

Controlling for natural variability in assessing the response of fish metrics to human pressures for lakes in north-east USA

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ABSTRACT

1. While fish-based Indices of Biotic Integrity (IBIs) have been developed for a wide array of lotic systems, equivalent tools have seldom been adapted to the monitoring and assessment of lakes. Major difficulties arise in such work: (i) collecting data that allow statistically robust analyses, (ii) choosing the relevant variables to describe the biotic, environmental and anthropogenic data sets and (iii) assessing the relative importance of the latter two in explaining the former. The aim of the present paper is to produce such an assessment for the fish communities of the lakes of north-east USA.

2. Fish surveys, environmental features and catchment-scale descriptors of human stresses (agricultural and urban land-uses) were collected for 112 natural lakes.

3. Fish metrics, i.e. species richness and percentages of species belonging to reproductive, trophic, and tolerance guilds, were regressed against anthropogenic variables, then against anthropogenic variables and the natural environmental conditions.

4. It was shown that failing to control for the natural environmental conditions in the IBI construction led to selecting metrics (percentage of intolerant species and percentage of omnivorous species) that did not display response to stresses when the environment was controlled for. Moreover, controlling for natural variability of the metrics allowed identifying the impact of agricultural land-use on the percentage of diadromous species.

5. Fish communities appear valuable for the bioassessment of lakes. Appropriate statistical methods have proved that the natural variability in the bioassessment tools could be accounted for, thereby allowing assessments at the scale of multiple basins and ecoregions. This opens new perspectives for the development of IBIs for lentic systems in lake-poor regions, such as southern

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Europe, and therefore represents a significant contribution to the implementation of the European Water Framework Directive.

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INTRODUCTION

Apart from a limited community of scientists working on the alteration of ecosystems undergoing human impacts, environmental awareness has long been an attribute of politically engaged environmentalists. The debate opposed those giving priority to the conservation of species and ecosystems to those considering that such conservation objectives would be harmful to socio-economic development. The idea that the alteration of ecosystem functioning could greatly affect the human uses of these systems widened the stakes in environmental conservation (Baron *et al.*, 2002). From that point of view, freshwater ecosystems are of particular concern (Gleick, 2003). Access to water resources to meet human needs both qualitatively and quantitatively is now considered a prerequisite for human development (Jackson *et al.*, 2001; Baron *et al.*, 2002; Gleick, 2003). This shift in awareness has been accepted by at least some political authorities in many parts of the world, leading to regulations aimed at protecting and/or improving the integrity of hydrosystems (e.g. the European Water Framework Directive (WFD), or the Clean Water Act in the USA). A guiding spirit of these regulations was that ensuring the ecological integrity of water bodies was the best guarantee of the sustainability of the services and commodities provided by freshwater ecosystems.

The concept of biological integrity of ecosystems was defined by Karr and Dudley (1981) as 'the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity and functional organisation comparable to that of natural habitat of the region'. Although this is an ecosystem-level definition, most studies assessing ecological integrity rely upon biological community-, guild- or population-level indicators.

Multimetric fish-based indices, such as the Index of Biotic Integrity (IBI) first formulated by Karr (1981), have been developed for a wide array of lotic systems. However, equivalent tools have seldom been adapted to the monitoring and assessment of lakes (but see Dionne and Karr, 1992; Hughes *et al.*, 1992; Minns *et al.*, 1994; Jennings *et al.*, 1995, 1999; Whittier, 1999; Appelberg *et al.*, 2000; Drake and Pereira, 2002). Most of these studies were only preliminary even if some assessed the response of individual fish metrics to human stresses such as acidification (Appelberg *et al.*, 2000), eutrophication (Jennings *et al.*, 1999) or land use (Drake and Pereira, 2002). However, a major difficulty in identifying which bioassessment metrics perform best (those that clearly respond to human pressures) is that these metrics generally also display natural patterns of variation (Karr *et al.*, 1986; Karr, 1999; Smogor and Angermeier, 1999; Oberdorff *et al.*, 2002). It is necessary to adjust the metrics, therefore, to account for this natural variability before analysing their relationship with human stresses, which has not been done, or only partially (i.e. adjusting metrics to a single environmental gradient), in the studies listed above dealing with standing waters.

Thus, the aim of the present study is to demonstrate the importance of environmental control in assessing the response of fish metrics for north-east USA lakes to catchment-scale human pressures. Because good quality data on lentic fish communities are lacking in southern Europe, we believe this study of lakes in north-east USA will support the implementation of the WFD for European lakes.

MATERIALS AND METHODS

The data set

The data were collected between 1991 and 1994 from 196 natural lakes and reservoirs in north-east USA by the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP; Larsen *et al.*, 1991; Whittier and Paulsen, 1992). The lakes were selected using a probability design to be representative of regional conditions (Larsen *et al.*, 1994). Each summer, five or six crews were employed to sample 49–68 lakes, on a 4-yr rotation. A random subset of 48 lakes received one, two or three repeat samples, with no more than two visits in any summer. For this study only data from the first visit were assessed. Sampling was conducted from early July until mid-September, during the period of lake stratification. The sampling schedule was arranged to remove (as much as practically possible) spatial bias from the sampling dates. Fish assemblages were sampled with overnight sets of gillnets, trapnets and minnow traps, and by night seining (Baker *et al.*, 1997; Whittier *et al.*, 1997). A standardized level of effort, as a logarithmic function of lake size, ranged from one to 10 sets of each passive gear and up to six seining sites (Baker *et al.*, 1997). The sampling objective was to collect a representative sample of the fish assemblage at each lake, without regard to any particular species, or concentrated sampling of species-rich habitats. Fish were identified to species, and counted. Voucher specimens were archived at either the Harvard University Museum of Comparative Zoology (Cambridge, MA) or the New York State Museum (Albany, NY).

The field sampling protocols (Baker *et al.*, 1997) are available at the EMAP website <http://www.epa.gov/emap/html/pubs/docs/groupdocs/surfwatr/field/97fldman.html>. For each lake, the fish community was represented as the sum of the catch data from all gear.

The classification of species into trophic guilds (Table 1) was based on a literature survey (Goldstein and Simon, 1999; Whittier, 1999; Bruslé and Quignard, 2001). The reproductive guild classification mainly follows Simon (1999) with some additions from Balon (1975) and online resources (see in reference list). *Noturus insignis* was considered benthic invertivorous based on other *Noturus* species listed in Simon (1999). Tolerance classifications were from Halliwell *et al.* (1999). They correspond to a general assessment of the species' environmental niche breadth.

Ten traits (Table 2) were derived from the community guilds: four from the trophic guilds (piscivorous, invertivorous, omnivorous and benthivorous), four from the reproductive guilds (litho-psammophilous, phytophilous, guarder and diadromous) and two from the tolerance guilds (tolerant and intolerant). Using species' migratory and parental care characteristics is not common in IBI metrics, but it was hypothesized that these traits, being important features of the species life-history strategies, might display responses to human disturbance (Winemiller and Rose, 1992). Other life-history traits (growth rate, for example) could be valuable in this perspective but they were not available for these data.

Ten guild-based metrics were expressed as proportions of species (i.e. number of species sharing a trait divided by the total number of species in the lake) to which the total species richness metric was added (Table 3). Non-native species were not omitted because they were considered as part of the resident species pool (Halliwell *et al.*, 1999); both native and non-native species have been included in the metric calculations. Alternative ways of combining faunal sampling and guild assignment to obtain metrics could have been used, for example, to obtain the percentage of individuals per guild, but the use of abundance and/or biomass estimates for fish in deep and heterogeneous environments, such as lakes and reservoirs, always gives rise to sampling issues (Jackson and Harvey, 1997).

Environmental variables, catchment-scale measures of land use and human pressures were obtained from digitized maps (Table 4). The environmental variables used can be considered as the main abiotic determinants of richness and structure of fish assemblages in natural lakes (Amarasinghe and Welcomme, 2002; Irz *et al.*, 2007). The assemblage and habitat data analysed here are available at the EMAP website (<http://www.epa.gov/emap/html/dataI/surfwatr/data/nelakes>).

Table 1. Assignment of the fish species into trophic, reproductive (Repro.) and tolerance (Tol.) guilds. The codes refer to Table 2 for the trophic and reproductive guilds. Tolerance guilds are from Halliwell *et al.* (1999). I, intolerant; MT, intermediate tolerance; T, tolerant

Species	Trophic guild	Repro. guild	Tol. guild	Species	Trophic guild	Repro. guild	Tol. guild
<i>Alosa pseudoharengus</i>	KI	A.1.4+Diad	MT	<i>Margariscus margarita</i>	GF	A.1.3	MT
<i>Ambloplites rupestris</i>	IC	B.2.2	MT	<i>Micropterus dolomieu</i>	TC	B.2.2	MT
<i>Ameiurus natalis</i>	GF	B.2.7	T	<i>Micropterus salmoides</i>	IC	B.2.2	MT
<i>Ameiurus nebulosus</i>	GF	B.2.7	T	<i>Morone americana</i>	IC	A.1.4+Diad	MT
<i>Amia calva</i>	TC	B.2.5	T	<i>Moxostoma macrolepidotum</i>	BI	A.1.3	MT
<i>Anguilla rostrata</i>	IC	A.1.1+Diad	T	<i>Moxostoma valenciennesi</i>	BI	A.1.3	I
<i>Aplodinotus grunniens</i>	GF	A.1.1	MT	<i>Notemigonus crysoleucas</i>	GF	A.1.5	T
<i>Carassius auratus</i>	BI	A.1.5	T	<i>Notropis bifrenatus</i>	CI	A.1.5	I
<i>Carpoides cyprinus</i>	GF	A.1.2	T	<i>Notropis heterodon</i>	CI	A.1.5	I
<i>Catostomus catostomus</i>	BI	A.1.2	I	<i>Notropis heterolepis</i>	BI	A.1.5	I
<i>Catostomus commersoni</i>	GF	A.1.2	T	<i>Notropis hudsonius</i>	BI	A.1.2	MT
<i>Coregonus artedi</i>	KI	A.1.1+Diad	I	<i>Notropis volucellus</i>	GF	A.1.5	MT
<i>Coregonus clupeaformis</i>	BI	A.1.2+Diad	I	<i>Noturus gyrinus</i>	BI	B.2.7	MT
<i>Cottus cognatus</i>	BI	B.2.7	I	<i>Noturus insignis</i>	BI	B.2.7	MT
<i>Couesius plumbeus</i>	IC	A.1.2	MT	<i>Oncorhynchus mykiss</i>	IC	A.2.3	I
<i>Culaea inconstans</i>	CI	B.2.4	I	<i>Osmerus mordax</i>	IC	A.1.2+Diad	I
<i>Cyprinus carpio</i>	GF	A.1.4	T	<i>Percina caprodes</i>	BI	A.2.3	MT
<i>Cyprinella spiloptera</i>	CI	A.2.4	T	<i>Perca flavescens</i>	IC	A.1.4	MT
<i>Dorosoma cepedianum</i>	KH	A.1.2	T	<i>Percopsis omiscomaycus</i>	CI	A.1.3	MT
<i>Erimyzon oblongus</i>	GF	A.1.2	I	<i>Phoxinus eos</i>	GF	A.1.5	MT
<i>Esox lucius</i>	TC	A.1.5	I	<i>Phoxinus neogaeus</i>	IN	A.1.4	MT
<i>Esox niger</i>	TC	A.1.5	MT	<i>Pimephales notatus</i>	GF	B.2.7	T
<i>Etheostoma fusiforme</i>	BI	A.1.5	I	<i>Pimephales promelas</i>	GF	B.2.7	T
<i>Etheostoma olmstedii</i>	BI	B.2.7	MT	<i>Pomoxis nigromaculatus</i>	IC	B.2.5	MT
<i>Exoglossum maxillingua</i>	BI	B.2.3	I	<i>Pungitius pungitius</i>	CI	B.2.4+Diad	MT
<i>Fundulus diaphanus</i>	CI	A.1.5	T	<i>Rhinichthys atratulus</i>	BI	A.1.2	T
<i>Gasterosteus aculeatus</i>	CI	B.2.4+Diad	MT	<i>Rhinichthys cataractae</i>	BI	A.1.2	MT
<i>Hybognathus regius</i>	BH	A.1.4	I	<i>Salmo salar</i>	IC	A.2.3+Diad	I
<i>Ictalurus punctatus</i>	IC	B.2.7	MT	<i>Salmo trutta</i>	IC	A.2.3+Diad	I
<i>Labidesthes sicculus</i>	CI	A.1.4	I	<i>Salvelinus alpinus</i>	IC	A.2.3+Diad	I
<i>Lepisosteus osseus</i>	TC	A.1.4	MT	<i>Salvelinus fontinalis</i>	CI	A.2.3+Diad	I
<i>Lepomis auritus</i>	CI	B.2.3	MT	<i>Salvelinus namaycush</i>	IC	A.2.3	I
<i>Lepomis gibbosus</i>	IC	B.2.2	MT	<i>Scardinius erythrophthalmus</i>	GF	A.1.4	T
<i>Lepomis macrochirus</i>	GF	B.2.2	T	<i>Semotilus atromaculatus</i>	IC	A.2.3	T
<i>Lepomis microlophus</i>	BI	B.2.2	MT	<i>Semotilus corporalis</i>	IC	A.2.3	MT
<i>Lota lota</i>	BI	A.1.2	MT	<i>Sander vitreus</i>	TC	A.1.2	MT
<i>Luxilus cornutus</i>	GF	A.2.3	MT	<i>Umbra limi</i>	GF	B.1.4	T

Analytical procedure

The procedure was designed (i) to analyse the relationship between the fish community metrics and the anthropogenic features of the lakes without control of the environment, (ii) to analyse the relationship between the fish community metrics, and the environmental and anthropogenic features of the lakes and (iii) to partition the variation in fish community metrics into four components: purely environmental, purely anthropogenic, covariation relationships between environmental and anthropogenic, and unexplained.

The large number of predictor variables (Table 4) and the correlation among them required factor analysis to reduce dimensionality and avoid collinearity. This was achieved by means of standardized

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Table 2. Correspondence between trophic and reproductive guilds and the modalities used to derive the metrics

Guild	Description	Piscivore	Invertivore	Omnivore	Benthic feeder	Guarder	Litho-psammophilous	Phytophilous	Diadromous
BH	Benthic herbivore	0	0	0	1				
BI	Benthic invertivore	0	1	0	1				
CI	Water column invertivore	0	1	0	0				
GF	Generalist feeder (omnivore)	0	0	1	0				
IC	Invertivore/piscivore	1	1	0	0				
IN	Invertivore	0	1	0	0				
KH	Filter-feeding herbivores	0	0	0	0				
KI	Filter-feeding invertivore	0	1	0	0				
TC	Top carnivore (piscivore)	1	0	0	0				
A.1.1	Nonguarders – Open substratum spawners – Pelagophils				0	0	0	0	
A.1.2	Nonguarders – Open substratum spawners – Lithopelagophils				0	1	0	0	
A.1.3	Nonguarders – Open substratum spawners – Lithophils				0	1	0	0	
A.1.4	Nonguarders – Open substratum spawners – Phytolithophils				0	1	1	1	
A.1.5	Nonguarders – Open substratum spawners – Phytophils				0	0	0	1	
A.2.3	Nonguarders – Brood hiders – Lithophils				0	1	0	0	
A.2.4	Nonguarders – Brood hiders – Speleophils				0	1	0	0	
B.1.4	Guarders – Substratum choosers – Phytophils				1	0	1	1	
B.2.2	Guarders – Nest spawners – Polyphils				1	1	1	1	
B.2.3	Guarders – Nest spawners – Lithophils				1	1	1	0	
B.2.4	Guarders – Nest spawners – Ariadrophils				1	1	1	1	
B.2.5	Guarders – Nest spawners – Phytophils				1	0	0	1	
B.2.7	Guarders – Nest spawners – Speleophils				1	1	1	0	
C.1.4	Bearers – External brooders – Gill-chamber brooders				1	0	0	0	
Diad	Diadromous								1

Table 3. Description of the fish metrics

Metric name	Description
SpRichness	Number of species in the sample
%_LithPsam	Percentage of lithophilous or psammophilous species
%_Phyto	Percentage of phytophilous species
%_Guarder	Percentage of nest-guarder species
%_Diad	Percentage of long-range diadromous species
%_Pisc	Percentage of piscivorous species
%_Inv	Percentage of invertivorous species
%_Omn	Percentage of omnivorous species
%_Benth	Percentage of benthivorous species
%_Tol	Percentage of species tolerant to environmental variations
%_Intol	Percentage of species intolerant to environmental variations

Table 4. Environmental and anthropogenic variables included in the analysis with basic statistical descriptions of their distributions. Urbanization variables are related to URB_TOT, HOUDENKM, POPDENKM and RD_DEN

	Variable	Description	Min.–Max.	Median	
Environmental variables	AREA_WS	Area of the catchment (ha)	31–792 100	1564	
	AV_DEP	Estimated mean depth (m)	0.5–21.8	4.6	
	ELEV	Lake altitude (m)	16–569	247	
	HI_PT	High point of catchment (m)	81–1483	279	
	KM_SEA	Distance from the ocean (km)	6–330	139	
	LKVOL2M3	Estimated lake volume (m ³)	16 410–5.42 × 10 ⁸	2 689 000	
	LK_HA	Lake surface area (ha)	3–3306	64	
	LTROFF_M	Long-term average annual runoff (m)	0.34–0.77	0.61	
	PRECIP_M	Long-term average precipitation (m)	0.80–1.28	1.09	
	RETENT	Estimated water retention time for lakes (yr)	0.01–5.60	0.40	
SHR_LTH	Length of shoreline including islands (m)	748–111 500	6317		
Anthropogenic variables	Urbanization variables	URB_TOT	% catchment urban (non-residential + residential)	0–37.8	0
		HOUDENKM	Housing unit density (housing km ⁻²)	0–120.2	2.6
		POPDENKM	Population density (persons km ⁻²)	0–310.2	2.5
		RD_DEN	Road density (m ha ⁻¹)	0–54.6	8.8
		AG_TOT	% catchment agricultural	0–59.3	0

principal components analysis (PCA). The principal components (PCs) are independent of each other and summarize the variance in the data matrix. A first PCA was carried out on the log-transformed environmental matrix, of which the first three PCs (env1 to env3) were kept for further analysis. The four variables describing human pressures related to urbanization were highly correlated, so they were synthesized into a single variable that was the first PC of a PCA carried out on these four variables. The percentage of agricultural lands in the catchment (AG_TOT) was transformed to $\arcsine\sqrt{X}$ to approach normality. This transformation is classically recommended for percentage variables (Sokal and Rohlf, 1994).

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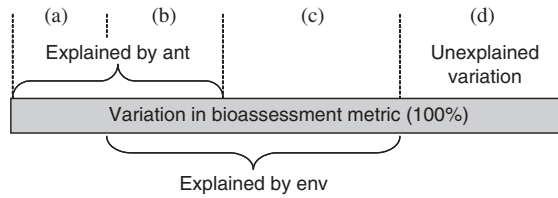


Figure 1. Partition of the variation of a bioassessment metric into four components. [a] exclusively anthropogenic, [b] combined between anthropogenic and environmental, [c] exclusively environmental and [d] unexplained. Adapted from Legendre and Legendre (1998)

Each fish metric was transformed to $\arcsin\sqrt{X}$ and regressed against the environmental and anthropogenic variables in multiple linear regressions (MLR). The significance of the models was assessed using an F -test. Visual examination of residual values was performed at each step of the procedure to identify potential outliers.

Variance partitioning was then carried out for each fish metric following the four steps recommended by Legendre and Legendre (1998) in situations where two complementary sets of variables may contribute to the variation of an ecological variable (Figure 1):

- Step 1: The metric was regressed against the anthropogenic PCs in MLR. The corresponding coefficient of determination R_1^2 measured [a] + [b].
- Step 2: The metric was regressed against the environmental PCs in MLR. The corresponding coefficient of determination R_2^2 measured [b] + [c].
- Step 3: The metric was regressed against the environmental and anthropogenic PCs in MLR. The corresponding coefficient of determination R_3^2 measured [a] + [b] + [c].
- Step 4: Each component was obtained by subtraction: [a] = $R_3^2 - R_2^2$; [b] = $R_1^2 + R_2^2 - R_3^2$; [c] = $R_3^2 - R_1^2$; [d] = $1 - R_3^2$.

A negative component [b] indicates that the anthropogenic and environmental sets of variables together explain the metric variation better than the sum of the individual effects of these two sets of variables (Legendre and Legendre, 1998).

All analyses were computed with R software (Ihaka and Gentleman, 1996) and carried out on the subset of 112 natural lakes (including 'augmented lakes', i.e. lakes that existed before European settlement that have been deepened by > 30%). Reservoirs were excluded because a preliminary analysis had shown that both environmental and land-use variables differed between these two types of systems (Whittier *et al.*, 2002). Natural lakes with a total species richness of 3 or less were also omitted because IBI metrics have little chance of being relevant for species-poor sites (Fausch *et al.*, 1990). As some of the lakes had been surveyed on more than one occasion, and in order to avoid statistical biases (i.e. pseudoreplication), only the first sampling visit was included in the analyses.

RESULTS

The PCA carried out on the environmental variables (Table 5) showed that the variables related to lake size were strongly correlated and contributed to the first environmental PC (env1). The second axis (env2) summarized the geographical location of the lakes, with the variables related to the altitude and straight-line distance to the sea. Axis 3 (env3) carried the rainfall regime but its eigenvalue was rather low (corresponding to 13% of the total variance).

Table 5. Principal components analysis carried out on the environmental variables. Table entries are the variables scores on the first three axes of the PCA. Those loading most heavily on each PC are in bold

Inertia	Env1 41%	Env2 26%	Env3 13%
AREA_WS	0.80	-0.01	-0.38
AV_DEP	0.78	-0.04	0.14
ELEV	0.04	0.85	0.46
HL_PT	0.42	0.79	0.27
KM_SEA	0.17	0.91	0.14
LK_VOL2M3	0.99	-0.10	-0.05
LK_HA	0.95	-0.10	-0.14
LTROFF_M	0.16	-0.50	0.63
PRECIP_M	0.01	-0.64	0.60
RETENT	0.53	-0.14	0.39
SHR_LTH	0.92	-0.14	-0.10

Table 6. Regression of fish metrics (arcsine \sqrt{X} transformed) against the anthropogenic variables. Table entries are regression coefficients, *F* statistic and model significance

Metric	Intercept	Urb_PCA	AG_TOT	<i>F</i>	Significance level
%_Phyto	0.836***	0.068***	-0.105	16.5	<0.001
%_Guarder	0.598***	0.085***	-0.074	29.8	<0.001
%_Diad	0.298***	-0.028*	0.129	2.4	0.095
%_LithPsam	1.077***	-0.013	-0.056	1.9	0.151
%_Pisc	0.769***	0.063***	-0.154	10.9	<0.001
%_Inv	0.857***	-0.003	-0.105	1.4	0.239
%_Omn	0.613***	-0.019*	0.047	2.8	0.065
%_Benth	0.134***	-0.016	0.008	1.2	0.302
%_Tol	0.643***	0.005	-0.006	0.2	-0.836
%_Intol	0.287***	-0.042***	0.109	5.1	0.007
SpRichness	2.184***	0.038	0.233	3.1	0.051

*Significant at 0.05 level; ***Significant at 0.001 level.

Six of the 11 candidate fish metrics displayed a response to human pressures (Table 6). The only type of pressure significantly contributing to the models was Urb_PCA, indicating the predominance of catchment urbanization in influencing fish distribution and ecology. Lakes with urban catchments displayed a decrease in the percentage of diadromous (%_Diad), omnivorous (%_Omn) and intolerant (%_Intol) species, and an increase in the proportion of phytophilous (%_Phyto), guarder (%_Guarder) and piscivorous (%_Pisc) species.

Four fish metrics displayed a response to Urb_PCA when environment was controlled for (Table 7). Lakes with urban catchments displayed a decrease in %_Diad and an increase in %_Phyto, %_Guarder and %_Pisc species. A single reproductive-based metric displayed a positive response to the proportion of agricultural land-use in the catchment. Apart from %_Guarder, all other models included significant coefficients for at least one environmental PC, which underlines the importance of accounting for the natural patterns of variability when studying the response of bioassessment indicators to human pressures. The main natural factor contribution to the models was lake size (env1). The strongest response to human pressure was the increase in %_Guarder, with 30% of the variance attributed to the anthropogenic variables, then %_Phyto with 13%, %_Diad with 11% and %_Pisc with 9%. Three of the four models

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Table 7. Regression of fish metrics (arcsine \sqrt{X} transformed) against the environmental and anthropogenic variables. Table entries are regression coefficients, *F* statistic, model significance level and variance partitioning; *var env* [c] is the percentage of the total variation attributable to pure environmental effects, *var ant* [a] to pure anthropogenic effects, *var com* [b] combined between anthropogenic and environmental effects and *unexpl* [d] variation unexplained by the model

Env.PCs interpretation	Metric	Intercept	Urb_ PCA	AG_TOT env1 (size)	env2 (altitude/ distance sea)	env3 (runoff/ precipitation)	<i>F</i> level	<i>var env</i> [c]	<i>var ant</i> [a]	<i>var com</i> [b]	<i>unexpl</i> [d]
<i>N</i> = 112	%_Phyto	0.841***	0.058***	-0.150	-0.032***	-0.04*	11.5 < 0.001	12.05	13.34	9.87	64.74
	%_Guarder	0.600***	0.087***	-0.089	0.007	-0.003	11.8 < 0.001	0.44	29.94	5.42	64.20
	%_Diad	0.284***	- 0.049***	0.217*	0.030**	0.018	9.5 < 0.001	26.69	11.05	-6.83	69.09
	%_LithPsam	1.08***	0.005	-0.078	0.032***	0.019	10.7 < 0.001	30.04	0.75	2.66	66.55
	%_Pisc	0.767***	0.052**	-0.141	0.025*	-0.006	6.9 < 0.001	7.93	9.15	7.50	75.41
	%_Inv	0.854***	-0.004	-0.083	0.028	0.013	5.7 < 0.001	18.59	1.72	0.87	78.82
	%_Omn	0.616***	-0.015	0.025	-0.028***	-0.009	7.4 < 0.001	20.87	2.52	2.37	74.24
	%_Benth	0.136***	-0.005	-0.006	0.034***	0.013	5.2 < 0.001	17.60	0.22	1.95	80.23
	%_Tol	0.639***	-0.003	0.021	-0.015*	-0.001	1.8 0.111	7.67	0.11	0.22	92.00
	%_Intol	0.282***	-0.027	0.149	0.03*	0.046*	6.3 < 0.001	14.36	3.10	5.54	77.01
	SpRichness	2.21***	0.035	0.029	0.136***	-0.084**	26.8 < 0.001	50.48	1.88	3.45	44.19

*Significant at 0.05 level; **Significant at 0.01 level; ***Significant at 0.001 level.

displaying response to human pressures were related to the reproductive requirements, combined with a single trophic structure metric (%_Pisc).

DISCUSSION

Whatever the model developed (i.e. integrating or not natural environmental factors), species richness did not respond to the human pressures considered in this study. This was not surprising given that various responses of this metric have been reported, from an increase due to eutrophication (Dodson *et al.*, 2000; Mittelbach *et al.*, 2001) or species introductions (Irz *et al.*, 2004), to a decrease due to the extirpation of habitat-sensitive taxa (Corbacho and Sanchez, 2001). However, this metric is one of the most frequently included in IBIs developed for lakes (Hickman and McDonough, 1995; Jennings *et al.*, 1999; McDonough and Hickman, 1999; Whittier, 1999; Appelberg *et al.*, 2000; Drake and Pereira, 2002). Including non-responsive metrics in an index results in increasing the noise in the data and hence alters its ability to detect or assess the impact of human activities on ecological systems. Therefore, the IBIs that have been developed skipping the step of the evaluation of the response of individual metrics to stressors (step 4 in Whittier *et al.*, 2001) are unlikely to be optimized in terms of indicator properties.

The negative relationship between %_Intol and Urb-PCA is significant only when the natural environment is not controlled for. Most of the fish-based IBIs developed for lakes also include tolerance metrics (Hickman and McDonough, 1995; Jennings *et al.*, 1999; McDonough and Hickman, 1999; Whittier, 1999) that frequently exhibit clear relationships with the pressures. However, these studies do not control for the effects of differences in natural habitat conditions across lakes other than lake area (Whittier, 1999). This statement gives rise to substantial doubts about the ability of tolerance metrics to respond to anthropogenic stressors when the confounding environmental effects are discarded. It may be a consequence of the difficulty in assigning species to tolerance guilds. For the purpose of the present study, the choice was made to use the fish species tolerance rating according to Halliwell *et al.* (1999) rather than according to Whittier (1999) or Whittier and Hughes (1998). Although these latter studies were dedicated to the fish communities of the lakes studied here, we considered it to be more rigorous to assign tolerance guilds on the basis of a totally independent source that did not use the EMAP data set. It is clear that the assessment of species tolerance is highly dependent upon the regional context. For example, a species could be considered as intolerant in some regions where it is restricted to a particular type of environment (e.g. at the edges of its distribution area, see Karr (1991)), and tolerant in another region where it is widespread (e.g. at the centre of its distribution area). However, using the same data set to assess the species tolerance to human stresses and to analyse the response of tolerance metrics to the same stresses would have led to circular reasoning. Experimental tests of sensitivity to specific stresses would ensure the independence between the assessment of species sensitivity and the data set used to analyse the response of fish communities to human stresses, but would be beyond the scope of this study.

Two of four trophic composition metrics displayed relationships with human pressures without environmental control while one metric did with it. This was consistent with the frequent inclusion of trophic metrics in river IBIs (Hughes and Oberdorff, 1999; Belpaire *et al.*, 2000) and has been previously suggested with a different analytical procedure on a subsample of the present data set (Whittier, 1999), and on other lentic systems (Jennings *et al.*, 1999; Drake and Pereira, 2002). The strong positive relationship observed in the two models (i.e. integrating or not integrating natural environmental factors) between piscivorous species and urbanization may be explained by species manipulations in urban areas in response to anglers' demand. The negative bivariate correlation between urban development and %_Omn contrasted with those previously observed both on lakes (Schulz *et al.*, 1999; Drake and Pereira, 2002) and on rivers (Oberdorff *et al.*, 2002). However, this relationship was not significant when the effects of natural

environmental factors were controlled for, thereby suggesting that the correlations between natural environmental factors and anthropogenic stressors can lead to artificial metric-stress relationships.

Except for %_LithPsam, regardless of the models developed, all of the remaining spawning guild metrics were related to anthropogenic variables. Hence, the reproduction-based metrics were those that most frequently contributed significantly to the models. Furthermore, controlling for the environment allows identifying the effect of agricultural land use on %_Diad. In this case the variability in the metric attributable to the environment is likely to have blurred its response to land-use.

Reproductive metrics were not included in the early IBIs developed for lotic systems (Karr *et al.*, 1986; Karr, 1991; Hughes and Oberdorff, 1999) but have now been proved to be relevant (Oberdorff *et al.*, 2002; Pont *et al.*, 2006) and their response to anthropogenic stressors has never, to our knowledge, been shown for lacustrine environments. The availability of suitable spawning habitats is certainly one of the major factors driving the distribution of fish species (and guilds) in freshwater systems. These results indicate that the alteration of these habitats is likely to be responsible for major impacts on lentic fish communities.

Conservation and scale issues

It is now commonly accepted that local communities are shaped by an interplay between local and larger-scale processes (O'Neill, 1989; Levin, 1992; Ricklefs and Schluter, 1993). Consequently, the spatial scale is important when considering the assessment of human pressures. The functioning of freshwater ecosystems is highly dependent upon the catchment from which they receive most of their inputs (Baron *et al.*, 2002), but also on their connectivity with the downstream river network from which they receive most of the colonizing species, and on local human uses. In this study, only the catchment was considered. Thus, the metrics displaying no link with pressures at the catchment scale could respond to other local pressures such as hydroelectricity production, power boating, and flood control, as well as to broader-scale pressures.

A multiscale analysis is also critical to the design of conservation strategies (Lewis *et al.*, 1996; Turner, 2005). For example, impacts of invasive species, global change, air pollution or human-induced landscape alterations can hardly be assessed by local and short-term investigations because they imply relatively slow dynamics (compared with the duration of most ecological studies) and operate according to a hierarchical framework in which regional-scale alterations potentially lead to local impacts. Therefore, the implementation of efficient management strategies to mitigate these impacts requires an understanding of the mechanisms at various scales as well as the links between scales (Turner, 2005).

The contemporary technological and scientific contexts give the opportunity for broad-scale ecological investigations that both are scientifically innovative and provide support for ambitious environmental policies. Nevertheless, so far, general conservation issues and management decisions are still often discussed at a restricted scale compared with that required by the targeted ecological process. Considering that inland waters (e.g. lakes and rivers) belong to the most intensively human influenced ecosystems on Earth, partly owing to their interface position in the landscape and the fact that human population densities and associated activities are highest along river courses (Dudgeon *et al.*, 2006), developing large-scale conservation strategies becomes crucial for these ecosystems.

The pioneering work on IBIs has been carried out at relatively limited spatial scales in order to mitigate the 'uncontrolled' larger-scale processes. However, recent developments of bioassessment tools for lotic systems have proved that appropriate statistical methods could efficiently account for the natural variability of community attributes, thereby allowing working at the scale of multiple basins and ecoregions (Oberdorff *et al.*, 2002; Pont *et al.*, 2006). The present study shows that similar techniques can also be implemented for lake systems over broad geographic areas. This type of procedure opens new perspectives for the development of assessment tools for lentic systems in lake-poor regions, such as southern Europe. In these places working within basins would not allow the collection of a sufficient number of samples to

obtain statistically and ecologically sound assessments of the response of fish communities to human stresses.

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