	0	0	1	1	0	0	1	0	0	0
Blicca bjoerkna	0	1	0	0	1	0	1	1	0	0
Carassius auratus auratus	0	1	0	0	1	1	1	1	1	0
Carassius carassius	0	1	0	0	1	1	1	1	1	0
Coregonus lavaretus	1	0	1	1	0	0	1	1	0	0
Cottus gobio	1	0	1	1	0	0	1	0	0	0
Cyprinus carpio	0	1	1	0	0	1	1	1	0	0
Esox lucius	0	0	0	0	1	0	0	0	0	1
Gambusia affinis	0	1	0	0	0	0	1	1	0	0
Gobio gobio	0	0	1	0	0	0	1	0	1	0
Gymnocephalus cernuus	0	0	1	0	0	0	1	0	0	0
Hypophthalmichthys molitrix	0	1	0	0	0	0	0	1	1	0
Lepomis gibbosus	0	1	1	1	0	0	1	1	0	0
Leucaspius delineatus	1	0	0	0	1	0	1	1	0	0
Leuciscus idus	1	0	1	0	0	1	1	1	1	1
Leuciscus leuciscus	0	0	1	1	0	1	1	1	0	0
Liza aurata	0	0	0	0	0	1	0	1	1	0
Liza ramada	0	1	1	1	0	0	1	0	1	0
Lota lota	0	0	1	1	0	0	1	0	0	1
Oncorhynchus mykiss	0	0	1	1	0	0	1	0	0	1
Perca fluviatilis	0	1	1	0	0	0	1	0	0	1
Phoxinus phoxinus	0	0	1	1	0	0	1	0	0	0
Rhodeus amarus	1	0	0	0	0	0	1	0	1	0

Rutilus rutilus	0	1	1	0	0	1	1	1	1	0
Salaria fluviatilis	0	0	1	1	0	0	1	0	0	0
Salmo trutta fario	1	0	1	1	0	0	1	0	0	1
Salvelinus alpinus	1	0	1	1	0	0	1	0	0	1
Salvelinus namaycush	1	0	1	1	0	0	1	0	0	1
Sander lucioperca	0	0	1	0	0	0	0	0	0	1
Scardinius erythrophthalmus	0	0	0	0	1	1	1	1	0	0
Silurus glanis	0	0	0	0	1	0	1	0	0	1
Squalius cephalus	0	0	1	0	0	1	1	1	1	1
Telestes souffia	1	0	1	1	0	0	1	0	0	0
Thymallus thymallus	1	0	1	1	0	0	1	0	0	0
Tinca tinca	0	1	0	0	1	0	1	0	0	1