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Approche comparative des communautés piscicoles lacustres

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Pascal Irz. Approche comparative des communautés piscicoles lacustres. Ecologie, Environnement. Université Montpellier II - Sciences et Techniques du Languedoc, 2006. Français. NNT: . tel-00088836

HAL Id: tel-00088836

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UNIVERSITE MONTPELLIER II
SCIENCES ET TECHNIQUES DU LANGUEDOC

T H E S E

pour obtenir le grade de
DOCTEUR DE L'UNIVERSITE MONTPELLIER II

Discipline : Ecologie
Formation Doctorale : Ecologie des Systèmes Aquatiques Continentaux
Ecole Doctorale : Biologie des Systèmes Intégrés - Agronomie - Environnement

présentée et soutenue publiquement
par

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le 20 avril 2006

*Approche comparative des communautés
piscicoles des plans d'eau*

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Pour Félia.

Remerciements

Pour éviter les embarras de préséance, je remercie collectivement toutes les personnes qui m'ont accompagné au cours de cette thèse :

- les collègues qui m'ont supporté sur le terrain et lors du travail quotidien,
- les génies qui ont développé certains outils de gestion et d'analyse des données et m'ont ainsi permis d'avancer,
- les sages avec qui les discussions ont été stimulantes et constructives,
- les comiques qui ont contribué à maintenir autour de moi convivialité et sérénité,
- les courageux qui ont accepté d'évaluer ce travail,
- les malchanceux qui m'ont guidé,
- les flegmatiques qui ont permis mon investissement dans ce projet,

mais pas les autres. Pas de raison, non?

Table des matières

1	DEMARCHE D'ETUDE	3
1.1	PROBLEMATIQUE GENERALE	3
1.2	ORGANISATION DU MEMOIRE	6
2	MATERIELS ET METHODES	10
2.1	LES DONNEES	10
2.1.1	LES INVENTAIRES PISCICOLES DES PLANS D'EAU EN FRANCE	10
2.1.2	LES CARACTERISTIQUES DES PLANS D'EAU FRANÇAIS ET DE LEURS BASSINS VERSANTS	11
2.1.3	LES DONNEES SUR LES PLANS D'EAU DU NORD-EST DES ETATS-UNIS	11
2.1.4	LES CARACTERISTIQUES BIOLOGIQUES DES ESPECES	12
2.1.5	CONSIDERATIONS GENERALES SUR LES DONNEES	13
2.2	DESCRIPTION DES COMMUNAUTES	14
2.3	LES METHODES	14
3	SYNTHESE ET DISCUSSION DES RESULTATS	16
3.1	EFFET DES FACTEURS ENVIRONNEMENTAUX	16
3.1.1	SUR LA RICHESSE SPECIFIQUE	16
3.1.2	SUR LES ASSEMBLAGES D'ESPECES	19
3.2	EFFET DES INTERACTIONS AU SEIN DES COMMUNAUTES	21
3.3	IMPACTS ANTHROPIQUES	27
3.3.1	IMPACTS DIRECTS	29
3.3.2	IMPACTS INDIRECTS	30
3.4	PERSPECTIVE HISTORIQUE ET EVOLUTIVE	33
4	PERSPECTIVES	35
4.1	REGLES D'ASSEMBLAGE	35
4.2	LIEN ENTRE LES ECHELLES SPATIALES	36
5	CONCLUSION	42
6	REFERENCES	43
	ANNEXES - PUBLICATIONS ET MANUSCRITS	51

1 Démarche d'étude

1.1 Problématique générale

Il est aujourd'hui généralement reconnu que les mécanismes écologiques s'exerçant localement sont sous la dépendance de ceux opérant à des échelles spatiales supérieures (Ricklefs 1987 ; O'Neill 1989 ; Levin 1992 ; Ricklefs & Schluter 1993b). Ceci a été conceptualisé en présentant les communautés aquatiques locales comme résultant du passage d'un pool mondial d'organismes à travers une série de cribles, du plus grossier (continental) au plus fin (local), agissant en excluant à chaque étape certains organismes (Tonn 1990 ; Tonn *et al.* 1990 ; Poff 1997). Cette approche hiérarchique descendante a été reprise en Figure 1 et adaptée en considérant que seuls les éléments de discontinuité nette agissaient comme des filtres. Ainsi, les continents sont-ils des entités clairement distinctes les unes des autres, séparées par des étendues marines. De même, les bassins versants sont délimités par des milieux terrestres et marins, et les plans d'eau par des milieux terrestres et lotiques. Ces entités sont donc séparées par des milieux qui représentent des obstacles difficilement franchissables pour des poissons d'eaux douces et stagnantes. Dans le sens ascendant, le lien entre les échelles se fait par le *turnover* (Loreau 2000 ; Chase & Leibold 2002) ; par exemple c'est le *turnover* inter-bassins qui permet de retrouver l'ensemble de la faune du continent. La faune piscicole d'un bassin n'étant pas exclusivement constituée d'espèces lenticques, le *turnover* inter-lacs ne permet pas d'expliquer la totalité de la faune du bassin. Toutefois, la distinction entre milieux lotiques et lenticques étant largement une question de convention, et la plupart des espèces présentes dans les plans d'eau d'Europe de l'Ouest étant également largement distribuées dans les cours d'eau (Muus & Dahlstrom 1978 ; Mahon 1984), insérer un filtre « faune piscicole lacustre » aurait été discutable.

Ces considérations d'échelle spatiale trouvent leur pendant temporel puisque les processus écologiques que l'on peut observer actuellement, par exemple la compétition entre deux espèces, sont dépendants du contexte historique et évolutif qui a conduit à ce que ces espèces soient présentes dans une même région (Tokeshi 1999).

Enfin, les mécanismes opérant à un niveau d'intégration biologique donné (par exemple individuel) dépendent largement des niveaux d'organisation supérieurs tels que les populations, les communautés ou les écosystèmes (Begon *et al.* 2005).

Pour résumer, les échelles spatiales, temporelles et les niveaux d'intégration biologique larges fixent le cadre dans lequel se déroulent les processus écologiques aux échelles plus fines.

Un nombre croissant de questionnements adressés à la communauté scientifique concerne des phénomènes se déroulant à de larges échelles spatiales et temporelles (Lawton 1999 ; Gaston 2003 ; Turner 2005). Les impacts écologiques de la dissémination des espèces invasives, du changement global, des pollutions atmosphériques ou des modifications des paysages par l'Homme peuvent difficilement être appréhendés par des investigations limitées à un contexte local et sans recul temporel. La réponse écologique à de telles atteintes se manifeste en effet par une dynamique relativement lente (par rapport à la durée de la plupart des études) et selon un schéma d'échelles emboîtées où les perturbations à l'échelle régionale peuvent influencer sur les mécanismes locaux. La mise en œuvre de politiques de gestion efficaces pour limiter ces impacts suppose une bonne compréhension des mécanismes régissant les trajectoires des systèmes étudiés, compréhension qui ne sera possible qu'en saisissant la complémentarité des échelles d'investigation (Levin 1992 ; Rosenzweig 1995 ; Poff 1997) et non en promouvant une échelle aux dépens des autres.

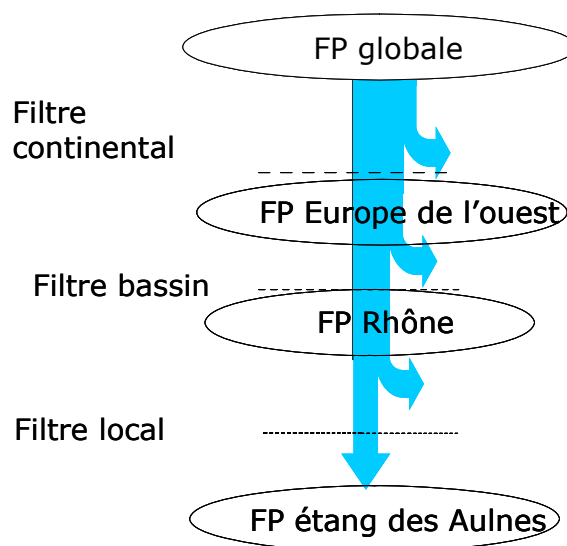


Figure 1 : Représentation du modèle selon lequel les faunes piscicoles (FP) locales résultent du passage d'un *pool* d'espèces au travers d'une série de cribles de plus en plus fins. Adapté de Tonn (1990).

Si l'intérêt d'études intégrant les mécanismes opérant à large échelle n'est pas une découverte récente, il n'en est pas de même des possibilités de mener à bien de telles études (Gaston 2003). En effet, le développement de modèles permettant de caractériser l'environnement sur de vastes zones (modèles numériques de terrain, modèles climatiques continus, réseau hydrographique, etc.) est récent car il fait appel à des données collectées par des moyens développés dans les dernières décennies (télédétection). Ces données doivent ensuite être administrées (bases de données en particulier à références spatiales) pour être accessibles à des utilisateurs équipés de moyens de calcul permettant l'analyse d'importantes masses de données. Dans un autre registre, les connaissances sur la biologie des espèces, nécessaires pour interpréter les variations de richesse et d'abondance entre les sites, se sont nettement affinées (Gaston 2003), même si les efforts de recherche portent essentiellement sur les groupes taxonomiques porteurs d'enjeux pour les activités humaines.

Le contexte technologique et scientifique actuel ouvre donc des possibilités d'investigation écologique à large échelle tout à la fois innovantes et susceptibles de contribuer à la définition de politiques environnementales ayant pour ambition de dépasser les contextes locaux.

Ainsi, le présent mémoire a pour objectif général de préciser les patrons de variabilité des attributs des communautés piscicoles entre les plans d'eau en vue de contribuer à la compréhension des mécanismes responsables des patrons, qu'ils soient naturels ou conséquences des activités de l'Homme.

La manipulation expérimentale de plans d'eau, si elle a déjà été menée (He & Kitchell 1990 ; Persson *et al.* 1999 ; Persson *et al.* 2003), est à la fois très lourde à mettre en œuvre et discutable sur le plan éthique. L'approche comparative, utilisant la variabilité entre des situations (Diamond 1983), est donc pratiquement la seule concevable pour aborder les questions sous-tendues par l'objectif général de cette thèse. Elle aurait potentiellement pu être développée selon deux axes : une approche sur un petit nombre de sites et un suivi temporel de long terme (utilisation de la variabilité temporelle) et une autre sans suivi temporel mais en intégrant de nombreux sites dans les analyses (utilisation de la variabilité spatiale). C'est le second axe qui a été retenu, tout d'abord pour des questions d'accessibilité aux données, mais aussi pour mettre en évidence les mécanismes essentiels de l'organisation des communautés piscicoles lacustres, et non ceux de tel ou tel système

local (Lévêque 2001). Ce type d'approche a reçu la dénomination de macroécologie, terme introduit pour désigner l'étude statistique des patrons d'abondance, de distribution et de diversité des espèces (Brown & Maurer 1989 ; Brown 1995) à des échelles larges, donc non compatibles avec l'expérimentation.

Dans ce mémoire, la communauté piscicole lacustre est considérée comme l'ensemble des populations de poissons qui cohabitent au sein d'un même lac, ce dernier terme désignant toute étendue stagnante d'eau douce, qu'elle soit d'origine naturelle ou créée par l'Homme. Le terme de plan d'eau en est synonyme.

1.2 Organisation du mémoire

Pour progresser vers l'objectif général énoncé ci-dessus, il a été nécessaire d'étudier les facteurs « naturels » qui influencent les communautés piscicoles locales, tels que les gradients environnementaux déterminant les conditions locales d'habitat, les interactions biotiques ou les caractéristiques du réseau hydrographique auquel le lac est connecté (physiques, *pool* d'espèces). Les impacts des activités humaines ont ensuite été approchés en les considérant comme une perturbation dans les patrons naturels de variabilité. Les deux types de pressions considérées ont été les introductions d'espèces non autochtones et l'occupation (agricole et urbaine) du bassin versant des plans d'eau.

Les résultats obtenus ont fait l'objet d'articles à différents stades d'avancement qui sont présentés en annexe :


- (P1) Irz P., Laurent A., Messad S., Pronier O. & Argillier C. (2002) Influence of site characteristics on fish community patterns in French reservoirs. *Ecology of Freshwater Fish*, 11, 123-136
- (P2) Irz P., Argillier C. & Proteau J.-P. (2004) Contribution of native and non-native species to fish communities in French reservoirs. *Fisheries Management and Ecology*, 11, 165-172
- (P3) Irz P., Argillier C. & Oberdorff T. (2004) Native and introduced fish species richness in French lakes: local and regional influences. *Global Ecology and Biogeography*, 13, 335-344
- (P4) Irz P., Odion M., Argillier C. & Pont D. (2006) Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs? *Aquatic Sciences*, 68, 109-116


(P5) Irz P., De Bortoli J., Michonneau F., Whittier T.R., Oberdorff T. & Argillier C. (en cours) Partitioning the variability in fish metrics into environmental and anthropogenic components for the bioassessment of Northeast U.S.A. lakes and reservoirs.


(P6) Irz P., Michonneau F., Oberdorff T., Whittier, T.R., Lamouroux N., Mouillot, D. & Argillier C. (en cours) Fish community convergence along environmental gradients in lakes of France and Northeast U.S.A.

De manière synthétique, les thématiques qui ont été abordées sont les suivantes :


1. Rôle structurant des facteurs « naturels »

 Facteurs environnementaux jouant sur les conditions locales d'habitat (P1, P6).

 Interactions biotiques (P3).

 Rôle du bassin (caractéristiques, *pool* de colonisateurs potentiels) (P2, P3, P4, P6).

2. Impacts anthropiques sur les communautés

 Introductions d'espèces (P2, P3).

 Occupation des sols sur les bassins versants (P5).

Ces thématiques n'étant évidemment pas indépendantes les unes des autres (par exemple les conditions d'habitat jouent sur les interactions biotiques), un même article se retrouve abordant plusieurs d'entre elles. Le dernier de ces articles, P6, en réalisant un test de convergence intercontinentale, présente une évaluation du caractère généralisable (i) des patrons observés séparément sur deux jeux de données indépendants (France et nord-est des Etats-Unis) et (ii) des mécanismes les plus probables pour expliquer ces patrons.

Les questions auxquelles les articles ont tenté de répondre, ainsi que les données qui ont été utilisées, sont précisées dans le Tableau 1 :

Tableau 1 : Questions abordées et données utilisées dans les articles de la thèse. Les données sont décrites au § 2.1. Pour la désignation des jeux de données, E-U=Etats-Unis, Fr=France.

	Lacs Fr	Retenues Fr	Cours d'eau Fr	Lacs E-U	Retenues E-U	Questions
P1		✓ (y compris de montagne)				<ul style="list-style-type: none"> • Les assemblages d'espèces varient-ils entre les sites selon des gradients continus ou selon une organisation discrète ? • Quels gradients environnementaux jouent sur cette organisation et sur la richesse spécifique ?
P2		✓				<ul style="list-style-type: none"> • Quelle est la contribution des espèces introduites aux richesses locales et régionales ?
P3	✓	✓				<ul style="list-style-type: none"> • Quel est le lien entre richesse locale et richesse du bassin ? • Suggère-t-il une saturation des communautés locales ? • Quelle est l'influence des espèces introduites sur ce lien quand les gradients environnementaux sont contrôlés ?
P4	✓	✓	✓			<ul style="list-style-type: none"> • Les retenues sont-elles des milieux intermédiaires entre lacs et cours d'eau du point de vue de l'abondance des espèces, de la richesse et du <i>turnover</i> entre espèces ?
P5				✓	✓	<ul style="list-style-type: none"> • Quelle est la réponse des communautés de poissons à l'occupation des sols ? • Les réponses sont-elles équivalentes entre lacs et retenues ?
P6	✓	✓		✓	✓	<ul style="list-style-type: none"> • Observe-t-on une convergence dans les réponses des communautés piscicoles lenticques aux gradients environnementaux entre la France et les Etats-Unis ?

Le mémoire de thèse est ainsi organisé de manière à synthétiser les avancées que représente chacun de ces articles. En effet, l'exercice de rédaction des articles impose que chacun soit focalisé sur des questions clairement délimitées, ce qui va à l'encontre de la vision synthétique d'un sujet plus large.

Si ce mémoire présente une synthèse relativement personnelle du sujet, les résultats obtenus et présentés dans les articles sont le fruit de travaux collectifs comme en atteste la liste des co-auteurs. J'ai également bénéficié de contributions

indirectes de nombreuses personnes lors des phases de collecte et de manipulation des données ainsi que lors de discussions informelles.

La présente première partie ayant posé la problématique générale, elle est suivie d'une brève description des données et des méthodes mises en œuvre. La troisième partie synthétise et discute les principaux résultats. Enfin, la quatrième partie propose des perspectives pour compléter ce qui a été réalisé au cours de cette thèse.

2 Matériels et méthodes

2.1 Les données

Les objectifs généraux de ce travail ont nécessité la collecte d'une importante masse de données, soit par l'analyse de la littérature, soit par des échantillonnages de terrain, soit par l'extraction à partir de bases existantes. Une description succincte en est fournie ci-dessous pour faciliter la lecture d'ensemble du document mais le détail de ces données figure dans les articles.

2.1.1 Les inventaires piscicoles des plans d'eau en France

Les inventaires piscicoles sur les plans d'eau de France ont été rassemblés à partir de nombreux documents de la littérature grise, de publications, ou ont été mis à disposition par les organismes ayant réalisé les pêches (Conseil Supérieur de la Pêche, Electricité de France, Universités, Instituts de recherche, bureaux d'étude, administrations, cf. Figure 2)

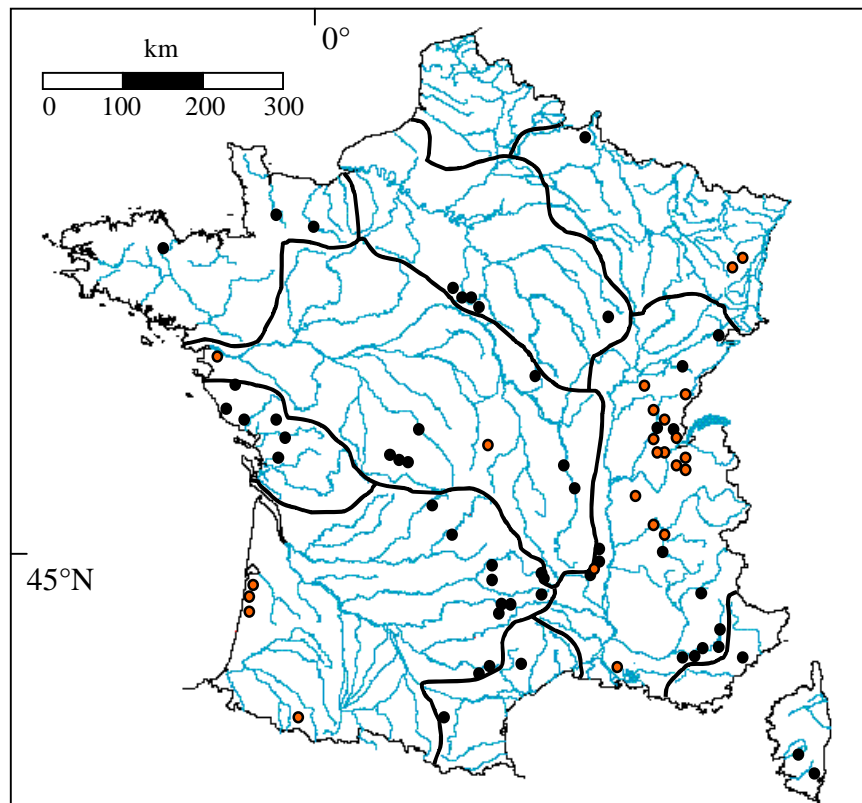


Figure 2 : Position des sites d'étude en France et délimitation des principales zones hydrographiques. En orange les lacs naturels et en noir les plans d'eau artificiels.

Les méthodes de pêche et les plans d'échantillonnage présentent une importante hétérogénéité. La plupart des inventaires ont été réalisés aux filets maillants. Toutefois, ceux réalisés par la collecte des poissons au moment de la vidange de certaines retenues ont été conservés pour certains volets de l'étude. Des descriptions plus précises sont disponibles dans les articles P1 et P3, dans la première thèse réalisée sur le sujet dans l'équipe actuellement dénommée "Ecosystèmes lacustres" de l'Unité de Recherche Hydrobiologie du Cemagref (Pronier 2000), et dans les articles issus de cette thèse et auxquels j'ai collaboré (Argillier *et al.* 2002b ; Argillier *et al.* 2002c).

2.1.2 Les caractéristiques des plans d'eau français et de leurs bassins versants

Les premiers travaux développés dans cette thèse ont fait appel aux caractéristiques morphologiques et géographiques des plans d'eau obtenues à partir de cartes à l'aide de planimètres et curvimètres (P2). Ensuite, le passage d'une base de données Paradox à un ensemble base de données "Access" + Système d'Informations Géographiques (SIG) "Arcview" a permis d'obtenir des informations telles que le régime climatique ou l'occupation du sol sur les bassins versants des plans d'eau. Les sources utilisées ont été :

- Carthage® pour le réseau hydrographique (Institut Géographique National),
- MNT 250m pour la topographie et la délimitation des bassins versants des lacs (Institut Géographique National),
- Corine Land Cover pour l'occupation des sols sur les bassins versants (Institut Français de l'Environnement),
- modèle thermique global (New *et al.* 2002),
- liste des plans d'eau soumis à la DCE (Agences de l'Eau, Ministère de l'Ecologie),
- diverses cartes aux échelles 1/25 000^{ème} à 1/250 000^{ème}.

2.1.3 Les données sur les plans d'eau du nord-est des Etats-Unis

L'US Environmental Protection Agency (USEPA) a mis en place en 1990 un programme de recherche en vue de développer les outils nécessaires à la surveillance de l'état des ressources écologiques (Larsen *et al.* 1994). Ce programme (Environmental Monitoring and Assessment Program, EMAP) comprenait en particulier un volet dédié aux lacs naturels et artificiels du nord-est des Etats-Unis. Un

échantillon de 365 plans d'eau (Figure 3) a été sélectionné pour représenter au mieux la diversité des plans d'eau de cette région (Larsen *et al.* 1994).

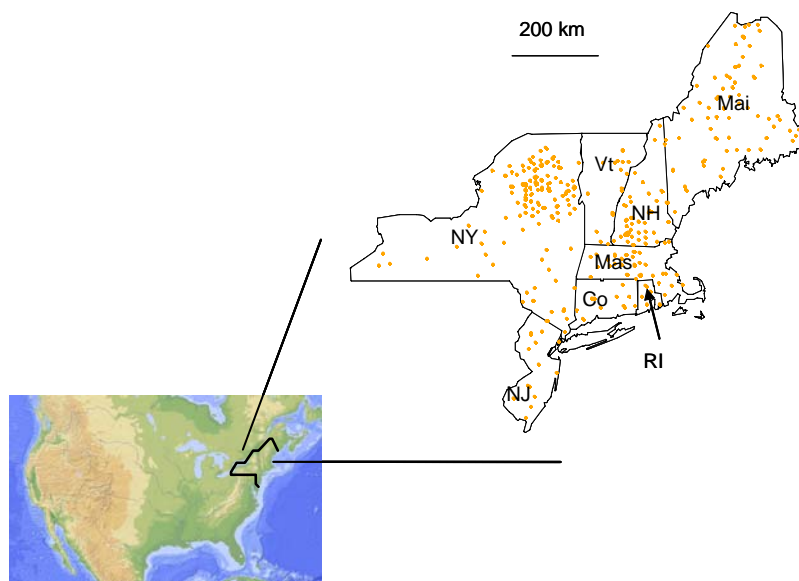


Figure 3 : Position des plans d'eau inventoriés par l'USEPA. Co=Connecticut, Mas=Massachusetts, Mai=Maine, NH=New Hampshire, NJ=New Jersey, NY=New York, RI=Rhode Island, Vt=Vermont.

Des modes opératoires standardisés ont été définis pour la collecte d'échantillons destinés à l'évaluation de la qualité de l'eau, de l'ichtyofaune, de l'avifaune, des diatomées, du macrobenthos et du zooplancton (Baker *et al.* 1997). Les campagnes de prélèvement ont été réalisées au cours des étés 1991 à 1994. Cent quatre-vingt seize de ces plans d'eau ont fait l'objet d'inventaires piscicoles. Ces données ont été complétées par des informations sur l'occupation du sol sur les bassins versants ainsi que par diverses variables décrivant les conditions d'habitat (collectées par SIG). La description précise de ces données est disponible dans des articles publiés antérieurement (Whittier & Hughes 1998 ; Allen *et al.* 1999 ; Whittier 1999 ; Whittier *et al.* 2002).

2.1.4 Les caractéristiques biologiques des espèces

Les caractéristiques biologiques des espèces ont été collectées par revue bibliographique (Tableau 2). Etant donné que l'ensemble des questions abordées au cours de cette thèse se place à l'échelle inter-spécifique, les variations intra-spécifiques ont été négligées. Caractériser les espèces par une valeur « moyenne » est certes réducteur, mais cette simplification a été imposée par l'absence de données sur la variabilité phénotypique intra- et inter- populations pour de

nombreuses espèces. Les variables ont été choisies, parmi les informations disponibles, pour décrire au mieux les exigences des espèces en termes d'habitat et de ressources trophiques.

Tableau 2 : Sources utilisées pour déterminer les guildes d'appartenance des espèces.

Guilde	Trophique	Reproductive	Tolérance
France	www.fishbase.org Michel & Oberdorff (1995) Bruslé & Quignard (2001)	Balon (1975)	www.fame.boku.ac.at
Etats-Unis	Whittier (1999)	Balon (1975) Simon (1999)	Halliwell <i>et al.</i> (1999)

Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada* **32**:821-864.

Bruslé, J., and J. P. Quignard. 2001. *Biologie des poissons d'eau douce européens*. Lavoisier Tec & Doc, Paris.

Michel, P., and T. Oberdorff. 1995. Feeding habits of fourteen European freshwater fish species. *Cybium* **19**:5-46.

Halliwell et al 1999, Simon 1999 et Whittier 1999: *in* T. P. Simon, editor. *Assessing the sustainability and biological integrity of water resource quality using fish communities*. CRC Press, Boca Raton, Florida.

2.1.5 Considérations générales sur les données

Il apparaît donc que le présent travail repose sur des données issues de sources variées qui n'ont pas été collectées pour répondre à son objectif. L'hétérogénéité des modes opératoires sur le terrain et des niveaux de définition, en particulier pour les bases à références spatiales, représente donc un facteur d'imprécision. Ces problèmes sont pratiquement inhérents à l'échelle à laquelle se place la présente étude. A de rares exceptions près, les investigations menées en macroécologie ou en biogéographie impliquent la mise en commun de données collectées par diverses équipes, selon des modes opératoires conçus pour répondre à des objectifs plus locaux. Que cela soit explicite ou non, ce type d'étude fait l'hypothèse que le rapport signal (=patron) / bruit (incluant les biais opératoires) est suffisamment élevé pour permettre, par l'emploi de méthodes statistiques adaptées, de révéler les patrons de variabilité de l'objet d'étude (Pielou 1977 ; Blackburn & Gaston 1998, 2004). Une des conséquences directes de cette variabilité dans les modes opératoires a été l'obligation, pour conserver un maximum de sites dans les analyses, d'homogénéiser le type d'information traitée en prenant en compte le plus petit dénominateur commun. C'est ce qui a conduit à mener la plupart des analyses sur des richesses spécifiques ou des occurrences d'espèces, sans pouvoir prendre en compte l'abondance de chaque espèce dans le milieu. De ce point de vue, le développement de réseaux de suivi environnemental à grande échelle (application de la DCE à

l'échelle européenne, EMAP aux Etats-Unis) s'appuyant sur des modes opératoires standardisés permettra certainement la collecte de données beaucoup plus précises et donc d'importants progrès dans les connaissances relatives aux mécanismes gouvernant la distribution spatiale et temporelle des espèces.

2.2 Description des communautés

Deux choix majeurs ont dû être faits pour cette étude : la définition de la communauté et la façon de la décrire. Le terme communauté a donc été défini selon des critères taxonomique (les poissons) et de délimitation géographique (les lacs) sans référence à de potentielles interactions. Ces communautés ont été caractérisées par plusieurs descripteurs qui autorisent des inférences complémentaires (Rodriguez & Lewis 1997 ; Samuels & Drake 1997).

- La richesse spécifique permet d'appuyer les analyses sur une abondante littérature aussi bien empirique que théorique (Magurran 1988 ; Ricklefs & Schluter 1993a ; Rosenzweig 1995 ; Gaston & Spicer 2004). Souvent utilisée comme un substitut de la biodiversité au sens large (Gaston & Spicer 2004), la richesse spécifique est un descripteur, certes simplifié à l'extrême, mais qui permet de nombreuses inférences sur les mécanismes qui gouvernent l'organisation des communautés.
- L'utilisation de guildes écologiques permet d'approcher les communautés sous un angle fonctionnel et donc de les comparer entre zones géographiques abritant des cortèges d'espèces différents.
- Les listes taxonomiques ont été analysées pour tenir compte de l'identité des espèces et de la manière dont elles coexistent au sein des plans d'eau.

Ces choix dans la façon de décrire les communautés influencent fortement les résultats obtenus (P5, P6).

2.3 Les méthodes

Les méthodes mises en œuvre sont celles classiquement utilisées en écologie comparative, à savoir des méthodes statistiques destinées à mettre en évidence des patrons de variabilité en comparant les assemblages d'un grand nombre de sites (Brown 1995 ; Gaston & Blackburn 2000). Elles sont basées sur les modèles linéaires, les modèles linéaires généralisés, les analyses de corrélation et les analyses multi-

variées. Ces dernières ont été utilisées pour l'exploration des données ou pour obtenir une vision synthétique de la variabilité des observations.

Ces méthodes ont été appliquées en début de thèse pour mettre en évidence des patrons de variation, puis dans le but de tester des hypothèses. Si la démarche a évolué au cours de l'étude, il n'en reste pas moins vrai que les analyses basées sur des corrélations ne permettent pas de démontrer l'existence de liens de causalité (Havens 1999). Elles permettent toutefois de confronter des observations à des situations attendues sous certaines hypothèses. Dans la plupart des cas, la principale difficulté réside dans le choix de l'hypothèse et dans sa formalisation. L'interprétation a également été délicate dans de nombreux cas puisque les questions étaient posées de manière simple, voire binaire (la richesse spécifique locale est-elle proportionnelle à - ou indépendante de - la richesse régionale ?), alors que les réponses se trouvaient dans une gamme continue de situations bornées par celles envisagées dans la question. Le type d'approche développé reposant par ailleurs sur l'analyse de patrons de variations, il est fréquent que différentes hypothèses puissent concourir à expliquer un même patron. Trancher entre ces hypothèses est généralement impossible de façon stricte car il est rare de pouvoir toutes les rejeter sauf une. Les conclusions sont donc plutôt appuyées sur des faisceaux d'indices concordants.

3 Synthèse et discussion des résultats

3.1 Effet des facteurs environnementaux

Chacun des gradients environnementaux correspondant aux dimensions de la niche écologique des espèces (Hutchinson 1957) peut influencer leur distribution et donc les attributs des communautés locales. Une synthèse (Matthews 1998) fait apparaître des liens entre les communautés piscicoles et :

- la qualité chimique de l'eau (pH, conductivité, teneur en oxygène),
- ses propriétés physiques (température, transparence, caractéristiques d'écoulement),
- la disponibilité en habitats (reproduction, abris) et en ressources alimentaires.

Ces propriétés locales sont liées à de nombreuses caractéristiques des milieux aquatiques (morphologie, taille, position géographique) et de leur environnement (climat et bassin versant en particulier). Il est rare que les données locales soient disponibles sur un nombre important de sites, aussi, dans cette thèse comme dans la plupart des études à grande échelle, il a souvent été fait appel à des gradients environnementaux généraux pour caractériser les conditions locales d'habitat.

3.1.1 Sur la richesse spécifique

Les résultats obtenus sur les relations entre facteurs environnementaux et communautés de poissons montrent que la richesse spécifique est avant tout expliquée par la surface du plan d'eau (P1, P3, P6). Cette relation linéaire, en échelle logarithmique, apparaît assez générale puisque de même pente entre les plans d'eau du nord-est des Etats-Unis et de France, de même qu'entre les lacs naturels et les retenues artificielles (P6). Le même type de relation a déjà été obtenu à de nombreuses reprises en Amérique du Nord (Tonn & Magnuson 1982 ; Eadie *et al.* 1986 ; Rago & Wiener 1986 ; Rahel 1986 ; Matuszek & Beggs 1988 ; Minns 1989 ; Mandrak 1995 ; Chapleau *et al.* 1997 ; Griffiths 1997 ; Magnuson *et al.* 1998 ; Matthews 1998 ; Allen *et al.* 1999 ; Whittier & Kincaid 1999) et dans d'autres régions (cf. Amarasinghe & Welcomme 2002 pour une revue).

Les mécanismes responsables de cette relation peuvent être recherchés dans l'abondante littérature dédiée aux relations aire-espèces (revues dans Magurran 1988

; Brown 1995 ; Rosenzweig 1995). L'augmentation de la richesse spécifique avec la surface d'une entité géographique est l'un des patrons les plus généraux de l'écologie des communautés (Rosenzweig 1995). Quatre explications ont été proposées à la relation aire-espèces, la dernière ayant été formulée spécifiquement pour les milieux aquatiques.

Premièrement, puisque les surfaces importantes abritent un nombre plus élevé d'individus, il est logique d'y trouver plus d'espèces que sur les petites surfaces. En effet, elles abritent une proportion plus importante du *pool* régional d'espèces (Coleman 1981 ; Coleman *et al.* 1982).

Il a également été fait référence à la théorie de la biogéographie insulaire (MacArthur & Wilson 1967). Les plans d'eau présentent en effet un certain nombre de similitudes avec les îles (Barbour & Brown 1974 ; Magnuson 1976 ; Browne 1981 ; Eadie *et al.* 1986 ; Magnuson *et al.* 1998). Ils sont isolés les uns des autres et les phénomènes de colonisation entre lacs sont rares car ils ne communiquent que par l'intermédiaire des cours d'eau. Dans cette théorie, la richesse est déterminée par l'équilibre entre des processus stochastiques de colonisation et d'extinction (MacArthur & Wilson 1967). Les premiers dépendent du degré d'isolement de l'île par rapport au continent qui abrite le *pool* d'espèces colonisatrices. Les probabilités d'extinction dépendent de la surface des îles car elles sont inversement proportionnelles à la taille des populations (MacArthur & Wilson 1967). La richesse à l'équilibre décroît donc avec l'isolement et croît avec la surface de l'île.

L'hypothèse a par ailleurs été posée que la surface n'agissait pas en tant que telle, mais au travers de son lien avec la diversité des habitats (Williams 1943 ; Diamond 1975). Les grandes surfaces, présentant généralement une hétérogénéité environnementale supérieure, permettraient la coexistence d'un plus grand nombre d'espèces en lien avec la théorie des niches (Hutchinson 1957 ; Giller 1984 ; Leibold 1995).

Enfin, il a été suggéré que cette relation résultait de la stabilité environnementale supérieure des grands plans d'eau par rapport aux petits (inertie physico-chimique). Cette stabilité limiterait les taux d'extinction (Jackson *et al.* 2001).

Une représentation schématique de ces hypothèses montre qu'elles ne sont pas indépendantes les unes des autres (Figure 4). Exception faite de la première, les différents mécanismes proposés jouent en effet tous sur les taux de colonisation et d'extinction. Dès lors, il est sans doute plus pertinent de poser la question de

l'importance relative de ces différents mécanismes que de tenter de tester chacune des hypothèses séparément. Bien que ne disposant pas à l'heure actuelle des données adéquates pour aborder la relation aire-espèces sous cet angle, il a été montré sur les plans d'eau du nord-est des Etats-Unis que la première de ces hypothèses (les grands plans d'eau sont plus riches car ils abritent plus d'individus) était loin d'expliquer à elle seule le lien entre la superficie du plan d'eau et sa richesse piscicole (P6).

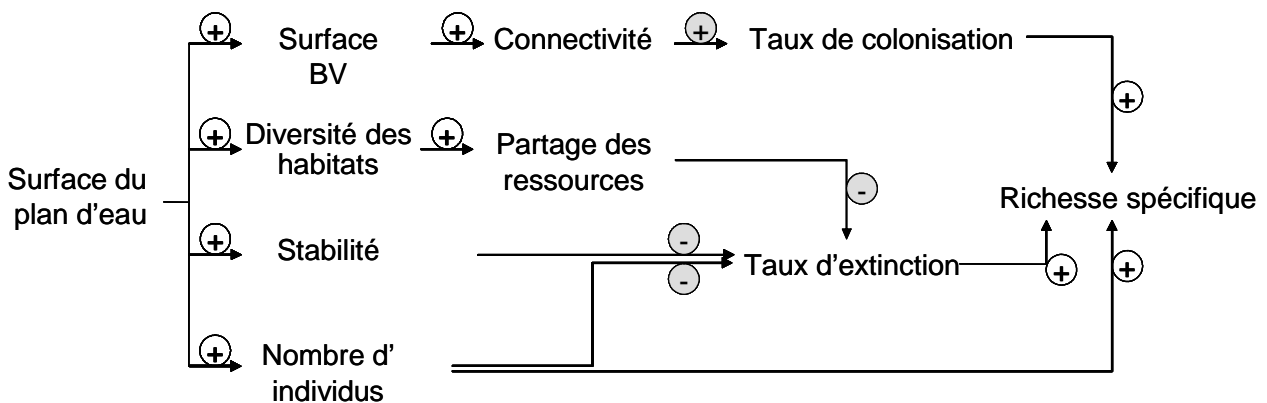


Figure 4 : Représentation des différents mécanismes par lesquels la surface d'un lac est susceptible d'agir sur la richesse spécifique. Les signes grisés correspondent aux processus influencés par le *pool* régional d'espèces.

La mise en oeuvre des réseaux de suivi des plans d'eau devrait à brève échéance mener à l'acquisition de données sur la diversité des habitats lacustres selon un mode opératoire standardisé (Rowan *et al.* 2003) ainsi que le suivi de la qualité physico-chimique de l'eau. Par ailleurs, un géo-référencement des barrages est actuellement en cours. Il apparaît donc que les données adéquates devraient être disponibles pour évaluer l'importance relative des différents mécanismes concourant potentiellement à expliquer la relation aire-espèces sur les plans d'eau.

La richesse spécifique augmente également avec la profondeur du plan d'eau, paramètre qui reflète, comme la surface, un aspect de la diversité des habitats. Proposer des mécanismes par lesquels la profondeur agirait sur la richesse est très délicat dans la mesure où ce paramètre est fortement corrélé à la surface du plan d'eau (P6).

Les effets conjugués de la surface et de la profondeur aboutissent logiquement à l'augmentation de la richesse avec le volume du plan d'eau.

Parmi les autres facteurs environnementaux pris en compte, l'altitude joue aussi sur la richesse spécifique (P1). Sur les retenues françaises, on observe une nette différence de richesse de part et d'autre d'un seuil situé autour de 1500m. Sous cette limite, la richesse moyenne est de 9,1 espèces contre 1,8 au-dessus. Il est clair que

l'altitude, comme la surface du plan d'eau, ne joue pas en tant que telle sur les communautés de poissons car elle ne représente pas un gradient environnemental le long duquel les espèces expriment leurs exigences écophysiologiques. C'est un facteur intégrateur dans le sens où il co-varie avec un grand nombre d'autres paramètres qui, eux, représentent des filtres environnementaux (température, substrats) ou des barrières à la dispersion (pente des cours d'eau). Il s'agit là d'une limite générale des approches expliquant statistiquement les attributs des communautés par des facteurs intégrateurs (tels que l'altitude). De tels travaux peuvent avoir un bon pouvoir prédictif mais pèchent dans leur caractère généralisable par leur absence de base mécaniste (Poff 1997).

Les travaux menés au cours de cette thèse ont ainsi permis de préciser les patrons de variabilité de la richesse spécifique en regard des facteurs de l'environnement et de faire apparaître des connexions, au travers des taux de colonisation et d'extinction, entre certaines hypothèses relatives aux mécanismes déterminant la richesse spécifique des milieux lacustres. En effet, les plans d'eau étant des entités relativement éphémères à l'échelle temporelle évolutive (Matthews 1998), les processus de spéciation et d'extinction totale ne jouent pas directement sur les faunes piscicoles qu'ils abritent. Pour autant, il apparaît délicat de déterminer, à partir de ces résultats, l'importance relative des processus de colonisation et d'extinction pour expliquer la richesse spécifique. Pour progresser vers cet objectif, il serait nécessaire de disposer de données suffisantes sur le réseau hydrographique et les communautés piscicoles qu'il abrite pour caractériser les probabilités de colonisation (cf. Magnuson *et al.* 1998).

3.1.2 Sur les assemblages d'espèces

Les travaux développés sur cet aspect font suite aux résultats obtenus quasiment sur le même jeu de données au cours de la thèse d'Olivier Pronier (Pronier 2000). Une analyse factorielle des correspondances (AFC) menée sur la table sites/espèces a montré que, sur la totalité des sites (lacs naturels et retenues artificielles), une nette dichotomie apparaît entre les sites situés de part et d'autre de la limite altitudinale évoquée précédemment (Argillier *et al.* 2002b). Au-dessus de cette limite, approximativement située à 1500m, que les plans d'eau soient naturels ou artificiels, les communautés sont majoritairement constituées de Salmonidés, le plus souvent introduits (la truite commune *Salmo trutta* et la truite arc-en-ciel *Oncorhynchus mykiss* étant les plus fréquents). En dessous, les lacs naturels se distinguaient par la

présence sur certains sites d'omble chevalier *Salvelinus alpinus* et de corégones (*Coregonus* sp.), tandis que les retenues pouvaient abriter des espèces considérées généralement comme rhéophiles telles que le barbeau (*Barbus barbus*) et le toxostome (*Chondrostoma toxostoma*) (Argillier *et al.* 2002c).

Au travers de l'étude menée en France sur les retenues artificielles de plaine (P1), les facteurs environnementaux agissant sur la richesse (cf. §3.1.1) ont également montré leur capacité à expliquer la structure taxonomique des communautés, en association avec l'âge de la retenue (c'est à dire le temps écoulé entre la mise en eau initiale de la retenue et la pêche d'échantillonnage). Les cortèges piscicoles des retenues se succèdent au fil du vieillissement du plan d'eau, depuis des peuplements constitués d'espèces rhéophiles issues de la rivière qui a été barrée vers des peuplements dominés par des espèces limnophiles, souvent peu exigeantes vis-à-vis de l'habitat. Cette trajectoire est homologue à un « glissement » de la retenue vers l'aval. Elle avait déjà été observée sur des retenues d'Europe centrale (Kubecka 1993) mais contraste singulièrement avec la stabilité des communautés piscicoles observées sur une quarantaine d'années sur la retenue de Texoma aux Etats-Unis (Gido *et al.* 2000).

Après la perturbation hydraulique majeure que représente le passage de conditions initiales courantes à un milieu stagnant, le processus de vieillissement des retenues se traduit par des modifications de l'habitat telles que l'augmentation de la productivité primaire, principalement phytoplanctonique, et des modifications des substrats sous l'effet de la sédimentation et de l'accumulation de matière organique. L'ensemble de ces évolutions de l'habitat tend vers des conditions plus fréquemment rencontrées en plaine que dans des zones de piémont.

Il est par ailleurs établi que les introductions d'espèces sont des pratiques communes dans ces milieux (Argillier *et al.* 2002a). Bien que celles-ci concernent essentiellement les espèces d'intérêt halieutique, il est fréquent que d'autres espèces soient déversées accidentellement, par exemple lors d'alevinages. Il est donc envisageable que la quasi-totalité des espèces présentes dans une région donnée ait été introduite au moins une fois dans la plupart des plans d'eau de cette région.

La conjonction des modifications des conditions d'habitat au cours du vieillissement des retenues et de récurrentes introductions de nouvelles espèces conduirait ainsi à une dynamique relativement rapide des communautés piscicoles qui pourraient continuellement s'adapter en réponse à la dynamique de l'habitat.

Il apparaît donc que la richesse et la composition des communautés piscicoles varient selon la position géographique et les caractéristiques de la cuvette lacustre.

3.2 Effet des interactions au sein des communautés

Les théories classiques de la compétition (Lokta 1925 ; Volterra 1931) et les modèles qui en découlent prédisent que le partage de ressources finies entre espèces limite le nombre de ces espèces pouvant coexister localement par exclusion compétitive. Pourtant, certaines communautés végétales comme animales sont constituées d'un grand nombre d'espèces semblant utiliser un nombre limité de ressources. Cette apparente contradiction résulte vraisemblablement des hypothèses simplificatrices de ces modèles qui considèrent que les habitats sont homogènes, stables et isolés (Levin 1974 ; Schoener 1974 ; Chesson 2000). Or, il est clairement établi que les fluctuations temporelles (Wiens 1977 ; Chesson 1981) et l'hétérogénéité de l'environnement peuvent favoriser la coexistence des espèces, aussi bien à l'échelle locale que régionale (Amarasekare & Nisbet 2001). Par ailleurs, d'autres mécanismes peuvent conduire à la coexistence d'espèces compétitrices en maintenant les populations à un niveau suffisamment bas pour éviter l'exclusion compétitive, comme dans le cas d'une forte pression de prédation (Paine 1966 ; Janzen 1970 ; Gurevitch *et al.* 2000 ; Chase *et al.* 2002) ou de perturbations récurrentes (Connell 1978 ; Hastings 1980).

Les contextes historiques et évolutifs contribuent également à expliquer l'intensité des interactions compétitives observables actuellement. En effet, les mécanismes d'interaction biotique se déroulent entre individus d'espèces coexistant à une échelle locale, donc au sein d'un sous-ensemble de la faune régionale (Figure 1). Or, cette dernière est marquée, outre par la diversité des habitats régionaux, par une histoire qui lui est propre. Ces influences historiques sont particulièrement nettes dans les zones tempérées actuelles qui ont connu des bouleversements climatiques majeurs récents à une échelle temporelle évolutive (Brown & Lomolino 1998). Les alternances d'épisodes glaciaires et inter-glaciaires au cours du Pléistocène ont conduit à des extinctions de masse, aussi bien locales que totales. Si la théorie de la niche (Hutchinson 1957 ; Chase & Leibold 2003) prédit que les interactions compétitives exercent une pression sélective en direction d'une spécialisation des espèces (Giller 1984), les variations temporelles des conditions d'habitat telles que celles engendrées par les fluctuations climatiques du Pléistocène tendent à

sélectionner les espèces les plus généralistes aussi bien du point auto- que syn-écologique (Leigh 1990). Dans le contexte actuel, où nombre d'espèces ayant peuplé les eaux douces d'Europe occidentale ont disparu (Banarescu 1989), il est tout à fait plausible que la compétition interspécifique soit limitée, à l'image des situations rencontrées sur des îles océaniques pauvres en espèces car très isolées des sources de colonisation (MacArthur & Wilson 1967). Il est également concevable que la compétition passée entre espèces ait conduit à une coévolution tendant à une divergence de leurs niches (Connell 1980 ; Tokeshi 1999), et que les espèces actuelles ne connaissent plus, de ce fait, de compétition intense pour les ressources qu'elles utilisent. Cette tendance s'oppose à l'inertie phylogénétique qui contraint les espèces proches à certaines similarités de niche.

Evaluer si la compétition est un mécanisme contribuant significativement à expliquer la variabilité des communautés piscicoles entre plans d'eau est donc loin d'être évident.

Mises à part les études prenant en compte des traits morphologiques censés refléter certains axes de la niche des espèces (taille corporelle), les relations interspécifiques sont généralement délaissées par les études macroécologiques et délicates à mettre en évidence en milieu naturel (Giller 1984). En effet la plupart des scientifiques qui se sont penchés sur cette question ont eu recours à de l'expérimentation à petite échelle, généralement avec des communautés simplifiées à l'extrême et évoluant en milieu fermé (Schoener 1983). Les modèles de communautés ont également contribué au développement des connaissances sur le sujet. Cependant, la modélisation et l'expérimentation reposent sur des hypothèses simplificatrices (Levin 1992). Les résultats obtenus par ces méthodes ont fréquemment mis en évidence de manière convaincante le processus compétitif. Il est pourtant légitime de s'interroger non seulement sur la transférabilité de tels résultats vers des communautés réelles, riches en espèces, évoluant dans des lacs renfermant une diversité d'habitats, échangeant des individus avec les milieux environnants ; mais aussi sur l'effet des processus compétitifs sur la richesse spécifique (Blackburn & Gaston 2004 ; Ricklefs 2004), la liste faunistique ou les attributs fonctionnels des communautés locales.

C'est ainsi que se sont développées des recherches visant à mettre en évidence les processus compétitifs par l'analyse des patrons de distribution des espèces (Diamond 1975 ; Connor & Simberloff 1979). Une méta-analyse des études de co-occurrences des espèces conclut à un caractère général de patrons non aléatoires

conformes aux attendus générés par l'exclusion compétitive malgré des différences selon les groupes taxonomiques (Gotelli & McCabe 2002). Toutefois, le faible nombre des études de ce type réalisées sur les poissons (seulement trois incluses dans cette méta-analyse) ne permet aucune conclusion étayée pour ce groupe taxonomique.

Au cours de cette thèse, une approche indirecte des processus d'interactions interspécifiques au sein des communautés de poissons des plans d'eau a été développée en analysant la relation entre la richesse spécifique locale (=du lac) moyennée par bassin hydrographique (par exemple celui de la Loire) et la richesse régionale (=du bassin). Deux cas de figure extrêmes, encadrant un continuum de possibilités, permettent de cerner les processus gouvernant la richesse spécifique locale (Figure 5). La proportionnalité entre richesses locale (D_{α}) et régionale (D_{γ}) indique que c'est le réservoir de colonisateurs potentiels, et non les interactions entre espèces, qui fixe la limite à la richesse locale. Les communautés sont donc peu interactives. A l'inverse, si la richesse locale est indépendante de la richesse régionale ou si la relation laisse apparaître une tendance asymptotique de la richesse locale dans les régions les plus riches, il est vraisemblable qu'elle soit régulée par des processus écologiques locaux, en particulier de nature interactive, au moins dans ces dernières régions (Ricklefs 1987 ; Cornell & Lawton 1992 ; Cornell 1993 ; Srivastava 1999).

Parmi les études publiées sur les communautés de poissons d'eau douce, certaines suggèrent une insaturation (Hugueny & Paugy 1995 ; Belkessam *et al.* 1997 ; Griffiths 1997 ; Hugueny *et al.* 1997 ; Oberdorff *et al.* 1998), tandis que d'autres font apparaître de faibles influences régionales sur la richesse spécifique locale (Jackson & Harvey 1989 ; Minns 1989 ; Tonn *et al.* 1990 ; Angermeier & Winston 1998 ; Matthews & Robison 1998).

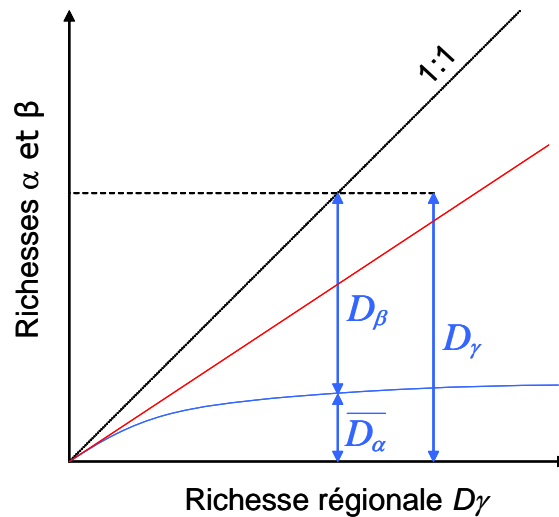


Figure 5 : Deux extrêmes de la relation entre richesses locales et régionales. Relation asymptotique (courbe bleue) et proportionnalité (droite rouge). Pour ce premier cas, la richesse régionale (D_γ) est représentés comme somme de la richesse locale moyenne (\bar{D}_α) et de la diversité inter-sites (D_β). D'après Loreau (2000).

Les richesses locales en espèces natives, non natives et totales ont donc été modélisées par régression en fonction de leurs richesses régionales respectives (terme simple et terme quadratique afin de mettre en évidence une éventuelle concavité de la relation) et des caractéristiques des plans d'eau (P3). Ces analyses ont été menées séparément pour les lacs naturels et artificiels. Pour les deux types de milieux, les modèles obtenus pour les richesses en espèces natives indiquent une relation linéaire entre richesses locale et régionale sans tendance asymptotique, suggérant une insaturation (P3). Il est aussi bien clair que les communautés piscicoles natives des plans d'eau de France peuvent être colonisées par de nouvelles espèces, comme le montre l'importance des espèces introduites (P2, P3), ce qui est également un signe de communautés insaturées. En revanche, si les communautés sont considérées dans leur ensemble, y compris les espèces introduites, la richesse locale totale devient indépendante de la richesse régionale, et avant tout déterminée par les caractéristiques des plans d'eau (P3). Il s'agit donc du cas de figure opposé à celui des espèces natives considérées seules, c'est-à-dire suggérant une saturation. Des résultats similaires ont été obtenus lors d'une étude sur des lacs d'Amérique du Nord (Griffiths 1997). Il est bien évident que scinder la richesse spécifique des plans d'eau en différentes composantes selon l'origine des espèces est une démarche artificielle et qu'il n'est pas possible d'interpréter séparément ces analyses, en particulier quand on vise à préciser les interactions entre les espèces. En effet il n'y a pas *a priori* de raisons pour que les espèces natives, translocatées (déplacées depuis un bassin

proche) et exotiques forment trois « communautés » n'entrant pas en interaction. Plusieurs hypothèses pourraient expliquer ces résultats. Si les introductions d'espèces, phénomène relativement récent, n'ont pas (encore) conduit à l'extinction locale des espèces natives, il est toutefois possible que ces introductions aient conduit à saturer les communautés. Il est également envisageable que les richesses natives locales que l'on observe actuellement aient été altérées par ces introductions, et ne représentent plus que la fraction des communautés originelles qui s'est maintenue face aux espèces introduites. Dans ce cas, la relation linéaire entre richesses locales et régionales pour les espèces natives ne serait plus représentative de la situation antérieure aux introductions.

De manière synthétique, et avec les réserves qu'impose le faible nombre de sites représentant certains bassins, nos résultats indiquent que les introductions conduisent à une augmentation forte des richesses locales (D_α) et régionales (D_γ) dans les bassins originellement pauvres en espèces (Corse, Côte d'Azur, cf. Figure 6), mais essentiellement à une augmentation des richesses régionales dans les bassins riches en espèces natives (Loire, Rhône, Rhin-Meuse). Ceci a été représenté schématiquement sur la Figure 7 où la pente des flèches indique l'importance relative de l'accroissement des richesses locales et régionales due aux espèces introduites.

Le fait que les introductions perturbent la relation entre richesses locales et régionales montre que les espèces natives et non natives diffèrent en terme de distribution spatiale. En effet, ces deux richesses sont reliées par D_β (Whittaker 1977 ; Lande 1996 ; Loreau 2000), qui représente la variabilité inter-sites, au travers de la relation $D_\gamma = \bar{D}_\alpha + D_\beta$ (Lande 1996), ce qui est schématisé en Figure 5. Il apparaît donc que dans les bassins riches, l'accroissement de diversité régionale conséquence des introductions soit essentiellement dû à une augmentation de D_β tandis que dans les bassins plus pauvres, il traduit avant tout une augmentation de D_α . En d'autres termes, la distribution spatiale des espèces introduites apparaît plus homogène (plus grand nombre de sites colonisés) dans les bassins pauvres que dans les bassins riches. Au moins deux hypothèses peuvent être envisagées pour expliquer ce phénomène. Tout d'abord, il a été montré que les bassins pauvres présentaient des communautés locales également peu diversifiées (pour les plans d'eau, mais ce résultat est sans doute généralisable aux autres parties du réseau hydrographique, cf. Oberdorff et al. 1998), ce qui a souvent été considéré comme un facteur de vulnérabilité aux invasions (Case 1991). Il est ainsi possible que l'extension de la distribution des espèces

introduites, après la première implantation dans un bassin, soit d'autant plus facile que ce bassin est pauvre en espèces natives. Une hypothèse alternative est liée au fait que les bassins pauvres soient également ceux de moindre surface. Ils seraient donc plus rapides à coloniser dans leur ensemble et présenteraient une hétérogénéité d'habitats moindre.

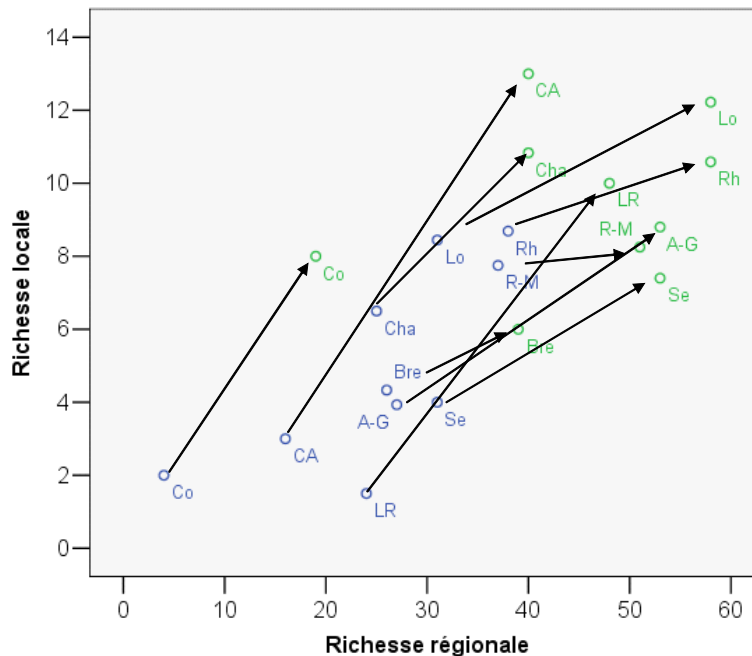


Figure 6 : Effet des introductions d'espèces sur la relation entre richesses locales (moyennes) et régionales en combinant lacs naturels et artificiels. En bleu, les richesses natives et en vert les richesses totales. Les flèches relient les points correspondant à un même bassin, donc la trajectoire induite par les introductions d'espèces. R-M : Rhin-Meuse, Se : Seine, Bre : Bretagne, Lo : Loire, Cha : Vendée-Charente, A-G : Adour-Garonne, Rh : Rhône, LR : Languedoc-Roussillon, CA : Côte d'Azur, Co : Corse.

Interpréter les relations entre richesses locales et régionales en terme d'importance des interactions biotiques au sein des communautés est un exercice délicat (Lawton 1999 ; Srivastava 1999 ; Hillebrand & Blenckner 2002 ; He *et al.* 2005 ; Hillebrand 2005 ; Shurin & Srivastava 2005). De nombreux facteurs (en interaction), tels que l'hétérogénéité environnementale, la capacité de dispersion, les taux d'extinction ou la dynamique de la colonisation influencent la forme de ce type de courbe (Mouquet & Loreau 2003 ; Mouquet *et al.* 2003 ; He *et al.* 2005).

Les résultats obtenus sur les communautés piscicoles des plans d'eau contribuent ainsi à mieux cerner les liens entre les communautés locales et les processus se manifestant à des échelles plus vastes. Cependant, ils ne permettent pas de statuer clairement sur le rôle des interactions pour expliquer la variabilité inter-lacs des communautés. En l'absence d'estimation des densités des peuplements piscicoles sur les milieux pris en compte au cours de cette thèse, il n'a pas été possible de tester la

compensation de densité à l'image de ce qui a été réalisé sur les cours d'eau (Oberdorff *et al.* 1998). Les analyses prévues pour compléter les résultats obtenus dans le manuscrit P6, ainsi que l'étude des règles d'assemblage (§4.1), devraient permettre de préciser le rôle des interactions biotiques comme mécanisme structurant des communautés.

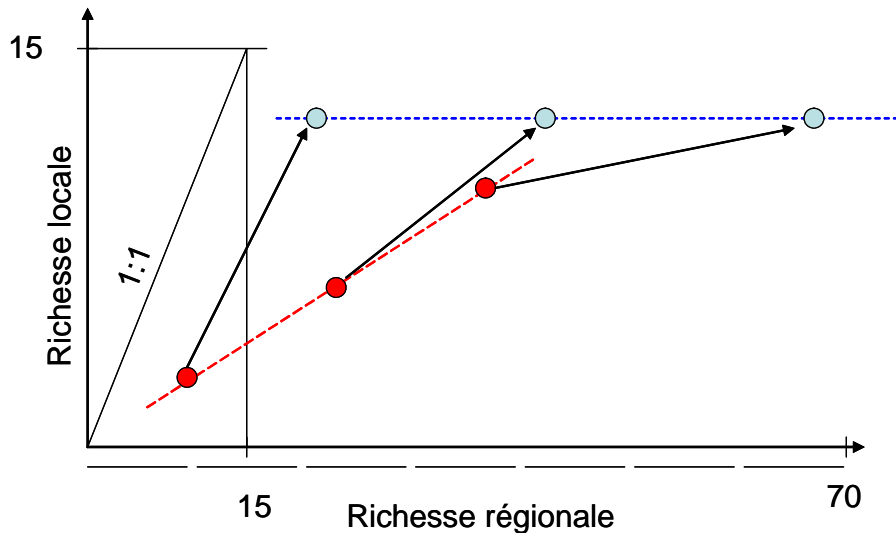


Figure 7 : Représentation schématique des relations entre richesses régionales et locales en espèces natives (points rouges) et totales (points bleus). Les flèches relient les points correspondant à un même bassin, donc la trajectoire induite par les introductions d'espèces.

Enfin, l'effet de la prédation sur les patrons de distribution et de richesse des communautés piscicoles d'eau douce a été montré en de nombreux cas (Jackson *et al.* 1992 ; Chapleau *et al.* 1997 ; Whittier *et al.* 1997) mais n'a pas pu être abordé au cours de cette étude. Il le sera, à brève échéance, par une étude des règles d'assemblage au sein des communautés piscicoles lacustres (cf. §4.1).

3.3 Impacts anthropiques

Durant de nombreuses décennies, hormis la communauté des scientifiques étudiant les impacts d'activités anthropiques sur les organismes vivants et leur milieu, les préoccupations environnementales étaient le fait de groupes politiquement engagés. L'opposition était alors claire entre ceux qui donnaient priorité à la protection des espèces et des milieux, et ceux qui considéraient que toute mesure de conservation allait à l'encontre du développement économique et donc du bien-être humain. Si un rapide regard sur l'actualité internationale montre que cette opposition est loin d'être caduque, même les plus fervents promoteurs du développement économique ont pu constater que les hydrosystèmes subissaient des dégradations qui, dans de nombreux cas, aboutissaient à la remise en cause des

usages qui en étaient faits par l'Homme. Il est donc apparu que des compromis étaient à trouver entre usages et conservation des milieux aquatiques. Cette prise de conscience a considérablement élargi le champ des préoccupations de conservation (Baron *et al.* 2002 ; Gleick 2003) et s'est traduit par des textes réglementaires tels que la Directive Cadre Européenne sur l'Eau (DCE) en Europe, ou le Clean Water Act (CWA) aux Etats-Unis. Ces réglementations reposent sur l'idée selon laquelle le maintien de l'intégrité écologique des milieux aquatiques est la meilleure garantie de la durabilité des services que ces milieux peuvent offrir aux sociétés humaines. Le niveau de dégradation d'un hydrosystème y est évalué par l'écart entre son état observé et un état de référence reflétant une situation exempte d'impact. Si ce cadre conceptuel a le mérite de la simplicité, la mise en œuvre de ces réglementations nécessite le développement de connaissances sur ce que devrait être l'état des hydrosystèmes en l'absence d'impact anthropique. Comme les impacts ont généralement précédé les études écologiques (et souvent même les descriptions des naturalistes), il est rarement possible d'utiliser des données historiques pour définir les états de référence. Une approche alternative basée sur des données collectables actuellement est de considérer les impacts sur les communautés vivantes comme des altérations des patrons naturels de variabilité des communautés. Il s'agit donc de distinguer ce qui, dans la variabilité inter-sites des attributs des communautés, est attribuable aux facteurs naturels de ce qui est une réponse à des pressions anthropiques. Une telle démarche permet d'appréhender l'effet soit direct (introductions d'espèces, pêche), soit indirect (dégradation des habitats, perturbations de la connectivité entre éléments du réseau hydrographique, pollution) des pressions anthropiques sur les milieux aquatiques à différentes échelles, ainsi que les effets conjoints de plusieurs types d'atteintes. En revanche, si elle permet de mesurer des impacts actuels, semble peu adaptée pour prévoir les trajectoires futures, ce qui représente un autre enjeu, surtout pour des organismes à temps de génération relativement long comme les poissons. La réversibilité des impacts est enfin une question qui reste entièrement posée, exception faite pour les cas d'extinction totale d'espèces.

Les parties précédentes visaient à analyser la réponse des communautés à des contraintes environnementales naturelles s'exerçant à différentes échelles (même si le cas des espèces introduites a été abordé). La présente a pour objectif d'évaluer si une part de la variabilité qui n'est pas expliquée par les facteurs de l'environnement peut l'être par des pressions anthropiques.

3.3.1 Impacts directs

Les impacts directs sur les communautés sont ceux impliquant le prélèvement ou le déversement d'individus dans le milieu. Les introductions d'espèces sont des pratiques très répandues (Williamson 1996), en particulier dans les milieux aquatiques continentaux (Welcomme 1988), surtout pour ce qui est de la faune ichthyologique (Holcik 1991 ; Cowx 1997 ; Argillier *et al.* 2002a). En France, les 23 espèces piscicoles non autochtones présentes dans les eaux douces comptent pour un tiers du total des espèces recensées dans le réseau hydrographique (Keith 1998). La question de l'impact de ces introductions sur les communautés piscicoles lacustres est assez controversée. Si, dans certains cas, il a été clairement démontré que l'introduction de prédateurs était à l'origine de l'extinction d'espèces proies autochtones, comme dans le cas de la perche du Nil (*Lates niloticus*) dans le lac Victoria (Witte *et al.* 1992) ou du sandre (*Sander lucioperca*) en Anatolie (Crivelli 1995), les effets découlant de processus compétitifs sont nettement moins évidents. Après avoir tenté d'expliquer la richesse piscicole des plans d'eau par les facteurs environnementaux (§ 3.1.1), l'étude ayant fait l'objet de P2 a montré l'importance de la contribution des espèces non autochtones à la richesse piscicole des retenues artificielles. La richesse spécifique a été scindée en plusieurs composantes : native, translocatée (originaires d'une autre région française) et exotique (naturellement absente en France). Aucune corrélation n'a été mise en évidence entre les richesses régionales en espèces natives et non natives (=exotiques + translocatées), indiquant que le nombre des espèces introduites est similaire dans les bassins naturellement riches et ceux naturellement pauvres. Il en résulte qu'en proportion, les espèces non autochtones représentent l'essentiel de la richesse dans les régions naturellement peu riches (plus de 50% dans les petits bassins côtiers Méditerranéens). Une corrélation négative entre les richesses locales en espèces natives et non natives a été mise en évidence sur les retenues artificielles (P2), qui en première approche aurait pu suggérer un impact des introductions, mais une analyse plus complète (P3) a montré que cette corrélation ne tenait plus lorsque les facteurs environnementaux étaient contrôlés et qu'elle était même positive pour les lacs naturels.

Cette approche n'a donc pas fait apparaître d'impact des introductions sur les richesses locales et régionales en espèces natives. Ceci ne signifie absolument pas que ces pratiques soient inoffensives pour les faunes piscicoles des plans d'eau français, mais simplement que la richesse spécifique est un attribut des communautés et des

bassins qui ne répond pas clairement à ces pratiques dans la fenêtre de temps écoulée depuis que la majorité de ces introductions a été réalisée. Des approches prenant en compte l'identité des espèces et/ou basées sur un suivi temporel permettraient certainement de mieux cerner l'effet des introductions et de la dispersion des espèces introduites sur les communautés natives des plans d'eau.

Les prélèvements réalisés par la pêche, de même que les empoisonnements destinés à soutenir les populations exploitées, représentent également des impacts directs sur les communautés (Argillier *et al.* 2002a), mais n'ont pas été abordés au cours de la présente étude. L'évaluation de ces impacts nécessiterait la collecte de données halieutiques ainsi que des relevés des déversements réalisés par les gestionnaires de la pêche.

3.3.2 Impacts indirects

Les impacts indirects peuvent être considérés comme ceux affectant les communautés au travers des conditions d'habitat au sens large (y compris la connectivité). Ils ont été appréhendés en analysant, sur les lacs du nord-est des Etats-Unis, les liens entre les attributs de ces communautés et l'utilisation des sols dans les bassins versants des plans d'eau (P5). Réaliser un travail équivalent sur les plans d'eau de France aurait certes été préférable pour la cohérence de cette thèse, mais les données collectées par l'USEPA (Baker *et al.* 1997) et rendues publiques présentaient une meilleure homogénéité dans les modes de collecte et ont été acquises sur des sites sélectionnés pour être représentatifs des plans d'eau de la région (Larsen *et al.* 1994).

L'utilisation des communautés piscicoles comme bioindicateur s'est considérablement développée depuis les travaux ayant précisé le concept d'intégrité biotique et donné dans les grandes lignes la méthode à suivre pour mettre au point des indices (IBIs - Indexes of Biotic Integrity) pour la mesurer (Karr 1981 ; Karr *et al.* 1986). Le nombre des articles publiés sur des adaptations de l'indice original pour les cours d'eau de diverses régions atteste du succès rencontré par cette méthode (Roset *et al.* in press). En comparaison, les plans d'eau semblent avoir reçu nettement moins d'attention. Certaines études ont bien été inspirées par la démarche appliquée aux cours d'eau (Dionne & Karr 1992 ; Hughes *et al.* 1992 ; Minns *et al.* 1994 ; Jennings *et al.* 1995 ; Jennings *et al.* 1999 ; Whittier 1999 ; Appelberg *et al.* 2000 ; Drake & Pereira 2002 ; Drake & Valley 2005), mais elles restent très partielles dans la mesure où aucune ne respecte l'ensemble des conditions suivantes :

- un contrôle des facteurs environnementaux,
- une sélection des métriques basée sur leur réponse à des pressions,
- une méthode d'agrégation des métriques optimisant la discrimination entre sites perturbés et non perturbés,
- une validation de l'indice sur un jeu de données indépendant.

Ce manque d'outils est par ailleurs encore plus criant pour les retenues artificielles que pour les lacs naturels.

Les résultats obtenus au cours de cette thèse ont montré que, sur 11 métriques candidates sélectionnées pour refléter, outre la richesse spécifique, la composition de la communauté en guildes trophiques, d'habitat et de tolérance, six répondaient significativement à l'anthropisation des bassins versants des plans d'eau. Sur les lacs naturels, les proportions d'espèces phytophiles, piscivores et pratiquant des soins parentaux augmentent avec l'urbanisation des bassins versants. Bien que les mécanismes expliquant ces réponses soient loin d'être clairement identifiés, on peut par exemple raisonnablement penser que l'urbanisation en amont des plans d'eau augmente les flux de nutriments vers ces milieux. Cet enrichissement conduirait à l'augmentation de la productivité primaire sous forme phytoplanctonique ou macrophytique, ce qui favoriserait les espèces phytophiles. L'accumulation de matière organique non dégradée au fond du plan d'eau tendrait à colmater les substrats minéraux nécessaires aux lithophiles pour leur reproduction. Cette modification des habitats physiques bénéficierait donc aux phytophiles. L'augmentation de la proportion de piscivores peut, quant à elle, être rapprochée des diverses hypothèses qui ont été proposées pour lier l'énergie disponible à la structure trophique des communautés (Abrams 1995 ; Srivastava & Lawton 1998 ; Bohannan & Lenski 2000). Il est également possible que la fréquence des introductions d'espèces d'intérêt halieutique, donc souvent prédatrices, augmente avec la proximité de centres urbains.

Une étude méthodologique a par ailleurs été réalisée pour évaluer si de tels résultats étaient sensibles (i) à l'inclusion ou l'exclusion des jeunes de l'année (0⁺) capturés lors des inventaires, (ii) à la nature des métriques (nombres ou proportions d'individus ou d'espèces) et (iii) au choix de la méthode de modélisation. Au final, cette étude montre que les alternatives ci-dessus ont peu d'influence sur les résultats. Sans extrapoler à d'autres régions, types de systèmes ou échelles d'approche, ceci suggère que les données supplémentaires apportées par un plan d'échantillonnage destiné à estimer les abondances, y compris des juvéniles, sont peu informatives en

terme de relation pression-impact. Collecter de telles données représente un surcroît de travail de terrain. Une baisse de l'effort porté sur chaque plan d'eau et une augmentation du nombre de sites prospectés pourrait donc s'avérer plus efficace en termes d'allocation de moyens. Une partie des moyens dégagés pourrait également être consacrée à un suivi temporel de certains sites. La question de la variabilité temporelle de court terme (entre saisons et entre années consécutives) mériterait en effet d'être examinée de façon à évaluer si des tendances de long terme (réponses au changement climatique, à l'altération des habitats, aux espèces introduites) peuvent être détectées par ce type de réseau et avec quelle incertitude.

Il est également clairement apparu que les métriques répondant à l'utilisation agricole et urbaine des sols sur les bassins versants étaient différentes entre les lacs naturels et les retenues (P5). Certes, les gammes de variation de ces deux catégories d'occupation du sol sur les bassins versants des deux types de plans d'eau ne sont pas équivalentes, ce qui peut expliquer en partie ces résultats, mais ces derniers sont de nature à porter le doute sur la possibilité d'utiliser les lacs naturels comme références à atteindre pour les retenues artificielles. Or, cette question de la référence à prendre en compte pour évaluer l'état écologique des retenues est très actuelle puisque ces milieux entrent dans le champ d'application de la DCE (P4).

La mise au point d'outils de bioindication basés sur les communautés piscicoles des plans d'eau semble un objectif réaliste mais nécessitant encore des développements scientifiques et l'acquisition de données orientée vers cet objectif. La démarche engagée pose les bases du développement de tels outils dans la mesure où elle a permis l'identification de facteurs environnementaux à contrôler, initié la caractérisation de pressions et proposé une première sélection de métriques. Dans l'idéal, ils devraient permettre, outre l'évaluation de l'intégrité écologique des milieux, de poser des diagnostics sur les causes des éventuels dysfonctionnements, voire de tester des scénarii de réponse à des actions de gestion. Pour ce faire, il sera important d'améliorer la caractérisation des pressions subies par les plans d'eau pour obtenir des évaluations des flux de polluants (au moins pour ce qui est des nutriments) et prendre en compte les pressions s'exerçant localement, telles que les altérations du régime naturel de marnage ou l'aménagement des berges.

3.4 Perspective historique et évolutive

Comparer les biocénoses de régions éloignées, ayant connu des histoires évolutives différentes, est un moyen à la fois d'évaluer le caractère généralisable de résultats obtenus dans un contexte donné et de tester si l'on observe des convergences. Les communautés actuelles ont convergé si elles sont plus semblables que ne l'étaient les communautés ancestrales (Orians & Paine 1983). La convergence entre communautés éloignées au plan phylogénétique suggère que les conditions environnementales contemporaines exercent une forte pression de sélection sur les communautés (Winemiller 1991 ; Losos *et al.* 1998). En revanche, elle est peu probable si les situations actuelles reflètent avant tout l'inertie phylogénétique et les contingences historiques (Price *et al.* 2000 ; Verdu *et al.* 2002).

Tester la convergence entre régions au niveau des communautés est délicat puisque les caractéristiques des communautés ancestrales ne sont pas connues (alors qu'il est possible de se baser sur des données paléontologiques pour tester la convergence au niveau des espèces). Une méthodologie basée sur l'analyse de variance a toutefois été proposée pour tester la convergence lorsque des observations réalisées dans différents types d'habitats au sein de chaque région sont disponibles (Schluter 1986). Elle revient à partitionner la variance des attributs des communautés en une composante inter-habitats et une composante inter-régions. Cette méthode a été appliquée pour tester la convergence des communautés piscicoles lacustres du nord-est des Etats-Unis et de France en considérant d'une part la richesse spécifique et d'autre part l'importance relative de guildes trophiques et reproductives (P6). Les analyses ont été menées sur les lacs naturels et artificiels en excluant les plans d'eau de montagne. La surface du plan d'eau et la température moyenne de l'air ont été utilisées pour caractériser les conditions d'habitat.

En résumé, il a été montré que :

- si les richesses spécifiques sont plus élevées, pour une surface donnée, sur les retenues et aux Etats-Unis, les pentes des relations aire-espèces ne diffèrent pas entre les types de plans d'eau et les continents,
- les traits reproductifs des communautés convergent en terme de réponse à la température,
- la structure trophique des communautés ne répond aux gradients environnementaux que sur les plans d'eau des Etats-Unis.

Certaines hypothèses écologiques ont été proposées pour expliquer ces patrons (P6), mais cette étude a aussi mis en relief l'importance des contraintes qu'exerce la distribution à l'échelle des familles sur les processus écologiques. Par exemple, l'absence des Ictaluridés et des Centrarchidés dans le cortège des espèces natives en France influence nettement les traits reproductifs des communautés. La comparaison des communautés piscicoles non totalement indépendantes mais différentes en termes d'espèces a donc révélé des patrons de convergence délicats à interpréter par des mécanismes.

4 Perspectives

4.1 Règles d'assemblage

Parmi les approches complémentaires au travail déjà réalisé, les tests d'hypothèses relatifs aux règles d'assemblage des communautés (Diamond 1975), associations non aléatoires d'espèces ou de groupes taxonomiques ou fonctionnels (Jackson *et al.* 1992 ; Kodric-Brown & Brown 1993), et basés sur des méthodes de permutation de type « modèles nuls » (Gotelli & Graves 1996), devraient autoriser des démarches rigoureuses d'inférence des processus à partir des patrons observés. En effet, l'une des principales difficultés des travaux à large échelle est l'absence de « témoins » comme ceux utilisés en plan d'expérience (Blackburn & Gaston 1998). Les modèles nuls peuvent dans une certaine mesure fournir ces témoins auxquels il est possible de confronter des observations (Connor & Simberloff 1979 ; Gotelli & Graves 1996). Ils sont construits en référence à un jeu de données réel en gardant constants certains éléments des données alors que d'autres sont autorisés à varier aléatoirement (test de permutation) pour générer de nouveaux patrons. Pour tester l'importance d'un mécanisme écologique, les permutations sont conçues pour produire les patrons attendus en l'absence de ce mécanisme particulier, toutes choses étant maintenues constantes par ailleurs (Gotelli & Graves 1996).

Le principal écueil de telles approches est la pertinence dans le choix de ces hypothèses nulles et donc dans le choix des méthodes de permutation (Connor & Simberloff 1979 ; Gotelli & Graves 1996 ; Gotelli 2000).

A titre indicatif, les hypothèses suivantes, concernant les règles d'assemblages, pourraient être confrontées aux modèles nuls.

- 🌍 Les communautés de poissons lacustres présentent des patrons emboîtés, c'est-à-dire que les communautés locales des sites les moins riches tendent à être des sous-ensembles des communautés des sites plus riches (Brown 1995). De tels patrons peuvent résulter de divers processus (Gaston & Blackburn 2000) tels que des taux de colonisation et d'extinction différents selon les sites, des influences historiques, des artefacts d'échantillonnage ou de différences inter-sites (surface, diversité d'habitats), mais ils ont rarement été considérés pour expliquer la

structure des communautés piscicoles. Les patrons emboîtés peuvent être mis en évidence au moyen de différentes statistiques (Patterson & Atmar 2000).

- Les espèces ne sont pas distribuées indépendamment les unes des autres. Certaines combinaisons d'espèces sont observées plus rarement ou plus fréquemment qu'escompté sous hypothèse d'indépendance (Diamond 1975 ; Gotelli & McCabe 2002). Ce cas peut résulter de l'exclusion compétitive ou de la prédation, mais aussi de réponses différentielles des espèces à des gradients environnementaux. Il peut donc être nécessaire de contrôler ces gradients environnementaux dans les modèles (Peres-Neto *et al.* 2001).
- Les espèces cohabitant au sein d'un même plan d'eau présentent des niches écologiques plus proches ou plus éloignées qu'un tirage aléatoire parmi le *pool* régional de colonisateurs potentiels. Le premier cas suggérerait que les contraintes environnementales dominent au sein du filtre local (Weiher & Keddy 1995), alors que dans le second les interactions compétitives pourraient limiter la co-occurrence d'espèces proches (MacArthur & Levins 1967). Ces hypothèses pourraient être testées en utilisant les données collectées sur la caractérisation écomorphologique des espèces piscicoles (Lanoiselée 2004).
- Les abondances relatives des espèces révèlent une organisation conforme à l'une des distributions prédites par les modèles de partage de niche (Tokeshi 1999). Ces modèles théoriques, au nombre de six, présentent des explications mécanistes à la forme des distributions des abondances relatives dans les communautés.

4.2 Lien entre les échelles spatiales

Du fait de leur relatif isolement les uns par rapport aux autres et par rapport au réseau hydrographique, les plans d'eau peuvent être considérés comme des entités fonctionnelles. C'est donc l'échelle qui a été retenue pour appliquer la DCE, chaque plan d'eau étant considéré comme l'entité dont l'état est évalué et qui se voit assigné des objectifs. Pour autant, les phénomènes de colonisation et d'extinction (naturels ou résultant des activités de l'Homme) sont largement responsables des assemblages d'espèces qui vont cohabiter au sein d'un même lac (Olden *et al.* 2001), d'où le parallèle avec la biogéographie insulaire (Barbour & Brown 1974 ; Magnuson 1976 ; Eadie *et al.* 1986 ; Magnuson *et al.* 1998). Les phénomènes de colonisation dépendent du bassin dans lequel se trouve le lac (nombre et écologie des espèces potentiellement colonisatrices, obstacles aux migrations). En revanche, les

extinctions sont essentiellement fonction des conditions locales (régime thermique, disponibilité en ressources, morphologie de la cuvette, qualité de l'eau, interactions biotiques), largement influencées par l'amont du plan d'eau ainsi que par des gradients environnementaux généraux, par exemple climatiques (Magnuson *et al.* 1998). De ce point de vue les situations locales dépendent de processus agissant à différents niveaux de la Figure 1.

A plusieurs reprises, les résultats obtenus au cours de cette thèse ont mis en évidence ces connexions entre échelles, en particulier pour expliquer la richesse spécifique. Les analyses menées sur la relation entre richesses régionales et locales ont clairement montré que ces dernières étaient liées à la fois aux conditions environnementales locales et au contexte biogéographique (variabilité entre bassins).

Néanmoins, intégrer une composante régionale pour expliquer les patrons locaux représente avant tout un choix et on pourrait tout aussi bien se poser la question inverse, qui est la dépendance des situations régionales vis-à-vis de la diversité des situations locales qu'elles englobent (Cornell & Lawton 1992 ; Cornell 1993). La démarche ascendante est pourtant rarement adoptée (Lawton 1996). Aucune de ces approches n'est plus légitime que l'autre et l'essentiel est d'aborder les questions de manière hiérarchisée (Ricklefs 2004) pour saisir le lien entre les différentes échelles (Tonn *et al.* 1990 ; Levin 1992).

Si, comme indiqué précédemment, la présente étude a bénéficié d'avancées considérables de contexte (puissance de calcul, bases de données), il est clair que ce mouvement s'accélérera encore dans les années à venir. La généralisation des bases à référence spatiale (modèle numérique de terrain de haute définition, réseau hydrographique qui « coule », inventaire des rejets de polluants par les Agences de l'Eau, géo-référencement des barrages, etc.) devrait permettre d'obtenir des données nouvelles et/ou plus précises, telles que :

- des données biologiques issues des réseaux de suivi environnemental,
- une définition plus précise des contours des bassins versants et donc de leurs caractéristiques,
- une évaluation des charges polluantes reçues par les plans d'eau,
- des éléments de caractérisation de la connectivité entre éléments du réseau hydrographique tels que la pente des cours d'eau et les barrages,
- des données environnementales, comme la température, selon des modèles continus.

L'accès à de telles données permettra une approche des communautés piscicoles intégrant les phénomènes de dispersion entre communautés locales au sein des bassins hydrographiques. En effet, une des limites des travaux développés au cours de cette thèse tient à la difficulté de prendre en compte les échelles spatiales dépassant le plan d'eau. Bien que certaines caractéristiques des bassins aient été intégrées pour expliquer les communautés trouvées localement, les résultats obtenus en comparant les communautés des lacs, des retenues et des cours d'eau (P4) suggèrent que certains processus à l'origine des patrons de distribution des espèces piscicoles en milieu lentique s'expriment également en milieu lotique et/ou que les échanges entre plans d'eau et cours d'eau ont une influence importante sur les communautés lacustres.

Par ailleurs, divers constats montrent que les échanges entre plans d'eau et cours d'eau sont importants :

- les espèces présentes dans les plans d'eau y sont arrivées par les cours d'eau (exception faite des introductions par l'Homme ou de phénomènes de spéciation, ces derniers étant négligeables à cette échelle d'étude),
- certaines espèces considérées comme typiquement rhéophiles (barbeau, vandoise, truite commune...) sont présentes dans des milieux lenticques où elles ne peuvent se reproduire (P1, Hladik & Kubecka 2003),
- la dynamique des communautés piscicoles dans les retenues artificielles à partir de leur création (Krizek 1987 ; Vostradovsky *et al.* 1989 ; Kubecka 1993) indique que les retenues connaissent des épisodes de colonisation suffisamment fréquents pour que leurs peuplements connaissent des successions d'espèces en réponse aux modifications de l'habitat.

Les ruptures dans les gradients environnementaux ont souvent conduit à définir des "types" de masses d'eau (lacs, retenues, ruisseaux, rivières, annexes fluviales, étangs, zones humides, nappes) et à les étudier séparément. Pourtant, ces "types" ne sont pas autre chose que des éléments d'une même mosaïque de paysages (Wiens 2002), interdépendants car échangeant des organismes vivants (Jackson *et al.* 2001), de la matière et de l'énergie (Kling *et al.* 2000). Mener des programmes de recherche considérant que les processus agissent selon un continuum spatial et temporel (Ricklefs 2004) depuis l'échelle de la station jusqu'à celle du bassin pourrait être riche d'enseignements, en particulier pour étudier des organismes aussi mobiles que les poissons (P4). L'étude des communautés de poissons à l'échelle des bassins versants (intégrant l'ensemble des types d'hydrosystèmes continentaux) serait par

ailleurs tout à fait pertinente pour répondre à des questions appliquées dans la mesure où la recherche d'états de référence pour les plans d'eau, demandée par la DCE, nécessite la compréhension de la réponse écologique locale aux pressions anthropiques locales, mais également régionales (fragmentation, pollutions diffuses, altérations du régime climatique). La théorie des métacommunautés fournit un cadre théorique à une telle approche. Une métacommunauté peut être définie comme un ensemble de communautés locales liées par la dispersion (Hanski & Gilpin 1991). Il s'agit donc d'une approche qui ne considère pas les communautés locales comme fermées, mais comme échangeant avec les autres communautés locales des individus, soit d'espèces nouvelles (colonisations), soit déjà présentes (par exemple dans le cas des dynamiques type source-puits). Parmi les bases théoriques proposées pour le fonctionnement des métacommunautés (Leibold *et al.* 2004), celle basée sur la théorie de la niche (Hutchinson 1957 ; Giller 1984 ; Chase & Leibold 2003), et désignée *species-sorting* (Leibold *et al.* 2004), semble particulièrement adaptée au contexte de métacommunautés de poissons à l'échelle des bassins. En effet, cette théorie repose sur l'hypothèse, vérifiée en France à notre échelle d'étude aussi bien sur les plans d'eau (P1) que sur les cours d'eau (Oberdorff *et al.* 2001), que les communautés varient en réponse à des gradients environnementaux. Elle est envisageable dans des systèmes présentant une hétérogénéité suffisante pour affecter la distribution des assemblages d'espèces, ce qui est typiquement le cas dans un bassin versant (gradients amont-aval de température, hydrologie, substrats ; alternance de zones courantes et stagnantes, etc.). La correspondance entre conditions environnementales et distribution des espèces piscicoles, qui permet de modéliser les secondes en fonction des premières, suggère que la dispersion est suffisante pour permettre aux différentes espèces de coloniser l'essentiel des sites répondant à leurs exigences à l'intérieur d'un bassin. Toutefois, la présence, en milieu lacustre, d'espèces ne s'y reproduisant pas, suggère également que certains phénomènes de dispersion se rapprochent d'un fonctionnement de type source-puits (*mass effect*, Leibold *et al.* 2004) pour une sous partie des communautés lacustres.

Une méthode a récemment été proposée pour évaluer l'importance relative de composantes environnementales et spatiales dans l'organisation des communautés (Cottenie 2005). Basée sur l'analyse de redondance, elle pourrait être appliquée dans un contexte de bassin versant. Si elle mettait en évidence une forte structuration spatiale des communautés indépendante des effets environnementaux, la démonstration serait faite de l'importance des échanges d'individus entre localités

pour expliquer les patrons de distribution. Or, ces bassins sont fortement fragmentés depuis que l'Homme, pour répondre à de nombreux usages, a construit des ouvrages de stockage, de régulation ou de dérivation des eaux. Les grands barrages, généralement infranchissables par les poissons, sont présents dans la plupart des bassins hydrographiques du globe (Dynesius & Nilsson 1994 ; Nilsson *et al.* 2005). Les petits ouvrages, même s'ils peuvent être franchis dans certaines conditions de débit, sont très nombreux et limitent également les échanges entre parties des réseaux hydrographiques. Il est donc vraisemblable que cette fragmentation ait des impacts sur le fonctionnement des métacommunautés, même si la dynamique relativement lente de réponse écologique ne permet pas de les déceler (Diamond 1983) ou si d'autres types d'altération des milieux ont des effets plus évidents (Cumming 2004).

Par ailleurs, les modèles de métacommunautés permettent non seulement de faire un lien direct entre échelles spatiales (les communautés régionales n'y sont pas autre chose que l'agrégation des communautés locales), mais également de prédire les variations de richesse entre localités et les distribution d'abondance des espèces à diverses échelles (Mouquet & Loreau 2003). Dans cette étude reposant sur des communautés simulées, les diversités D_γ , \bar{D}_α et D_β toutes choses étant égales par ailleurs, dépendent nettement de l'importance de la dispersion entre localités. Il s'agit là d'une des principales difficultés pour tester la validité de ces principes à partir de données de terrain car l'évaluation de cette dispersion est pour le moins délicate. Par ailleurs, la théorie des métacommunautés ne prend généralement pas en compte explicitement la dimension spatiale des distributions des espèces (Leibold *et al.* 2004). Or, les échanges d'individus entre localités dépendent de leur proximité et de leur connectivité, donc de leurs positions relatives, ainsi que de celles des barrières à la dispersion. Dans les études telles que celles menées au cours de cette thèse, l'autocorrélation spatiale, aussi bien dans la distribution des organismes que dans les gradients environnementaux, représente un biais important et rarement contrôlé. Ainsi, la prise en compte de la dimension spatiale dans la distribution des organismes, de leurs habitats et des barrières à leur dispersion, à l'image des approches développées en écologie du paysage (Ward *et al.* 2002 ; Wiens 2002), contribuerait certainement à cerner les liens entre échelles spatiales. Il serait donc nécessaire de développer des modèles spatialisés à l'échelle du bassin versant. Les communautés lotiques et les caractéristiques abiotiques du bassin contribueraient ainsi à expliquer des attributs des communautés lacustres. Une telle approche

permettrait également aux écologistes des milieux courants de mieux apprécier l'effet des eaux stagnantes et des barrages sur leur objet d'étude.

5 Conclusion

Cette étude a abordé diverses questions relatives aux communautés piscicoles des plans d'eau, avec un fil conducteur qui a été la recherche de patrons récurrents de variabilité dans les attributs de ces communautés. Elle a mis en évidence les principaux facteurs abiotiques auxquels ces communautés répondent et a souligné que les situations observables au niveau des plans d'eau sont largement dépendantes des autres parties du réseau hydrographique. Ces avancées ont ensuite permis de poser les bases du développement d'un outil d'évaluation, au moyen des communautés piscicoles, de l'intégrité écologique des plans d'eau.

Identifier des processus écologiques à partir de patrons est toujours délicat dans la mesure où plusieurs processus, voire des artefacts statistiques, concourent potentiellement à expliquer ces patrons. Les débats autour de l'interprétation des relations aire-espèces ou richesse locale-richesse régionale l'illustrent clairement. En effet, la démonstration théorique qu'un mécanisme particulier peut donner naissance à un patron n'apporte en aucun cas la preuve d'une relation de causalité (Levin 1992). La tâche est encore complexifiée par le fait qu'en général, les patrons ne résultent pas d'un unique processus, mais d'un ensemble de mécanismes liés les uns aux autres et dont l'importance relative dépend de l'échelle d'observation et du type de système écologique (Lawton 1996). Pour autant, les études expérimentales en écologie sont généralement menées à des échelles spatiales et temporelles différentes de celles auxquelles opèrent les mécanismes régissant la distribution des organismes vivants sur Terre. Faire le lien entre la distribution des organismes vivants et les mécanismes écologiques locaux représente ainsi un enjeu majeur pour l'écologie scientifique, mais aussi pour la conception de stratégies efficaces de protection des milieux.

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Annexes - Publications et manuscrits

P1	INFLUENCE OF SITE CHARACTERISTICS ON FISH COMMUNITY PATTERNS IN FRENCH RESERVOIRS	53
P2	CONTRIBUTION OF NATIVE AND NON-NATIVE SPECIES TO FISH COMMUNITIES IN FRENCH RESERVOIRS	69
P3	NATIVE AND INTRODUCED FISH SPECIES RICHNESS IN FRENCH LAKES: LOCAL AND REGIONAL INFLUENCES	79
P4	COMPARISON BETWEEN THE FISH COMMUNITIES OF LAKES, RESERVOIRS AND RIVERS: CAN NATURAL SYSTEMS HELP DEFINE THE ECOLOGICAL POTENTIAL OF RESERVOIRS?	91
P5	PARTITIONING THE VARIABILITY IN FISH METRICS INTO ENVIRONMENTAL AND ANTHROPOGENIC COMPONENTS FOR THE BIOASSESSMENT OF NORTHEAST U.S.A. LAKES AND RESERVOIRS	101
P6	FISH COMMUNITY CONVERGENCE ALONG ENVIRONMENTAL GRADIENTS IN LAKES OF FRANCE AND NORTHEAST U.S.A.	127

P1: Influence of site characteristics on fish community patterns in French reservoirs

Irz P., Laurent A., Messad S., Pronier O. & Argillier C. (2002)

Ecology of Freshwater Fish, 11, 123-136.

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Influence of site characteristics on fish community patterns in French reservoirs

Irz P, Laurent A, Messad S, Pronier O, Argillier C. Influence of site characteristics on fish community patterns in French reservoirs. *Ecology of Freshwater Fish* 2002: 11: 123–136. © Blackwell Munksgaard, 2002

Abstract – The objectives of this paper are to describe the fish assemblages in French reservoirs and to relate them to the sites' characteristics. The results of 43 fishing surveys were collected and completed with environmental descriptors. Fish assemblages differ between salmonids-dominated mountain sites and lowland ones. The latter show higher species diversity and a distinction between rheophilic- and limnophilic-type communities. This distinction can be explained by the reservoir age, location in the catchment and depth. The response of fish communities to these variables was investigated by canonical correspondence analysis. It shows that rheophilic species are typically abundant in upper basin, deep and recently created reservoirs. The fish community response to the aging process corresponds to an addition of lowland standing waters species and an extinction of the native riverine ones. The structuring role of the sites' depth, location and age is discussed, considering their relationship with the water body trophic status.

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Key words: ageing process; environmental variables; fish community; France; reservoir

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Accepted for publication January 4, 2002

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Due to its geological and climatic history, the French territory has few lakes. The construction of dams in the past decades considerably increased the potential fish yield from freshwater bodies. These environments now sustain recreational fisheries which locally represent an important source of revenue in rural regions. However, the management of these fisheries, based on stocking and species introductions, is seldom efficient (Argillier et al. 2002) due to insufficient knowledge of these systems functioning. Yet few studies have investigated the relationship between European reservoir fish communities and site characteristics. The purposes of the present paper are to investigate the patterns of fish communities in French reservoirs and to identify the parameters structuring them. This requires a wide-scale community-level approach in order to detect general trends that cannot be assessed either by case

studies or by species focused works (Tonn & Magnuson 1983).

The site → reach → catchment hierarchy proposed for rivers (Imhof et al. 1996) helps define the different scales of interactions governing freshwater systems. The dependence of riverine fish assemblages upon the catchment, natural and human features is now established (Marsh-Matthews & Matthews 2000). Lake fish fauna follows similar patterns (Jackson & Harvey 1989). Fish habitat characteristics also depend, at the lake scale, on its morphometry (Hondzo & Stefan 1996), macrophyte cover (Eadie & Keast 1984) and internal biochemical processes (Matthews 1998). The presence of deep areas favors the development of a pelagic fish community (Stefan et al. 1995), whereas the lake shoreline features condition the type of habitat available for littoral species (Eadie & Keast 1984; Mandrak 1995). Despite their apparent similarities, reservoirs cannot be considered as natural lakes due to

numerous functional differences. Wetzel (1990) provides a comparative overview of how these systems function. The specificity of reservoirs essentially originates in their location in the catchment area with low hydraulic residence time and high organic, particulate and nutrient input loads. Dam operation also generates irregularly pulsed level fluctuations and water movements. These conditions lead to severe pressure on the living communities.

Major efforts have to be made to collect important datasets so that general trends in fish associations can be detected and related to the water bodies descriptors. This type of work was therefore carried out in few areas of the world and most of the cited literature originates from northern America. However, Godinho et al. (1998) showed the preponderance of longitudinal variables (elevation and temperature) and their correlates (rainfall) in structuring fish communities from Portuguese reservoirs. Similar observations were made earlier on riverine systems (Huet 1949; Illies & Botosaneanu 1963). The River Continuum Concept (Vannote et al. 1980) provides an energy-based framework to the biota distribution. Typically, the fish species richness increases downstream the river course (Oberdorff et al. 1993), resulting in a combination of zonation and downstream addition of species (Rahel & Hubert 1991). These similarities suggest that the processes governing reservoir fish communities could be midway between those occurring in lakes, as a result of an isolation limiting immigration possibilities (Magnuson et al. 1998) and the riverine continuity.

Materials and methods

The dataset

The dataset pools the information collected over 30 years for the needs of case studies. The sources are fully listed in Pronier (2000). Most of the 43 study sites are located in south-eastern France (Fig. 1), where the landscape is favorable to hydroelectric power generation. The main characteristics of these artificial lakes are summarized in Table 1. They represent a variety of environmental conditions (Table 2).

Ichthyological data were collected during either impoundment draining for dam investigation or gillnetting surveys. These surveys were carried out using two different sampling schemes. The first one is mostly empirical, relying on the setting of horizontal gillnet series overnight with knot-to-knot mesh sizes ranging from 10 to 60 mm in geometrical progression. The sampling sites are

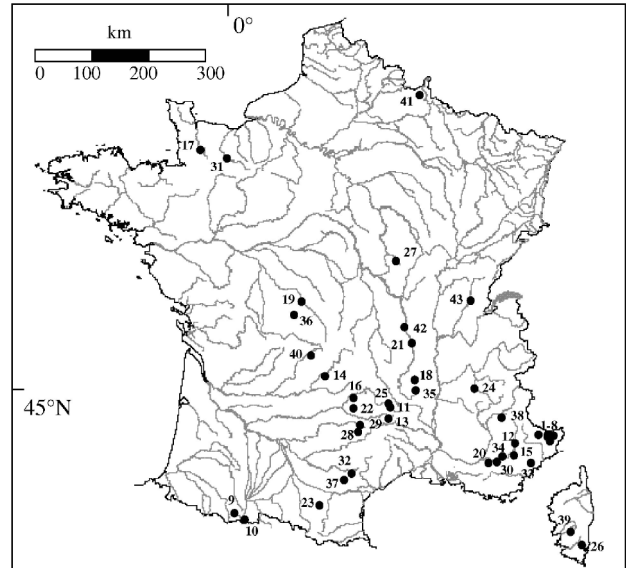


Fig. 1. Location of the 43 study sites on the French hydrographic network. The site numbers refer to Table 1.

chosen so that the whole water column may be prospected and to cover most of the habitats diversity. The second methodology uses vertical gillnet series in the deep areas, whereas the littoral zone is sampled with multimesh gillnets. The nets are then set for approximately 24 h. These two methods proved to be equally efficient in terms of accuracy on species diversity and show overall similar distributions on the relative abundance of species (Irz 1998). The efficiency of both gillnetting methods was successfully compared with a total census of the standing stock on the occasion of the total draining of La Ravière and Treignac reservoirs (unpublished data).

From the overall 37 species present in the samples, only 22 were common enough to be kept for the analysis. The species that were omitted were either sparse (less than five occurrences) or not properly sampled by gillnetting. Some related species with similar habitat requirement were pooled into a single group (Table 3). The numerical relative abundance (RA) of each species was calculated as the ratio of the number of individuals per species versus the number of fish caught during the survey. These abundances were then encoded into three categories corresponding to the absence, low abundance, and high abundance of the species. The cut-off level between low and high abundances is the median relative abundance.

Environmental descriptors were chosen among the parameters available in the database. They were selected from the existing bibliography for their relevance in structuring fish communities.

Table 1. Main characteristics of the studied reservoirs. Each reservoir is coded with three letters corresponding to its name and a number corresponding to a French administrative department.

Map number	Code	Name	River basin	Area (ha)	Altitude (m)	Mean depth (m)
1	BAS06	Basto	Coastal south	24	2341	5.9
2	CAR06	Carbon	Coastal south	6	2179	5
3	FOU06	Fourcat	Coastal south	4.5	2165	2.6
4	LLS06	Lac long sup.	Coastal south	12	2111	6.5
5	LM006	La Muta	Coastal south	8	2274	5
6	NOI06	Noir	Coastal south	11	2278	4.7
7	TRE06	Trécolpas	Coastal south	1.4	2150	2.5
8	VER06	Vert	Coastal south	15	2221	7.1
9	CDL65	Cap de long	Garonne	118	2161	45
10	ESC65	Escoubous	Garonne	2	2235	3.5
11	ARM48	Mas d'Arman	Loire	12	1000	4.5
12	CAS04 ^a	Castillon	Rhône	450	880	33.1
13	CHA19	Chastang	Dordogne	538	262	34.7
14	CHA48	Charpal	Garonne	180	1320	4.5
15	CH004	Chaudanne	Rhône	70	790	22.8
16	COU12	Couesque	Garonne	260	290	21.6
17	DAT14	Dathée	Coastal north	44	160	2.5
18	DEV07	Devesset	Rhône	50	1074	4.74
19	EGU36	Eguzon	Loire	270	202	16
20	ESP04	Esparron	Rhône	330	360	24.24
21	GRA42 ^a	Grangent	Loire	365	420	15.7
22	MAU12	Maurly	Garonne	160	588	20.6
23	MON11	Montbel	Garonne	585	400	18
24	MON38	Monteynard	Rhône	657	490	41.87
25	NAU48	Naussac	Loire	1050	1000	18
26	OSP2A	L'Ospédale	Coastal south	42	949	6.8
27	PAN58	Pannecière	Seine	520	324	15.86
28	PAR12	Pareloup	Garonne	1260	805	12.5
29	PDS12	Pont de Salars	Garonne	190	720	10.8
30	QUI04 ^a	Quinson	Rhône	191	404	20
31	RAB61	Rabodanges	Coastal north	97	125	4.64
32	RAV34	La Raviège	Garonne	439	662	10.2
33	SCA83	Saint-Cassien	Coastal south	374	147	16
34	SCR04 ^a	Sainte-Croix	Rhône	2182	477	50
35	SMA07	Saint-Martial	Rhône	13	830	5
36	SPA87	Saint-Pardoux	Loire	330	360	7
37	SPE81 ^a	Saint-Peyres	Garonne	211	670	16.43
38	SPO05	Serre-Ponçon	Rhône	3200	780	37.5
39	TOL2A	Tolla	Coastal south	115	560	30
40	TRE19	Treignac	Dordogne	101	513	7.4
41	VFO08	Vielles Forges	Meuse	136	320	3.3
42	VIL42	Villerest	Loire	800	316	22
43	VOU39 ^a	Vouglans	Rhône	1600	429	37.8

^aSampled twice.

Table 2. Summary of the environmental characteristics of the studied reservoirs.

Parameter	Mean	SD	Range
Altitude above sea level (m)	947	753	125–2341
Distance to source (km)	36	47	0–177
Catchment area (km ²)	784	1435	1–6520
Lake area (ha)	396	632	1–3200
SLDF ^a	3.20	1.87	1.04–8.50
Perimeter (km)	22	23	0.1–107.0
Water level range (m)	12	15	0–60
Mean depth (m)	16	13	3–50
Reservoir age (years)	35	31	4–71

^aCalculated as: $\sqrt{4\pi \times \text{surface}}$.

Only long-term stable parameters were taken into account in order to provide a secondary source of data when the database was incomplete. This includes large-scale as well as local parameters (Table 2). The large-scale parameters, related to the position of the reservoirs in the watershed, were measured from 1/50 000th to 1/1 000 000th digitized topographical maps using Autocad[®] software. The lakes' area and perimeter were measured on 1/25 000th maps. These two parameters allowed to calculate the shoreline development factor (SLDF) characterizing the reservoir shape and ranging from 1 (round lake) to over 10 when the perimeter is very long when

Common name	Group code	Species	Frequency (%)	Average RA (%)	Average RA when present (%)
Barbel	BAR	<i>Barbus barbus</i>	18	1.0	5.3
Black bullhead ^a	BBH	<i>Ictalurus melas</i>	13	1.4	11.1
Bleak	BLK	<i>Alburnus alburnus</i>	36	2.9	8.0
Bream	BRE	<i>Abramis brama</i>	44	5.3	12.1
Brown trout	BWT	<i>Salmo trutta fario</i>	64	14.7	23.0
		<i>S. trutta lacustris</i>			
Common carp ^a	CAR	<i>Cyprinus carpio</i>	49	0.8	1.6
Chub	CHU	<i>Leuciscus cephalus</i>	54	2.8	5.3
Dace	DAC	<i>L. leuciscus</i>	18	0.3	1.5
		<i>L. leuciscus burdigalensis</i>			
French nase	FNS	<i>Chondrostoma toxostoma</i>	13	0.8	6.4
Gudgeon	GUD	<i>Gobio gobio</i>	33	1.6	4.8
Perch	PER	<i>Perca fluviatilis</i>	72	13.3	18.1
Pike	PIK	<i>Esox lucius</i>	54	0.4	0.7
Pikeperch ^a	PKP	<i>Stizostedion lucioperca</i>	33	1.3	3.9
Pumkinseed ^a	PUM	<i>Lepomis gibbosus</i>	18	0.2	1.2
Rainbow trout ^a	RBT	<i>Oncorhynchus mykiss</i>	46	10.4	22.5
Roach	ROA	<i>Rutilus rutilus</i>	72	34.0	47.3
Rudd	RUD	<i>Scardinius erythrophthalmus</i>	36	3.0	8.5
Ruffe	RUF	<i>Gymnocephalus cernua</i>	21	0.6	3.0
Tench	TEN	<i>Tinca tinca</i>	62	1.6	2.6

^aIntroduced species.

Table 3. Species occurrence, frequency, average numerical relative abundance (RA) and average RA excluding the absence cases.

the area is considered. The reservoir mean depth and the water level range, considered as the difference between the highest and lowest exploitation levels, were obtained from the dam operators.

Data processing

The relationship between fish diversity (i.e. the number of species present in each site) and several parameters was firstly studied by bivariate linear regression.

Further analyses, apart from the design of a longitudinal gradient index, were only carried out on the 33 reservoirs below 1500 m in altitude because all the fish populations in mountain lakes result from species introductions. Multivariate analysis was carried out using ADE-4 software (Thioulouse et al. 1997).

The faunal and environmental matrices were then analyzed separately. A correspondence analysis (CA) was processed on the species abundance indexes in order to identify the structure of the assemblages. The significance of between-species associations were then tested using Spearman correlation.

The environmental descriptors were submitted to a standardized principal components analysis (PCA) to study the correlation between these variables. This analysis of the environmental matrix allows selection of the variables providing

the best description of the reservoirs for further analysis. Careful selection avoids most of the redundancy between the selected descriptors. A second PCA was then processed on the most correlated and redundant variables. The decomposition of the site scores on the first two components of the PCA enabled clustering of the sites and thus to summarize these parameters into a single ordinal variable.

The relationship between the selected environmental descriptors and the fish communities was investigated by means of canonical correspondence analysis (CCA) (Ter Braak 1986). CCA is an ordination method that selects a series of linear combinations of environmental variables called canonical axes, which are uncorrelated. This method was designed to relate the dispersion of the species to the environmental descriptors. Therefore, it meets the needs of community ecologists and was successfully used in aquatic research (Dolman 1990; Godinho et al. 2000). It is a nonsymmetric approach that provides an assessment of the faunal inertia that is explained by environmental variables. The main result of the CCA is an ordination diagram displaying the pattern of community variation (reservoirs and species) along the environmental variables (Ter Braak 1987).

The method possesses specific properties to deal with the nonlinear relationship between the taxa abundance and environmental gradients

(Ter Braak 1986). It also performs well in the case of a large set of response variables (Prodon & Lebreton 1994), even when strongly correlated (Ter Braak 1987). The limited number of data available led us to retain only four explanatory descriptors chosen in the light of the initial PCA. This choice avoids the awkward interpretation of the results when numerous descriptors are correlated and ensures a tight restriction of the species scores by the explanatory variables.

The stability and significance of CCA results was assessed by a Monte Carlo test. This test is nonparametric and is based on random permutations of the lines of the observed faunal matrix. A value of the part of faunal inertia due to the environment is calculated for each combination and allows the validation of the observed explained value with simulated values (Efron 1982).

Results

Species occurrence

The species most frequently observed in the fish assemblages are, in decreasing order of occur-

rence, perch, roach, brown trout, tench, pike and chub (Table 3). The dominant species in these assemblages are roach and perch, which indicates their aptness for reservoir environments. Some of the more widespread species, such as carp and pike, always remain at a low relative abundance.

Species diversity

Species diversity was plotted against each environmental variable which were previously log-transformed. The correlation was significant for the catchment area, reservoir area, distance to the source and mean depth (Fig. 2). The best descriptors to predict the number of species in a reservoir are the reservoir area ($R^2=0.67$) and its watershed area ($R^2=0.54$). No continuous relationship was found between fish diversity and altitude, though the average diversity significantly differ ($P < 0.001$) between lowland (below 1500 m; mean = 9.1 species) and mountain sites (mean = 1.8 species), which confirms that fish assemblages follow different patterns below and over the 1500 m elevation threshold.

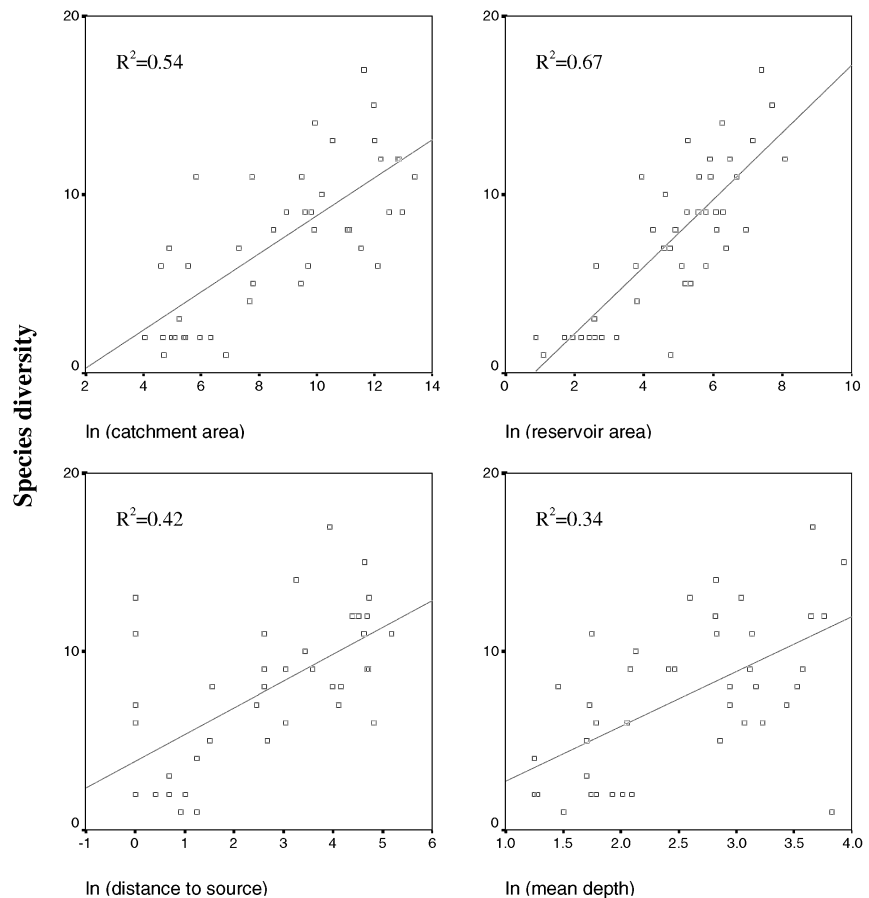


Fig. 2. Regression scatterplots of species diversity vs. the statistically significant variables.

Fish assemblages below 1500 m

The CA first axis clearly discriminates two types of fish communities (Fig. 3). The first one is composed of gudgeon, barbel, brown trout, French nase, chub and rainbow trout. These species are rheophilic and could originate from the riverine assemblages before the construction of the dams. The second group stretched along the second axis can be extended to the 13 other species, among which roach, perch, rudd and pike, i.e. limnophilic species are the most frequent. The opposition between tench, carp and pikeperch on one side, bream and bleak on the other side is difficult to interpret at this stage.

The between-species correlations confirm these results (Table 4). It shows the strong correlation among the first group of species, whereas the second group displays fewer significant correlations. The corresponding species represent an opposition to the first group but cannot be interpreted as a real assemblage due to their low co-occurrence rate.

Environmental descriptors of lowland sites

The PCA carried out on the environmental parameters provides an overview of their organization

(Fig. 4). The correlation matrix is given in Table 5. Depth, water level range, perimeter and reservoir area, all site-scale characteristics, appear correlated. These parameters represent the size of the lake. The catchment area and the distance to the source are positively correlated, and opposed to the altitude. This opposition summarizes the location of the sites in the catchment. SLDF is simultaneously correlated to site-scale descriptors and to the location in the catchment. Mountain water bodies are close to the river source and typically round-shaped (low SLDF), with a small catchment area. These parameters increase for downstream sites. Reservoir age is independent from all the other parameters.

Design of a longitudinal gradient index

Considering the strong correlations cited previously and the need to limit the number of explanatory variables for the CCA, a single longitudinal gradient index was searched for by means of PCA. The input parameters, altitude, distance to the river source, and catchment area, describe the location of the reservoirs on the hydrographic network.

The distribution of the 43 sites on the first two dimensions of the PCA enables the construction

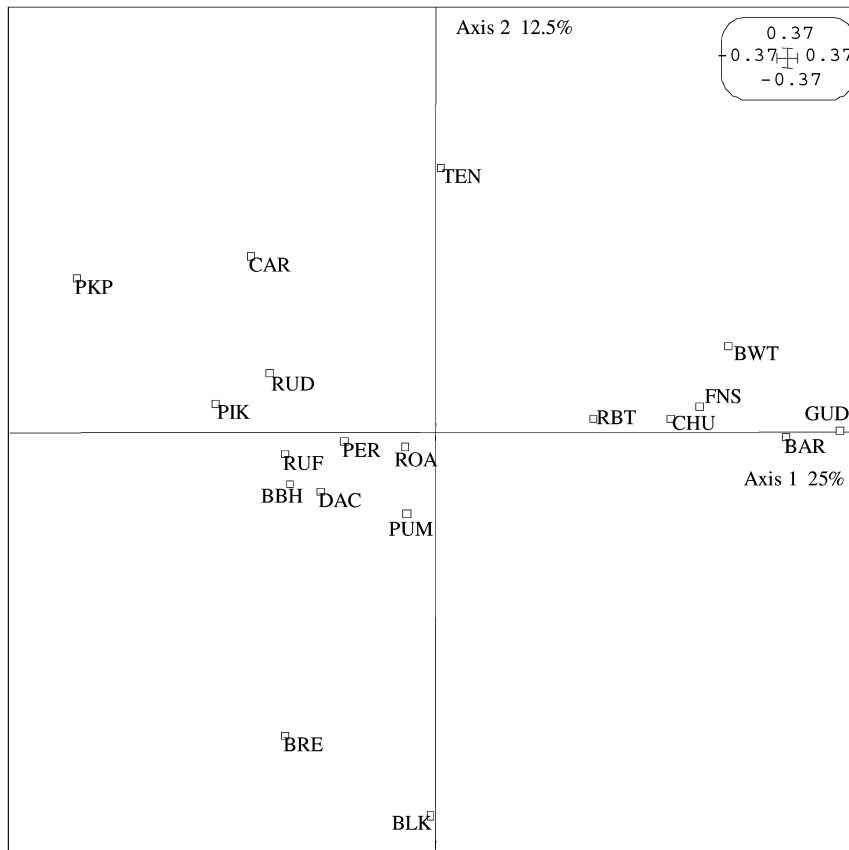


Fig. 3. Position of the fish taxa on the first two axis of the CA carried out on lowland sites (N = 33). The labels refer to Table 3.

Table 4. Spearman correlation between the species relative abundances in lowland sites.

	BAR	BBH	BLK	BRE	BWT	CAR	CHU	DAC	FNS	GUD	PER	PIK	PKP	PUM	RBT	ROA	RUD	RUF
BBH	-0.12																	
BLK	0.23	0.06																
BRE	0.06	0.37*	0.52**															
BWT	0.38*	-0.18	0.09	-0.10														
CAR	0.05	0.05	0.00	0.22	-0.06													
CHU	0.55**	-0.12	0.16	0.22	0.31*	-0.21	0.03											
DAC	-0.13	0.16	0.22	0.31*	0.08	0.01	0.44**	0.02										
FNS	0.78**	-0.02	0.08	0.07	0.29	-0.09	0.27	0.26	0.36*									
GUD	0.40**	-0.09	0.14	-0.14	0.51**	-0.32*	0.27	-0.26	-0.24	-0.32*								
PER	-0.31*	-0.02	0.02	0.08	-0.36*	-0.19	-0.14	0.01	-0.24	-0.31*	0.29							
PIK	-0.09	0.03	0.12	0.19	-0.41**	0.28	-0.26	0.22	-0.13	-0.31*	0.08	0.22						
PKP	-0.28	0.07	0.14	0.13	-0.32*	0.41**	-0.34*	0.29	-0.43**	-0.44**	0.08	0.01	-0.01					
PUM	0.02	0.14	0.22	0.37*	0.03	0.04	0.03	0.28	0.16	-0.06	0.15	0.01	-0.37*	0.32*				
RBT	0.27	0.00	-0.05	0.06	0.29	0.04	0.12	-0.06	0.51**	0.29	-0.14	0.15	-0.37*	-0.10				
ROA	-0.06	0.12	0.11	0.10	-0.20	0.09	-0.24	0.26	-0.04	-0.08	-0.30*	0.17	0.13	-0.08				
RUD	-0.04	0.37*	0.07	0.28	-0.24	0.17	-0.11	-0.14	-0.08	-0.12	0.27	0.21	0.17	0.14	-0.06	-0.46**		
RUF	-0.25	0.14	0.16	0.34*	-0.30*	0.22	-0.27	0.13	-0.13	-0.06	0.29	0.19	0.24	-0.01	0.14	0.14	-0.03	
TEN	0.06	-0.05	-0.16	-0.16	0.23	0.36*	0.05	0.02	0.13	0.01	-0.35*	0.02	0.14	0.03	-0.05	-0.05	0.07	0.03

*Correlation is significant at the 0.05 level.

**Correlation is significant at the 0.01 level.

of a longitudinal gradient index. This synthetic ordinal variable comprises five gradient classes, each corresponding to a group of reservoirs on the PCA diagram (Fig. 5). The fifth category contains all the mountain reservoirs.

The distribution of the environmental descriptors along the longitudinal gradient index is displayed in Fig. 6. These boxplots reveal the meaning of this index about altitude, distance to source and catchment area that were used to construct it. It also shows the homogeneous features of high-altitude reservoirs, apart from their age. It also appears that the index is correlated to SLDF, perimeter, and reservoir area. The longitudinal distribution of the sites also corresponds to strong morphological trends that oppose large, complex-shaped lowland reservoirs to small, round-shaped mountain ones. When class 5 sites are not considered, water level range ($P=0.22$) and reservoir age ($P=0.18$) are independent from the index, whereas it remains negatively correlated to the mean depth ($P<0.001$).

The occurrence rate of the fish species can be plotted against the gradient index (Fig. 7). This gradient provides a good explanation for the distribution of some species. Bleak and bream occur mainly in lowland sites (1–3). On the other hand, rainbow trout and brown trout are present more in the mountain sites (class 5). Some species like barbel, gudgeon, tench and French nase are obviously restricted to intermediate conditions. Roach and perch, the most widespread species in the reservoirs, are present in almost all the sites with the exception of mountain water bodies.

Ordination of fish communities restricted by environmental descriptors

Only four variables were kept for the CCA. The longitudinal gradient index is the single large-scale input parameter, whereas mean depth, water level range and reservoir age characterize the water body itself. These descriptors were chosen to remove most of the redundancy in the data as well as to limit the number of explanatory variables.

A Monte Carlo test ($P<0.001$, 1000 permutations) proves the significance of the analysis. It reveals that the four descriptors explain 20% of the variability within the fish assemblages (Table 6). The abundance of four species is well explained by the descriptors. Among these, barbel, French nase, and pikeperch are segregated along the first axis of the CCA biplot (Fig. 8). This axis accounts for 47% of the explained variability and can be interpreted by reservoir depth. The

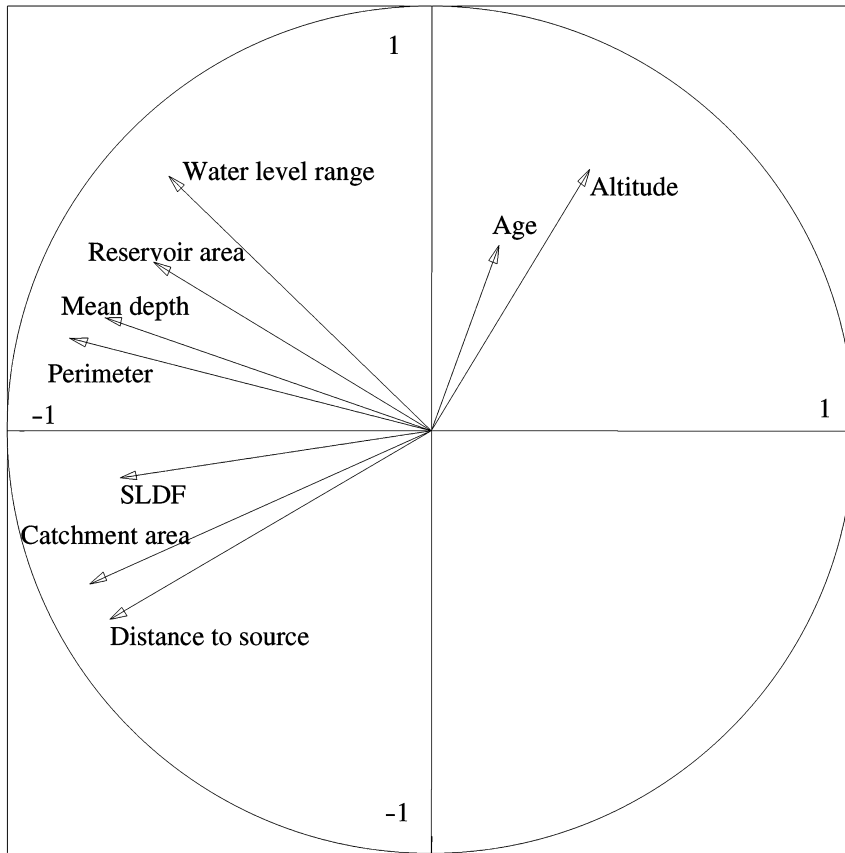


Fig. 4. Correlation circle of the PCA carried out on the environmental descriptors of 33 lowland sites.

abundance of French nase and barbel is positively correlated with this variable, whereas pikeperch populations are more abundant in shallow reservoirs. Depth is therefore the main parameter structuring the fish communities in the studied reservoirs. Along the second axis, which represents 26% of the explained variability, the longitudinal gradient is opposed to the age of the reservoir. These variables were not correlated

during the previous analysis. These independent descriptors have an opposite effect on the fish assemblages. Bleak is more abundant in old and/or lowland reservoirs, whereas rainbow trout develops in young and/or elevated ones. The age since first filling also has an effect on pikeperch which is most abundant in old water bodies. The group of rheophilic species observed in correspondence analysis (RBT, FNS, BAR, BWT, and

Table 5. Correlation matrix resulting from the PCA carried out on the environmental descriptors of 33 lowland sites.

	Distance to source	Altitude	Catchment area	Reservoir area	SLDF	Water level range	Mean depth	Reservoir age	Perimeter
Distance to source	1.00								
Altitude	-0.43*	1.00							
Catchment area	0.85**	-0.30	1.00						
Reservoir area	0.30	0.03	0.38*	1.00					
SLDF	0.49**	-0.40*	0.56**	0.16	1.00				
Water level range	0.17	-0.02	0.25	0.43*	0.42*	1.00			
Mean depth	0.55**	-0.16	0.47**	0.64**	0.30	0.65**	1.00		
Reservoir age	-0.17	0.15	-0.26	-0.20	0.10	0.19	-0.14	1.00	
Perimeter	0.41*	-0.18	0.56**	0.65**	0.80**	0.57**	0.50**	-0.05	1.00

*Correlation is significant at the 0.05 level.

**Correlation is significant at the 0.01 level.

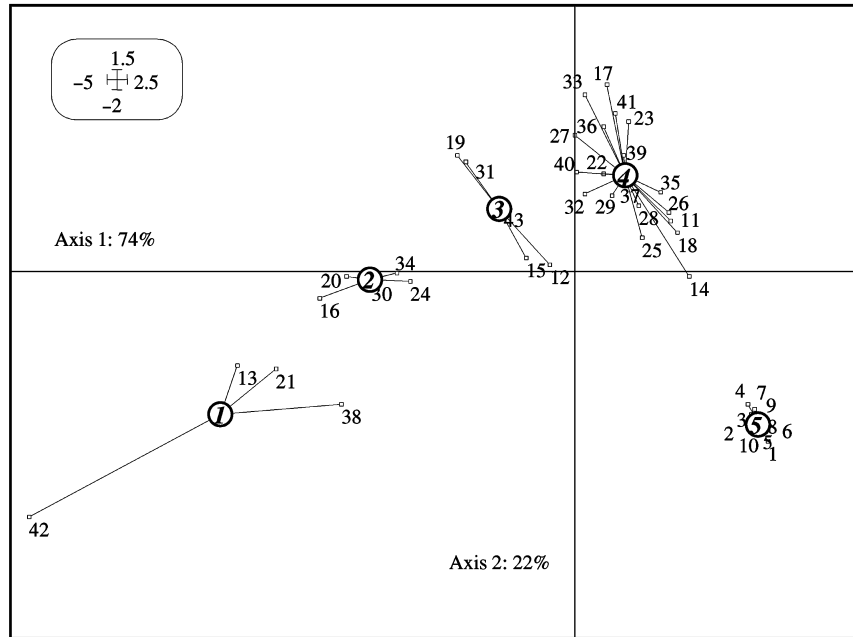


Fig. 5. Reservoirs scatterplot resulting from the PCA on the sites altitude, catchment area and distance to the source. The number inside each circle represents the inertia center of a class of gradient. The site numbers refer to Table 1.

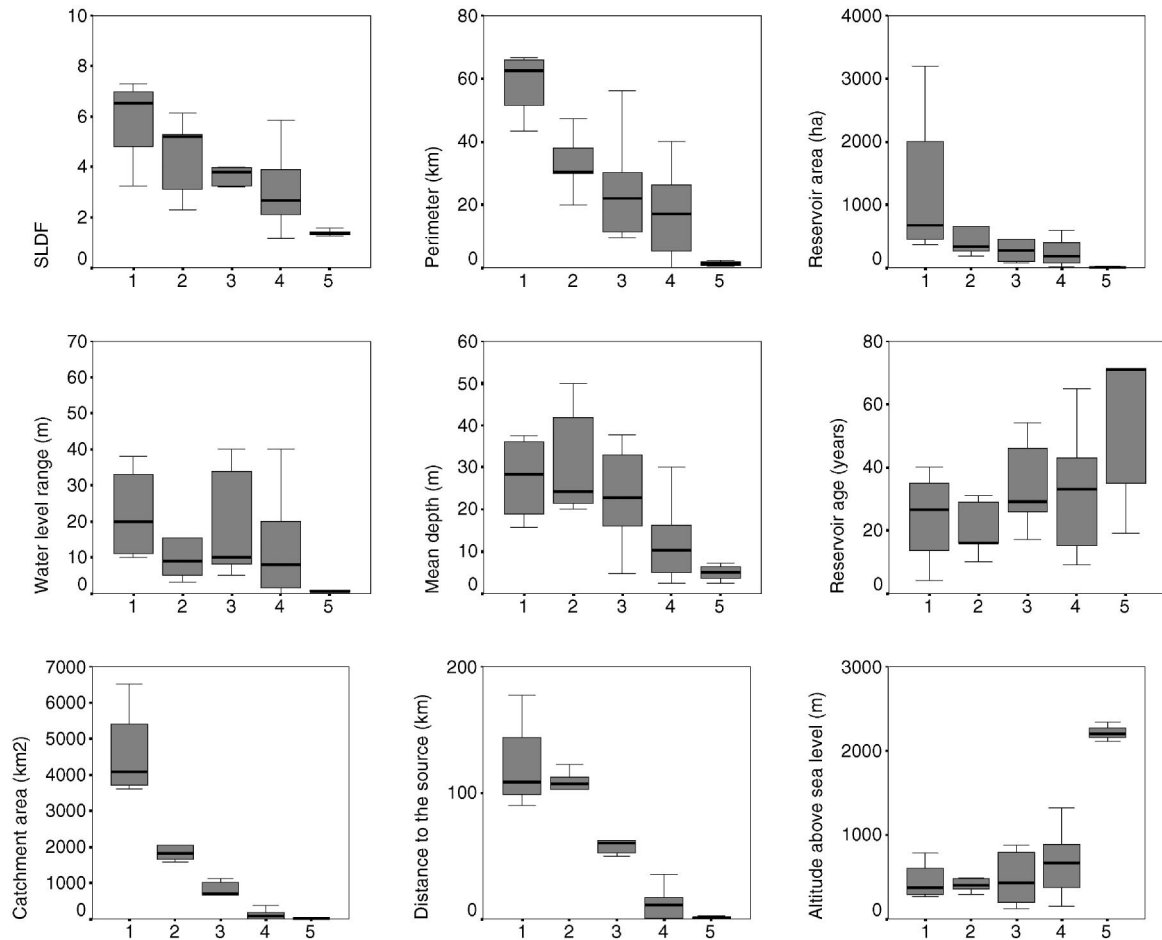


Fig. 6. Boxplot representation of the geographical and morphological signification of the longitudinal gradient index.

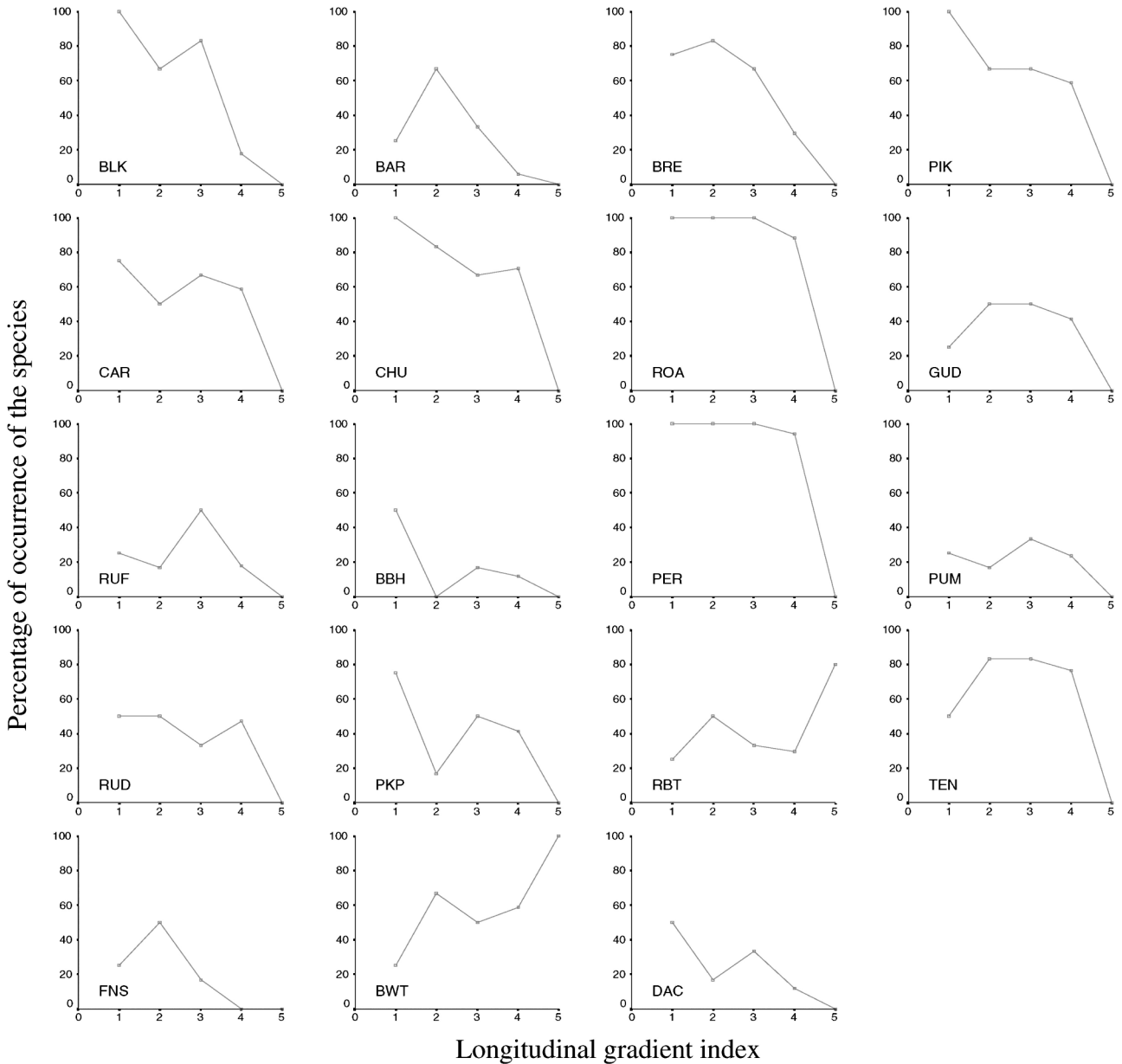


Fig. 7. Occurrence rate of the species along the longitudinal gradient.

GUD) appears characteristic of young reservoirs. The variation in abundance of perch is partly explained by the descriptors (27% of the variability explained). Its position on the biplot suggests that it is a species of intermediate longitudinal gradient and reservoir age. Water level range does not appear to be a good structuring variable for this dataset.

Discussion

The dataset processed in the present study reveals general patterns of the fish assemblages encountered in French reservoirs.

The observed taxa associations can be clustered into three types that are mountain sites, recently built lowland reservoirs, and older lowland reservoirs. The latter group is much more heterogeneous than the other two. The communities are influenced by local and regional parameters, and whereas reservoir morphology influences the abundance of particular species, large-scale descriptors tend to affect the assemblages.

The increase in species diversity with the reservoir size is coherent with the trends observed in Ontario lakes (Minns 1989) and northern Wisconsin lakes (Tonn & Magnuson 1982). This can be related to the relationship between the

Table 6. Projected inertia decomposition on a CCA subspace for the 19 species.

	Environmental subspace ($\times 10^{-3}$)	Orthogonal subspace ($\times 10^{-3}$)	Total inertia ($\times 10^{-3}$)	Explained inertia (%)
BAR	3.98	5.41	9.39	42.38
BBH	1.06	5.22	6.27	16.86
BLK	3.31	5.99	9.30	35.57
BRE	1.63	7.52	9.15	17.8
BWT	2.16	6.88	9.04	23.93
CAR	1.14	8.30	9.44	12.05
CHU	0.80	6.35	7.15	11.19
DAC	0.59	7.03	7.62	7.7
FNS	3.82	3.91	7.73	49.43
GUD	0.37	12.73	13.10	2.82
PER	1.41	3.89	5.30	26.67
PIK	1.83	7.31	9.14	20.04
PKP	4.00	7.43	11.44	35.01
PUM	0.21	7.72	7.92	2.59
RBT	2.11	4.29	6.40	32.9
ROA	0.30	4.91	5.21	5.72

water body surface area and the heterogeneity of its habitats (Eadie & Keast 1984; Benson & Magnuson 1992). The significance of the regressions between fish diversity and catchment area, distance to the source and reservoir depth should

be interpreted with care, considering the numerous correlations linking these descriptors. However, the effect of the catchment size on the fish communities can be considered indirectly through the downstream increase in nutrients loads, dissolved minerals, and conductivity. The longitudinal gradient index designed on the basis of the site location descriptors could also be regarded as a temperature, a trophic or a quality gradient. This longitudinal-based structure confirms the results of Godinho et al. (1998) on Portuguese reservoirs, although the species and sites characteristics are to a large extent different.

High-altitude rivers typically sheltered no native fish populations prior to human introductions of salmonids in the Pyrénées (Delacoste et al. 1997). This can be generalized to most mountain areas in France, and fishery legislation in such sites prohibits practices tending to sustain other fish taxa. Therefore, fish communities in mountain reservoirs are more likely to reflect human actions than biotic responses to environmental conditions.

Depth is the main parameter structuring fish communities in reservoirs below 1500 m in altitude. This observation suggests a trophic interpretation

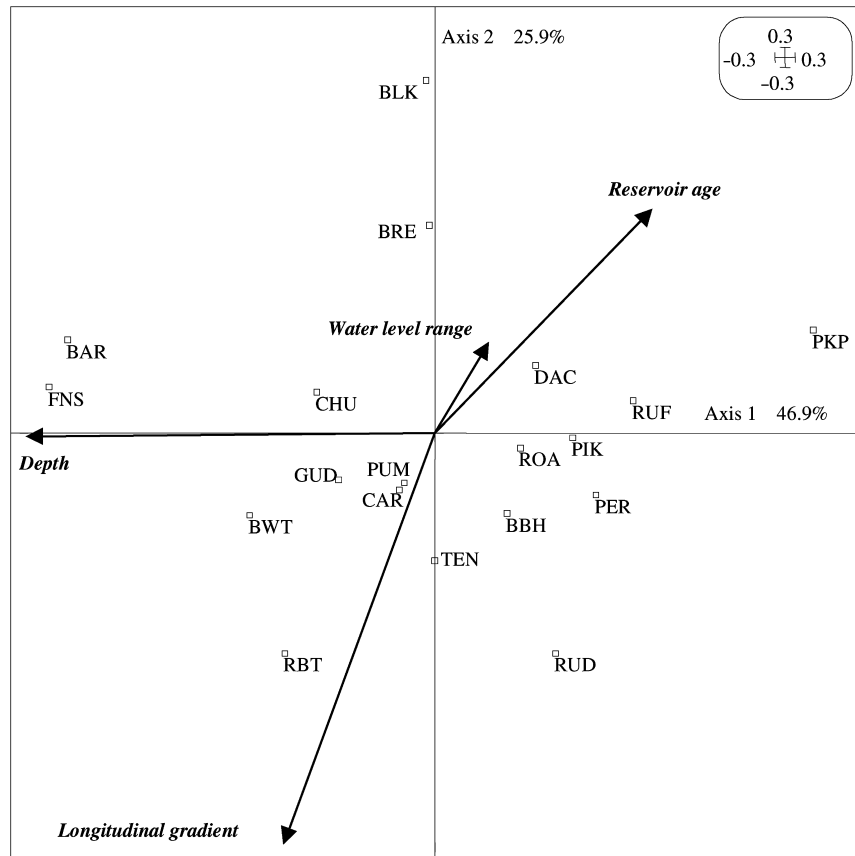


Fig. 8. CCA biplot superposing the environmental descriptors and the fish species. The scale box indicates the maximum value of the axis for the fish species. The maximum value of the axis is set to 1 for the descriptors.

related to the food resource availability. Deep water bodies submitted to temperate climate are seasonally stratified. These conditions are more favorable to pelagic fishes which are able to feed in open waters than to the benthivorous species then limited to the shallow littoral areas. Several biological and chemical processes have been shown to depend on the depth of the water body that was therefore included in the expression of synthetic models to assess the trophic status or to predict fish yield (Ryder et al. 1973). This interpretation of the effect of depth on fish communities is common with natural lakes, but reservoir-specific features increase the depth effect. A deep reservoir means that the dammed river had a steep slope. These intermediate riverine systems were described by Verneaux (1981) as, from upstream to downstream, brown trout, grayling (*Thymallus thymallus* L.) and barbel zones. French nase and barbel appear to be the species performing best in deep reservoirs, accompanied to a lesser extent by chub, bleak, rainbow trout, bream, gudgeon and brown trout, whereas pikeperch, ruffe, pike and perch are most abundant in shallow reservoirs. Furthermore the strong correlation between the reservoirs mean depth and their water level range can be considered as a general characteristics of these systems. The level fluctuations, whose effects have so far been difficult to distinguish from the effects of depth, also limit the possibilities for stable and rich benthic invertebrate and macrophytic communities to colonize the substrate. Such artificial and unpredictable conditions represent severe pressure for various functions of the fish life cycle. Most of the recorded fish species feed, at least at one development stage, on benthic invertebrates (Billard 1997). Their low abundance represent a resource gap. The absence of aquatic vegetation also considerably reduces the survival of juveniles due to the lack of shelters from predators and prevents some species to reproduce in the absence of suitable spawning habitat. The last direct impact of level variations is the risk for the eggs of shallow spawners to become emerged during lowering periods.

The CCA shows that the water body depth is a better explanatory variable of the fish community than the water level range. Nevertheless, the effects of level variations should be further investigated to draw general conclusions. A more precise description of the variations, including daily and seasonal fluctuation regimes, would provide more pertinent results than the simple annual level range.

Man-made reservoirs can be regarded as particularly interesting environments due to their

youth. Their rapid evolution, in comparison to natural hydrosystems, provides valuable information on the ecological successions following a major environmental disruption. Fish communities appear sensitive to reservoirs' aging process. The fish fauna of a newly built reservoir essentially originates from the dammed river. The dominant species at that stage are either rheophilic and limited to the mouth of the tributaries or come from the river pools. Few of them are generalist enough to remain competitive in a lacustrine environment. Pelagic habitats are to a large extent unexploited as these species find better living conditions in littoral shallow areas (Fernando & Holcik 1991). In most cases, the fish stock does not increase until species adapted to standing waters are introduced. Obviously, such management practices alter the natural evolution of biotic communities. Nevertheless, our observations show that the structuring role of site characteristics is not occulted by anthropogenic actions. Indeed, as shown by Argillier et al. (2002), stocking is rather inefficient in such environments. We hypothesize that species introductions do not challenge our approach, firstly because all the sites are similarly submitted to these practices, and secondly because the success of an introduced species depends on whether it meets favorable environmental conditions or not. Therefore, the abundance of the species can be regarded as a response to habitat characteristics despite stocking and introductions.

The brutal habitat disturbance due to the construction of the dam is followed by a rapid evolution in the created environment. Some authors consider three stages in this biogeochemical evolution. A short time after filling, a 'trophic upsurge' results from the nutrients' availability from inundated soils, then productivity decreases and then stabilizes at a level controlled by the external nutrients' loads from the inflow (Popp et al. 1996). In spite of the lack of water quality data, this model does not seem to fit our observations. French reservoirs appear sensitive to progressive eutrophication, the first algal blooms occurring a few decades after initial filling (unpublished data). Fish community response to these habitat alterations is quite similar to the pattern described by Kubecka (1993) with a shift from the original riverine community to cyprinids-dominated communities with important perch populations. Such a process certainly is accelerated by species introductions. The ultimate stage is characterized by the dominance of cyprinids, particularly bleak, and pikeperch that can be considered as the typical old reservoirs predator. These species are considered to be tolerant towards water

quality and their adaptive ability allows their populations to develop in unstable environments. Communities therefore seem to reflect the eutrophication trend.

The opposite effect of reservoir age and longitudinal gradient index shows that the response of fish assemblages to the aging process is similar to a progressive slide towards downstream-type communities. This confirms the trophic interpretation of the observed taxa successions, considering a longitudinal productivity gradient as a general feature of riverine systems.

Conclusions

This work provides an original overview of the features of fish communities in French reservoirs and highlights the different types of factors structuring them. Though the investigations were limited to easily collectable descriptors of the studied reservoirs, the general patterns in the species associations can be interpreted functionally. In the absence of reference conditions due to their artificial origin, reservoir fisheries management does not include any conservation purposes. Species introductions are widespread and accelerate the successions while reservoirs age. Further research aiming at designing a model to predict the fish potential yield and species adaptability should require the collection of water quality data.

Resumen

1. El objetivo de este trabajo es describir los ensamblajes de peces de los embalses franceses y relacionarlos con las características de las localidades. Los resultados de 43 muestreos fueron complementados con descriptores ambientales. Los ensamblajes de peces difirieron entre localidades de montaña dominadas por salmonidos y los de tierras bajas. Los embalses de montaña reflejan mas acciones humanas (re poblaciones e introducción de especies) que respuestas bióticas a las condiciones ambientales. Por debajo de los 1500 m de altitud, la diversidad de especies es mayor y se pueden distinguir comunidades reofilicas a limnofilicas. Esto puede estar relacionado con la edad, la profundidad y la localización geografica de la cuenca.
2. La respuesta de las comunidades a estas variables fue investigada a traves de Analisis de Correlacion Canónica. Los parámetros ambientales explicaron un 20% de la dispersión de las especies. Las comunidades estan influenciadas por parametros locales y regionales. Mientras que la morfología del embalse determina la abundancia de algunas especies, descriptores a gran escala tienden a afectar a los ensamblajes. Las especies reofilicas son tipicamente abundantes en las cuencas superiores, profundas y en los embalses recientemente creados. La respuesta de la comunidad de peces a la edad de los embalses tiende a ser la adición de especies de aguas quietas y a la extinción de especie de río. Discutimos ademas el papel estructural de la profundidad de las localidades, la edad y la localización, considerando estas

relaciones con el estado trófico y su significado en términos de habitat.

Acknowledgements

We would like to thank the numerous persons and institutions who provided data for this study, Conseil Supérieur de la Pêche, Ecole Nationale d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France. This work is part of a project funded by Conseil Supérieur de la Pêche.

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P2: Contribution of native and non-native species to fish communities in French reservoirs

Irz P., Argillier C. & Proteau J.-P. (2004)

Fisheries Management and Ecology, 11, 165-172

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Contribution of native and non-native species to fish communities in French reservoirs

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Abstract Previous studies showed that only 20% of the variability in fish community structure in French reservoirs could be explained by site characteristics. In addition, no relationship was found between the relative abundance of species and stocking effort. Therefore, deliberate or uncontrolled introductions are likely to be the source of a great part of the observed communities. The objective of this study was to assess the importance of species introductions in French reservoirs. Fifty-one reservoirs were sampled to obtain species presence/absence data. Local native (LNaR) and non-native (LNNR) species richness were negatively correlated. LNaR was strongly correlated to the lake surface area, depth and catchment area, whereas LNNR was independent of environmental variables. Furthermore, LNaR was positively correlated to regional native richness. Conversely, local total richness was independent of regional total richness, but was related to the reservoirs' environmental characteristics. It was hypothesised that the native fish communities in French reservoirs are unsaturated and species introductions lead to saturated communities.

KEYWORDS: environmental factors, interspecific interactions, reservoir, species introduction, species richness.

Introduction

Introduction of fish species in France has a long history but records exist mostly for the last two centuries (Keith & Allardi 1997). The 23 introduced fish species currently present in the country's water bodies account for one-third of the total number of species. Therefore, they are likely to affect native fish communities.

Introduced piscivores have frequently reduced the populations of prey species, occasionally leading to their extinction (Townsend 1996; Chapleau, Findlay & Szenasy 1997), thereby reducing native richness (Whittier, Halliwell & Paulsen 1997; Findlay, Bert & Zheng 2000) and altering fish community structure (Godinho & Ferreira 1998). Furthermore, previously predator-less native fish communities could be more sensitive to predation pressure (Townsend & Crowl 1991).

Competitive interactions are subject to debate. Frequently, diet analyses show that native and introduced species feed on similar resources and in similar habitats, but the severity of feeding competition is difficult to prove unless prey resources are assessed. The problem becomes even more complex when

considering that the interactions between two species are not restricted to feeding competition, but can depend on interactions with a third species (Bryan, Robinson & Sweetser 2002), and are influenced by habitat availability (Eklöv & Diehl 1994; Chick & McIvor 1997).

Ecologists have developed alternative methods and theories, frequently based on the niche theory (Hutchinson 1957), to assess directly interactions at the community level. Among those, the distinction between interactive and non-interactive communities (Cornell 1985; Cornell & Lawton 1992) is based on the hypothesis that local conditions result in a maximum carrying capacity. When species richness attains this capacity, interactive pressures are expected to condition subsequent community characteristics. Such communities are considered to be saturated. Conversely, species-poor communities, limited by regional biogeography, show limited niche overlapping and low interactions between species. Such situations provide greater chances for introduced species to develop and limits potential competitive risks with the original communities (Belkessam, Oberdorff & Hugueny 1997).

Local conditions strongly influence community characteristics (Eadie & Keast 1984; Hondzo & Stefan

1996) by providing the framework in which the structuring processes take place. Therefore, reservoir fish community composition can be partially explained by their location in the catchment, climatic conditions and reservoir morphometry (Godinho, Ferreira & Portugal e Castro 1998; Irz, Laurent, Messad, Pronier & Argillier 2002). A hierarchical conceptual framework was proposed to integrate the various spatial and temporal scales involved in structuring lacustrine fish communities (Tonn 1990). Thus, local assemblages are regarded as a subsample of the global fish pool. Consequently, an understanding of the key processes responsible for the standing communities requires a multiscale approach as well as an assessment of the relative importance of biotic, abiotic and regional factors (Jackson, Peres-Neto & Olden 2001), to which human interventions must be added.

The objectives of this paper are to: (1) investigate the relationship between native and non-native richness at a local scale; (2) correlate local richness to environmental variables; and (3) analyse the relationship between local and regional richness to evaluate community saturation.

Materials and methods

The data set

The data used in this study originated from various sources. The aim of the collection was to gather, as exhaustively as possible, existing information on fish communities in French reservoirs. This was achieved on the basis of numerous, mostly unpublished, reports from research institutes, administrations and consultants. These studies were carried out for local purposes. They were not part of a national monitoring network and thus were not based on any standardised fish sampling strategy. As a result, data acquisition procedures showed strong heterogeneity. Most of the surveys were carried out with gill nets, either horizontal or vertical, but fish censuses were also carried out when reservoirs were being drained. To reduce the bias related to the differences in sampling methods, fish data were only used to derive the total number of species in the sample, expressed as the reservoir's total species diversity (LToR).

The reservoirs' catchment area, maximum depth, surface area and altitude were either extracted from the reports or taken from 1:25 000 to 1:100 000 topographical maps. The scope of the study was limited to sites located below 1100 m altitude as this appeared to be a reasonable threshold, excluding the rather distinct mountain reservoirs located on streams that did not

originally host any fish populations prior to introductions. Such sites display little variability in species richness because they are limited to salmonids (Irz *et al.* 2002). Sufficient information was available for 51 reservoirs. The distribution of these sites in France is uneven (Fig. 1) and reflects both the actual distribution of reservoirs, which are mostly located in mountainous or hilly regions, and the degree of local interest for reservoir fisheries.

The classification of species as native, translocated or alien was based on historical records and riverine fish sampling (Keith 1998; Keith & Allardi 2001). This classification is given for each of the 10 hydrographic regions (Fig. 1). Species are considered as native if present in a catchment 5000 years BP, translocated when they were native in another French catchment, and alien when they were introduced from abroad. Tench, *Tinca tinca* (L.), was considered native in Côte d'Azur, as in the other mainland Mediterranean regions, despite the lack of precise information on the status of this species in Keith (1998) and Keith & Allardi (2001).

The reservoirs' (local) total species richness (LToR) could therefore be split into native (LNaR), translocated (LTrR) and alien (LAIR) richness. Local non-native richness (LNNR) is LTrR + LAIR. Regional total richness (RToR) was considered as the total species pool in each hydrographic region, regional

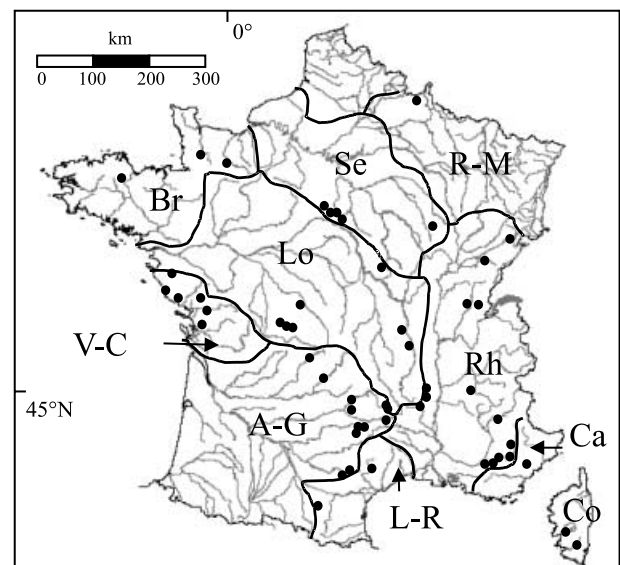


Figure 1. Map of France showing hydrographic regions (bordered by thick lines) according to Keith (1998) and location of the study reservoirs (solid circles). R-M: Rhine-Meuse; Se: Seine; Br: Bretagne; Lo: Loire; V-C: Vendée-Charente; A-G: Adour-Garonne; Rh: Rhône; L-R: Languedoc-Roussillon, Ca: Côte d'Azur, Co: Corse.

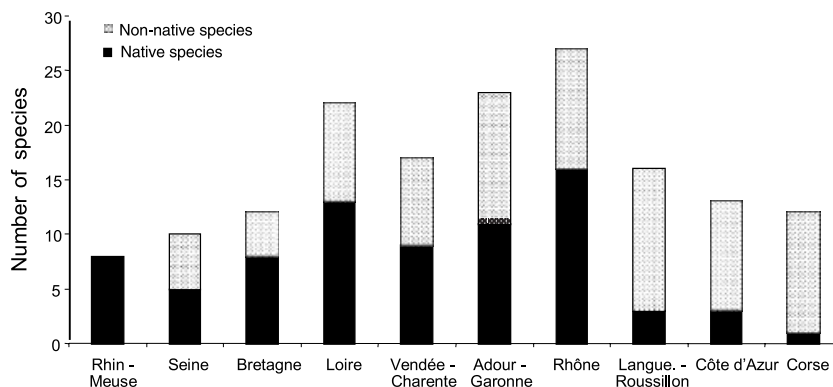


Figure 2. Number of native and non-native species recorded in the study reservoirs among hydrographic regions.

native richness (RNaR) being the total native pool in the region.

As the scale at which the status of species is given is the hydrographic region in which the lake is located, some of the species that are considered as native could have been introduced into the lake from another catchment of the same region.

Analytical procedure

Spearman correlation was used to study the bivariate relationship between LNaR, LTrR, LAIR and LNNR. As LNNR is the sum of LTrR and LAIR, these variables could not be considered independent and the correlation coefficients were not derived. Between-regions comparison of the environmental variables was processed by one-way ANOVA. The relationship between richness and environmental variables was investigated by bivariate Spearman correlation due to clear non-normal distributions of the environmental variables.

Plotting local vs. regional richness is the classical method for testing community saturation (Cornell 1985). The relationship was assessed using linear, power and quadratic regression between the mean value of local richness of each region and the regional richness. Pooling local richness into a single mean value of a region is recommended instead of using individual values of local richness for each sampling station to avoid pseudo-replication (Srivastava 1999).

All the statistical analyses were performed with SPSS software (SPSS Inc. 1999).

Results

Regional distribution of fish species

The total number of species recorded in the 51 reservoirs was 34, but varied from eight in Rhine-Meuse to

27 in Rhône (Fig. 2). These differences can be related to both the number of reservoirs in each region and to the regional species pool. Ten of these species were present only in a single region (Table 1).

Apart from Rhine-Meuse, represented by a single reservoir in the data, native and non-native species were found in all the regions. However, the balance between native and non-native was also dependent upon regions. Languedoc-Roussillon, Côte d'Azur and Corse, all small coastal Mediterranean catchments, limited in native richness, showed high proportions of introduced species (Fig. 2). Conversely, the proportion of introduced species was around 40% in the Seine, Loire, Adour-Garonne and Rhône, all large regions. The number of introduced species was similar between reservoirs of species-rich and species-poor regions.

Relationship between native and non-native richness

At the regional scale, the relationship between RNaR and RNNR was not significant ($r^2 = 0.012$, $P = 0.77$) while the correlation between RNaR and RToR was strong ($RToR = 18.5 + 1.06 RNaR$, $r^2 = 0.80$, $P < 0.001$).

At the local scale, the only significant correlation was a negative one between LNaR and LNNR (Table 2). However, LTrR ($P = 0.12$) and LAIR ($P = 0.21$) were also negatively related to LNaR, whereas LTrR and LAIR were positively correlated ($P = 0.09$), showing that some reservoirs were more subjected than others to introductions from either origin (close or alien) and/or allow these species persistence. The negative correlation between LNNR and LNaR suggests that such lakes, hosting numerous non-native species, tend to be poor in native species.

Table 1. List of the species recorded in the study reservoirs. The status is given per hydrographic region. Regional richness were taken from Keith & Allardi (2001) for Corse, and from Keith (1998) for all other regions

	Rhine- Meuse	Seine	Bretagne	Loire	Vendée- Charente	Adour- Garonne	Rhône	Languedoc- Roussillon	Côte d'Azur	Corse
Number of reservoirs	1	5	3	7	6	10	14	2	1	2
Regional native richness	37	31	26	31	25	27	38	24	16	4
Regional total richness	51	53	39	58	40	53	58	48	40	19
<i>Leucaspius delineatus</i>					NN		NN			
<i>Alburnus alburnus</i>			N	N	N	N	N	N	N	
<i>Barbus barbus</i>						N	N			
<i>Micropterus salmoides</i>		NN		NN	NN			NN	NN	
<i>Leuciscus soufia</i>							N			
<i>Blicca bjoerkna</i>	N		N	N	N	N	N	NN	NN	
<i>Abramis brama</i>	N	N	N	N	N	N	N	NN	N	
<i>Esox lucius</i>	N	N	N	N	N	NN	N	NN	NN	NN
<i>Carassius auratus</i>										NN
<i>Carassius carassius</i>				NN	NN	NN	NN	NN		NN
<i>Cyprinus carpio</i>		NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Leuciscus cephalus</i>				N		N	N	N		
<i>Coregonus</i> sp.							N			
<i>Salvelinus namaycush</i>							NN			
<i>Gambusia affinis holbrooki</i>						NN				
<i>Rutilus rutilus</i>	N	N	N	N	N	NN	N	NN	NN	NN
<i>Gobio gobio</i>			N	N	N	N	N			NN
<i>Gymnocephalus cernuus</i>	N		NN	NN	NN	NN	NN	NN		NN
<i>Chondrostoma nasus</i>							NN			
<i>Misgurnus fossilis</i>						NN	N			
<i>Lota lota</i>				N						
<i>Salvelinus alpinus</i>							NN			
<i>Ictalurus melas</i>		NN		NN	NN	NN	NN			
<i>Perca fluviatilis</i>	N	N	N	N	N	NN	N	NN	NN	NN
<i>Lepomis gibbosus</i>		NN		NN	NN	NN	NN	NN	NN	
<i>Scardinius erythrophthalmus</i>	N			N	N	N	N	NN	NN	NN
<i>Sander lucioperca</i>		NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Silurus glanis</i>				NN				NN		
<i>Oncorhynchus mykiss</i>			NN	NN		NN	NN	NN	NN	
<i>Tinca tinca</i>	N	N	N	N	N	N	N	N	N	NN
<i>Chondrostoma toxostoma</i>							N			
<i>Salmo trutta</i>				N		N	N			N
<i>Phoxinus phoxinus</i>						N				
<i>Leuciscus leuciscus</i>				N		N				

N, native; NN, non-native; blank, not recorded.

Table 2. Spearman correlation coefficients between local species richness

	Native richness	Translocated richness	Alien richness
Native richness	1		
Translocated richness	-0.220	1	
Alien richness	-0.180	0.235	1
Non-native richness	-0.286*	nc	nc

nc, Not calculated. * $P < 0.05$.

Influence of environmental variables

The sites displayed a wide range of variation in environmental characteristics (Table 3). Comparison of the environmental variables showed that only altitude presents significant between-regions differences ($P < 0.001$). The reservoirs of Corse, Rhône, Loire and Adour-Garonne were higher in altitude than those of the Seine and coastal regions.

The relationship between these variables and reservoirs' species richness showed that catchment area, lake area and maximum depth were positively correlated to LToR and LNaR but not to the richness in

Table 3. Range of variation of environmental variables

	Altitude (m)	Catchment area (km ²)	Lake area (ha)	Maximum depth (m)
Minimum	13	1	4	2
Maximum	1074	6520	3200	135
Mean	392	82.5	358	37.6
SD	297	1490	587	33.7

Table 4. Spearman bivariate correlation coefficients between species richness and reservoir characteristics

	Altitude	Catchment area	Lake area	Maximum depth
Native richness	0.141	0.500***	0.433**	0.288*
Translocated richness	-0.018	0.170	0.214	0.247
Alien richness	-0.183	-0.279*	-0.184	-0.155
Non-native richness	-0.056	-0.09	0.038	0.005
Total richness	0.092	0.407**	0.435**	0.395**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

introduced species (Table 4). The only exception was the negative correlation between LAIR and catchment area. Altitude was never a significant factor. Only native and total richness displayed environment-related patterns for the variables considered.

Saturating effect of species introductions?

The local-regional richness plot (Fig. 3) showed that LNaR was correlated to RNaR. The linear model fitted the data best ($n = 10$, $r^2 = 0.52$, $P = 0.012$) with no sign of reaching an asymptotic value, suggesting that native communities could be unsaturated. The slope was 0.195 and the intercept did not significantly differ from zero. Conversely, LToR appeared to be independent of

RToR ($n = 10$, $r^2 = 0.081$, $P = 0.43$). Such an independence could result from a local saturation in species.

Discussion

Regional scale

Fish species introductions are widespread in French reservoirs and occur in all regions, which is consistent with previous results obtained on rivers (Keith & Allardi 1997). When such introductions are voluntary, they generally aim at enhancing recreational fisheries and are carried out without any prior analysis of their chances of success or of their potential impact on native communities (Argillier, Pronier & Changeux 2002). These observations prove that reservoirs generally provide a favourable environment for the establishment of non-native species.

The number of introduced species in a region is interesting on a regional scale, but it is difficult to interpret because it depends on both the frequency of introduction attempts and the success rate of these attempts. However, it appears quite constant among regions and independent of the regional native pool. This suggests that the invasibility of species-poor regions is not markedly greater than that of species-rich ones.

Local scale

At the local scale, the negative correlation between native and non-native richness suggests that the success of introductions could be superior in species-poor environments, which would be consistent with other results showing that species-poor communities were in some cases less resilient to invaders (Lodge 1993). Furthermore, management authorities may be

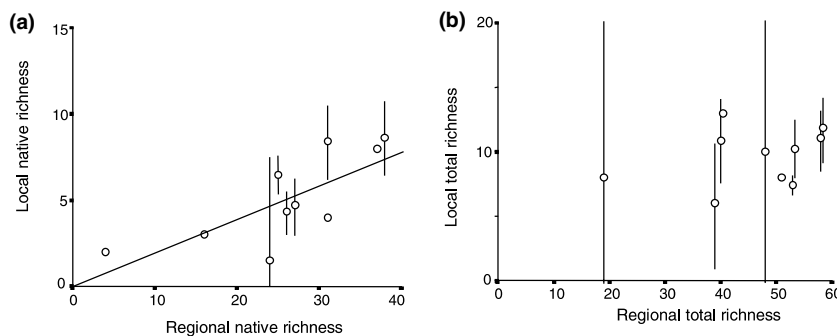


Figure 3. Relationship between regional and local species richness: (a) native richness; (b) total richness. Bars represent 95% confidence interval for the mean value.

more inclined to introduce species when recreational fisheries appear limited by local richness.

Environmental disruptions, such as dam construction, have also been proven to provide favourable conditions for the establishment of new species by modifying the competitive ability of native fauna (Moyle & Light 1996). The damming of the river also considerably alters the initial riverine habitat, thereby modifying the ecological niches available. The possibilities for the initial lotic fish species to occupy these niches are probably reduced because most of them may not be adapted to lentic conditions, which explains that in some cases in the years following the initial filling colonisation of a water body was restricted to its upper part and shallow areas (Fernando & Holcik 1991).

However, the success of introduced species also depends on their ability to cope with habitat conditions and environmental variability (Brown & Moyle 1997). The environmental variables considered in this study are not correlated to the number of introduced species, which shows that the reservoirs' physical features do not represent a major pressure on the number of non-native species, either translocated or alien. This does not mean that the fate of introduced species is independent of environmental conditions, but rather that whatever habitats are available, some of the introduced species find suitable conditions to settle. Native fishes exhibit patterns related to environmental variables. Catchment area can be considered as an indicator of the diversity of habitats upstream from the lake, whereas lake depth and surface area are related to the within-lake habitat diversity. Therefore, their positive correlation with native and total richness indicates the classical increase in richness with habitat diversity (Eadie & Keast 1984). It also suggests that migratory movements between the lake and the upstream hydrographic network have to be considered, which is confirmed by the presence in the data of numerous obligatory riverine species (according to Penczak & Kruk 2000).

The absence of an altitude effect is more puzzling because altitude is frequently recognised as a surrogate for the longitudinal succession of habitat conditions from upstream to downstream (Irz *et al.* 2002). It is possible that the range of variation in the sites' altitude (0–1074 m) was insufficient to make altitude an important explanatory variable to species richness.

Man-induced saturation?

The plots of local vs. regional richness (Fig. 3) suggest that native fish communities in reservoirs would be unsaturated (Cornell & Lawton 1992). In France, this

had already been observed in small coastal streams (Belkessam *et al.* 1997; Oberdorff, Hugué, Compin & Belkessam 1998) but not at a larger scale nor in lentic systems. In reservoirs, local native richness is limited because potential natural colonisation is restricted to a subsample of the upstream species pool that is sufficiently adapted to lentic environments. Therefore, native richness is likely to be below the levels leading to strong interaction between species, particularly when considering that the reservoir generally increases the diversity of habitats compared with the initial river.

Conversely, no linear relationship was found between local and regional total richness. This does not strictly prove that communities are saturated (Srivastava 1999). However, the strong relationships found between LToR and the environmental variables would be expected under a control of LToR by local conditions. Furthermore, the negative correlation between LNNR and LNaR, for which several interpretations were given above, could also reflect the impact of introductions on native communities and therefore a strong level of interspecific competition.

Comparing patterns of native and non-native richness suggests that introductions may be so frequent that they lead to increases in richness until communities become saturated, i.e. when no niche remains vacant.

Conclusion

In the absence of precise monitoring of lentic systems, including data on the extinction of native species at the local scale, the type of approach developed contributes to the understanding of the processes involved in structuring fish communities. In an applied perspective, it provides valuable information for the assessment of management practices because further introductions in already saturated communities could result in local extinction and thereby in a reduction in biodiversity.

Preliminary results from natural lakes (unpublished data) tend to confirm the hypothesis of man-induced saturation of fish communities. Further work will be carried out to check the trends observed in a broader framework for both natural and man-made lakes, with more attention to the underlying assumptions and analytical procedure.

Acknowledgments

We would like to thank the numerous persons and institutions who provided data for this study, Conseil

Supérieur de la Pêche, Ecole Nationale Supérieure d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France. We thank T. Oberdorff for his useful comments on the initial version of the manuscript.

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P3: Native and introduced fish species richness in French lakes: local and regional influences

Irz P., Argillier C. & Oberdorff T. (2004)

Global Ecology and Biogeography, 13, 335-344

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RESEARCH
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Native and introduced fish species richness in French lakes: local and regional influences

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ABSTRACT

Aim To analyse the importance of local and regional influences on the patterns of species richness in natural and man-made lakes and to infer the impacts of human-mediated introductions on these patterns.

Location France.

Methods Species occurrence data were gathered for 25 natural and 51 man-made lakes. Analysis is based on regression models of local richness against their related regional richness and lake environmental variables.

Results Local native richness was mostly controlled by the regional richness. Conversely, local total richness was mainly explained by local variables. These statements apply to both natural and man-made lakes. Lacustrine systems displayed weak resistance to invaders.

Main conclusions Species introductions have apparently contributed to saturate fish communities in these systems even if no clear negative effect on the survival of native species (i.e. species extinction) is detectable so far.

Keywords

Environmental factors, fish communities, interspecific interactions, lake, local vs. regional influences, reservoir, species introductions, species richness.

INTRODUCTION

The relative influence of biotic and abiotic factors in structuring ecological communities has long been discussed (Lawton & Strong, 1981; Schoener, 1983). This debate progressively shifted from the initial consideration of local scale factors to a multiscale approach (Levin, 1992). Recent advances have led freshwater fish ecologists to view species diversity as the result of hierarchical processes operating at different spatial and temporal scales (Hugueny & Paugy, 1995; Angermeier & Winston, 1998; Oberdorff *et al.*, 1998). The importance given to interspecific interactions is therefore likely to depend on the scale of investigation. Considering the local community as a sample extracted from the regional pool is a way of taking the regional contribution to local communities into account (Ricklefs & Schluter, 1993). This can be done by plotting local vs. regional species richness in order to assess whether communities are saturated or not (Cornell, 1985). If local richness increases linearly with regional richness, the regional pool of potential colonisers is likely to be the limiting factor to local richness. Conversely, saturation occurs when the local richness becomes independent from

regional richness. This pattern is classically interpreted as resulting from biotic interactions (Cornell & Lawton, 1992).

Although a vast literature exists on the effect of species introductions (Elton, 1958; Drake *et al.*, 1989; Williamson, 1996), these human practices have seldom been regarded as an increase in the species colonization rates. Nevertheless, introductions may cause diverse effects by a modification of the colonization/extinction equilibrium in biogeographical islands (MacArthur & Wilson, 1963, 1967). This is particularly likely when natural colonization is weak as a result of either a limited regional pool of species or of environmental isolation. Both of these conditions are met for the fish communities dwelling in the lakes of western Europe, weakly connected to each other by the riverine network. The fish fauna of western Europe is particularly depauperate since the last glaciations caused massive extinctions (Mahon, 1984; Oberdorff *et al.*, 1997). However, the introduction of fish species in inland waters has been widespread (Cowx, 1998) and generally carried out without any clear knowledge of its potential consequences on native communities (Welcomme & Bartley, 1998).

Introduced piscivores have, in some cases, been proved strongly to impact upon prey populations, leading locally to their

extinction (He & Wright, 1992; Chapleau *et al.*, 1997; Findlay *et al.*, 2000). The consequences of competitive interactions are more controversial. This might be due to difficulties in assessing competition intensity in natural environments at the community level. Most evidence of competition has been obtained for simple communities in artificial environments (Persson, 1987; Persson & Greenberg, 1990) and competition has been shown to depend upon numerous other factors such as environmental conditions (e.g. Taniguchi & Nakano, 2000). Testing whether communities are saturated or not is an alternative method that has seldom been implemented on fish communities. In streams, most of the studies published so far have concluded that local fish communities were not saturated with species, local richness being directly proportional to regional richness (Hugueny & Paugy, 1995; Belkessam *et al.*, 1997; Hugueny *et al.*, 1997; Oberdorff *et al.*, 1998), although some exceptions to this pattern were observed (Angermeier & Winston, 1998; Matthews & Robison, 1998). Studies of fish community saturation in lakes lead to somewhat conflicting results. Some of these studies suggest little regional influence on local species richness (Jackson & Harvey, 1989; Minns, 1989; Tonn *et al.*, 1990), while others have documented strong regional effects (Griffiths, 1997).

Our study focuses on the relationship between local and regional richness in fish species in French natural and man-made lakes. Species introductions are frequent in France (Persat & Keith, 1997), particularly in lacustrine systems (Irz *et al.*, in press) and provide opportunities to examine responses of local communities to invasions and to draw inferences about community saturation. Many of the authors who have documented the impact of species introduction into ecosystems have also commented on the difficulty of defining the specific role of introduced species on native communities, particularly for freshwater fish (Arthington, 1991). However, it is widely agreed that most fish introductions have a damaging effect on the receiving aquatic ecosystem and its indigenous fish fauna (Herbold & Moyle, 1986; Brown, 1989; Bianco, 1990; Holcik, 1991; Elvira, 1995; Rahel, 2000). Nevertheless, there are currently few studies that compare the community structure before and after introductions (Angermeier & Winston, 1998).

After stating the importance of non-native richness in French man-made lakes (Irz *et al.*, in press), this paper analyses the importance of local and regional influences on the patterns of species richness and infers the impacts of human-mediated species introductions on these patterns for both natural and man-made lakes.

MATERIALS AND METHODS

Data set

The data set is an extension of the one analysed in Argillier *et al.* (2002a) and Pronier (2000). It was compiled from various sources (mostly unpublished study reports). In the absence of a national monitoring network, these studies addressed local concerns. Most of the surveys were carried out with gillnets, either horizontal or vertical, but we also used fish censuses

produced when the reservoirs were drained. The complete list of the study lakes is given in Table 1.

The lakes' maximum depth, surface area and altitude were obtained from reports or 1/25,000–1/1,000,000 topographical maps. These variables have been used as inputs to explain the structure of the fish community in previous works on French lakes (Argillier *et al.*, 2002b; Irz *et al.*, 2004).

The lakes studied are not distributed uniformly across France (Fig. 1, Table 2). Their location reflects both the actual distribution of lakes, which are mostly located in mountainous or hilly regions, and the local concern of management authorities for lake fisheries.

The status of the species was established from historical research and actual riverine fish sampling (Keith, 1998). This work provided the status of each species for each of the 10 hydrographic regions of France (Fig. 1). These regions are bordered by natural catchment limits. Species were classified as native to a hydrographic region when they were present in that region 5000 years BP, translocated when they were native to another French region and exotic when introduced from abroad. Data for the Corse region were obtained from Keith & Allardi (2001).

The total species richness of a lake (LToR) was split into native (LNaR), translocated (LTrR) and exotic (LExR) richness. The autochthonous richness (LAuR) was further defined as the sum of native and translocated richness (LNaR + LTrR). Regional native (RNaR), translocated (RTrR), exotic (RExR), autochthonous (RAuR) and total richnesses (RToR) were built as the total species pool in each hydrographic region for each of these statuses following Keith (1998) (Table 2).

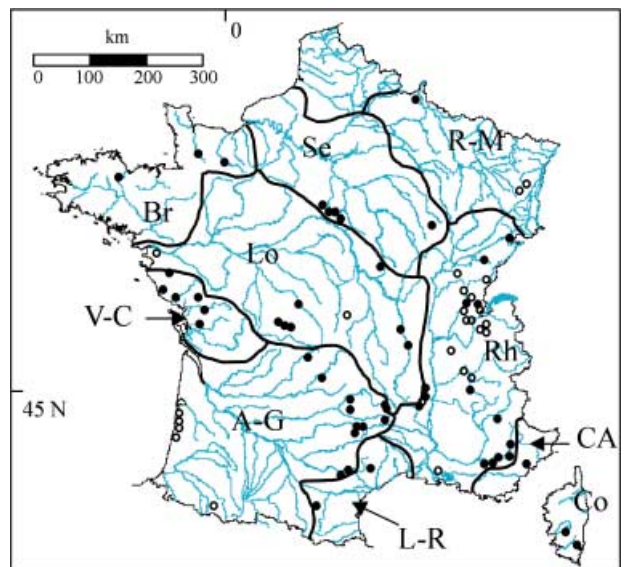


Figure 1 Map of France representing the hydrographic network and the natural (open circles) and man-made (solid circles) lakes of the study. Solid lines display the regional boundaries. A-M: Rhin-Meuse; Se: Seine; Br: Bretagne; Lo: Loire; V-C: Vendée-Charente; A-G: Adour-Garonne; Rh: Rhône; L-A: Languedoc-Roussillon; CA: Côte d'Azur; Co: Corse. Adapted from Keith (1998).

Table 1 List of the study lakes with their types and data sources. The sources are the institutions that provided the fish sampling data, not necessarily those that collected them

Name	Type	Source	Name	Type	Source
L'abbaye	N	Cemagref	Meinettes	A	AAPPMA
Aiguebelette	N	CSP	Mervent	A	AAPPMA
Angle guignard	A	AAPPMA	Moliets	N	Cemagref
Annecy	N	Cemagref	Montbel	A	EDF
Aulnes	N	Cemagref	Monteynard	A	CSP
Bage	A	University Toulouse	Nantua	N	CSP
Bourget	N	Cemagref	Naussac	A	Cemagref
Castillon	A	Cemagref	Noue mazonne	A	AAPPMA
Cazaux	N	Cemagref	Olivettes	A	Cemagref
Chastang	A	ENSAT	L'Ospédale	A	Agence eau
Chalain	N	AAPPMA	Paladru	N	CSP
Chaudanne	A	Cemagref	Pannecière	A	EDF
Couesque	A	Cemagref	Pareloup	A	EDF
Dathée	A	AAPPMA	Parentis	N	Cemagref
Devesset	A	CSP	Pont de salars	A	ENSAT
Divonne	A	Cemagref	Petichet	N	CSP
Eguzon	A	Cemagref	Pierre brune	A	AAPPMA
Esparron	A	Cemagref	Quinson	A	Cemagref
Estaing	N	ENSAT	Rabodanges	A	Cemagref
Etival	N	AAPPMA	Rabastens	A	ENSAT
Gué des cens	A	AAPPMA	La Raviège	A	Cemagref
Grand-lieu	N	Cemagref	Remoray	N	CSP
Gérardmer	N	Cemagref	Rochereau	A	AAPPMA
Gué l'évêque	A	AAPPMA	St-Cassien	A	Cemagref
Grangent	A	Cemagref	Ste Croix	A	Cemagref
Guerlédan	A	CSP	Saint Martial	A	AAPPMA
Ilay	N	CSP	Saint-Pardoux	A	ENSAT
Issarlès	N	DIREN	Saint Peyres	A	ENSAT
Laffrey	N	CSP	Serre-Ponçon	A	Cemagref
Laprade	N	Cemagref	Sylans	N	CSP
Lavaud-Gelade	A	EDF	Gour de Tazenat	N	University Clermont
Le Jaunay	A	AAPPMA	Tolla	A	Cemagref
Le Marillet	A	AAPPMA	Torcy	A	AAPPMA
Les Leschères	A	AAPPMA	Treignac	A	Cemagref
Longemer	N	Cemagref	Vielles Forges	A	EDF
Les Rousses	N	CSP	Villerest	A	Cemagref
Malsaucy	A	AAPPMA	Vouglans	A	Cemagref
Maury	A	EDF	Vaivre-Vesoul	A	Cemagref

N, natural lake; A, artificial lake. Cemagref: Centre d'Etude du Machinisme Agricole, des Eaux et des Forêts; CSP: Conseil Supérieur de la Pêche; DIREN: Direction Régionale de l'Environnement; AAPPMA: Association Agréée pour la Pêche et la Protection du Milieu Aquatique; EDF: Electricité de France; ENSAT, Ecole Nationale Supérieure d'Agronomie de Toulouse; University Clermont: Université Blaise Pascal, Clermont-Ferrand; University Toulouse: Université Paul Sabatier, Toulouse; Agence eau: Agence de l'Eau.

Sampling adequacy

In order to account for the differences in sampling schemes across lakes, we computed the Chao1 estimator of absolute species richness (Chao, 1984) in each lake using Estimates software (Colwell, 1997). This method is nonparametric and allows the estimation of species richness from samples on the basis of the species frequency data (Colwell, 1997). On an example data set (Colwell & Coddington, 1994), the Chao1 estimator displayed less underestimation of the asymptotic richness than a simple

accumulation curve, which means that it is less biased than the simple count of species in small samples. Such a procedure does not provide any guarantee against sampling biases but reduces the effect of differences in sample size (Gotelli & Colwell, 2001).

For the 45 lakes on which sufficient information was available, the number of fish caught per lake ranged from 141 (Devesset) to 5168 (Pannecière). Using bivariate Spearman's correlation, the total number of species in the sample (LToR) was significantly correlated with the sample size ($P = 0.005$, $R^2 = 0.17$) whereas the number of native species (LNAR) was not ($P = 0.13$, $R^2 = 0.05$).

Table 2 Number of studied sites and regional species richness among hydrographic regions according to the classification of Keith (1998)

Hydrographic region	No. natural lakes	No. man-made lakes	RNaR	RTrR	RExR	RAuR	RToR
Rhin-Meuse	2	1	37	7	20	44	51
Seine		5	31	3	17	34	53
Bretagne		3	26	4	9	30	39
Loire	2	7	31	11	13	42	58
Vendée-Charente		6	25	6	16	31	40
Adour-Garonne	5	10	27	11	15	38	53
Rhône	16	14	38	0	14	38	58
Languedoc-Roussillon		2	24	7	8	31	48
Côte d'Azur		1	16	5	10	21	40
Corse		2	4	13	11	17	19

Species richness: RNaR, Regional native; RTrR, translocated; RExR, exotic; RAuR autochthonous; RToR, total.

However, the Chao1 estimator of absolute total richness remained correlated to sample size ($P = 0.003$, $R^2 = 0.18$) and its correlation with LToR was so strong ($R^2 = 0.91$ excluding Saint Cassien with an atypical abundance pattern generating an outlier value of Chao1) that using the former in our case would be an unnecessary complication of the procedure. Despite the significant sampling effect, most of the variance in LToR was not explained by sampling effort and there was no significant difference in sample size among regions (Kruskal–Wallis test, $P > 0.05$). Thus, we judged that the underestimation of local species richness was likely to be equivalent among regions and that species richness was adequately assessed for our objectives.

As the reservoirs data set included both gillnetting surveys (37) and drainage censuses (14), we also checked that there was no major differential efficiency in the assessment of species richness. It is generally agreed that, everything else being equal, the lake area is an efficient predictor of fish richness with a classical power species–area relationship. Therefore, we performed an ANCOVA with $\text{Log}(\text{LToR})$ as the dependent variable, $\text{Log}(\text{lake area})$ as a covariate, and the sampling method as a factor. The slopes did not differ significantly ($P = 0.53$), thereby indicating that the two methods were comparable in terms of assessment of species richness.

Analytical procedure

The relationship between richness and habitat variables (maximum depth, surface area and altitude) was investigated using bivariate Pearson correlations, the first two habitat variables being log-transformed.

Testing for community saturation by analysis of local vs. regional richness with most rigour requires that habitats be identical among regions, which is not the case in our data set. Consequently, local richness (e.g. LNaR) was analysed by stepwise multiple linear regression in which regional richness (in this case RNaR), other local richness (in this case LTrR and LExR) and habitat variables were used as explanatory variables. The underlying hypothesis is that habitat may have a systematic effect

on the proportion of the regional pool present locally. Thus, this procedure allows us to assess the significance of the local–regional relationship, everything else being equal (Oberdorff *et al.*, 1998). To test more precisely the form of the relationship between local and regional richness, we included the square of the regional richness term and tested for its significance (Hugueny & Paugy, 1995; Caley & Schluter, 1997; Hugueny *et al.*, 1997; Oberdorff *et al.*, 1998). Curvilinearity provides sufficient evidence to reject the proportional relationship between local and regional richness as long as the regional species pool is correctly assessed to avoid ‘pseudosaturation’ (Oberdorff *et al.*, 1998; Srivastava, 1999). As local richness must, by definition, be equal to or less than regional richness, positive values of the intercept in the model are not theoretically consistent. Therefore, we started by fitting an unconstrained model and tested whether the intercept was significantly greater than zero (Griffiths, 1999). Only in this latter case did we constrain the regression model to pass through the origin (Hugueny & Paugy, 1995; Caley & Schluter, 1997; Hugueny *et al.*, 1997; Angermeier & Winston, 1998; Oberdorff *et al.*, 1998). In this case we entered the habitat variables as interaction terms with the regional richness variable, hence ensuring that local richness is always zero when regional richness is zero, irrespective of the values of the habitat variables.

Furthermore, if curvilinearity described the relationship better than linearity but was concave up (positive coefficient for the square of regional richness), rather than down as expected in the presence of species saturation, the quadratic term was removed from the final model (Caley & Schluter, 1997).

The statistical analyses were carried out with SPSS (SPSS Inc, 1999) and Systat (Wilkinson, 1990) software.

RESULTS

Habitat-related patterns

The observed range of the environmental variables (lake surface 4–6500 ha; altitude 0–1161 m; maximum depth 2–145 m) indicated that the data set represented a high diversity in lake

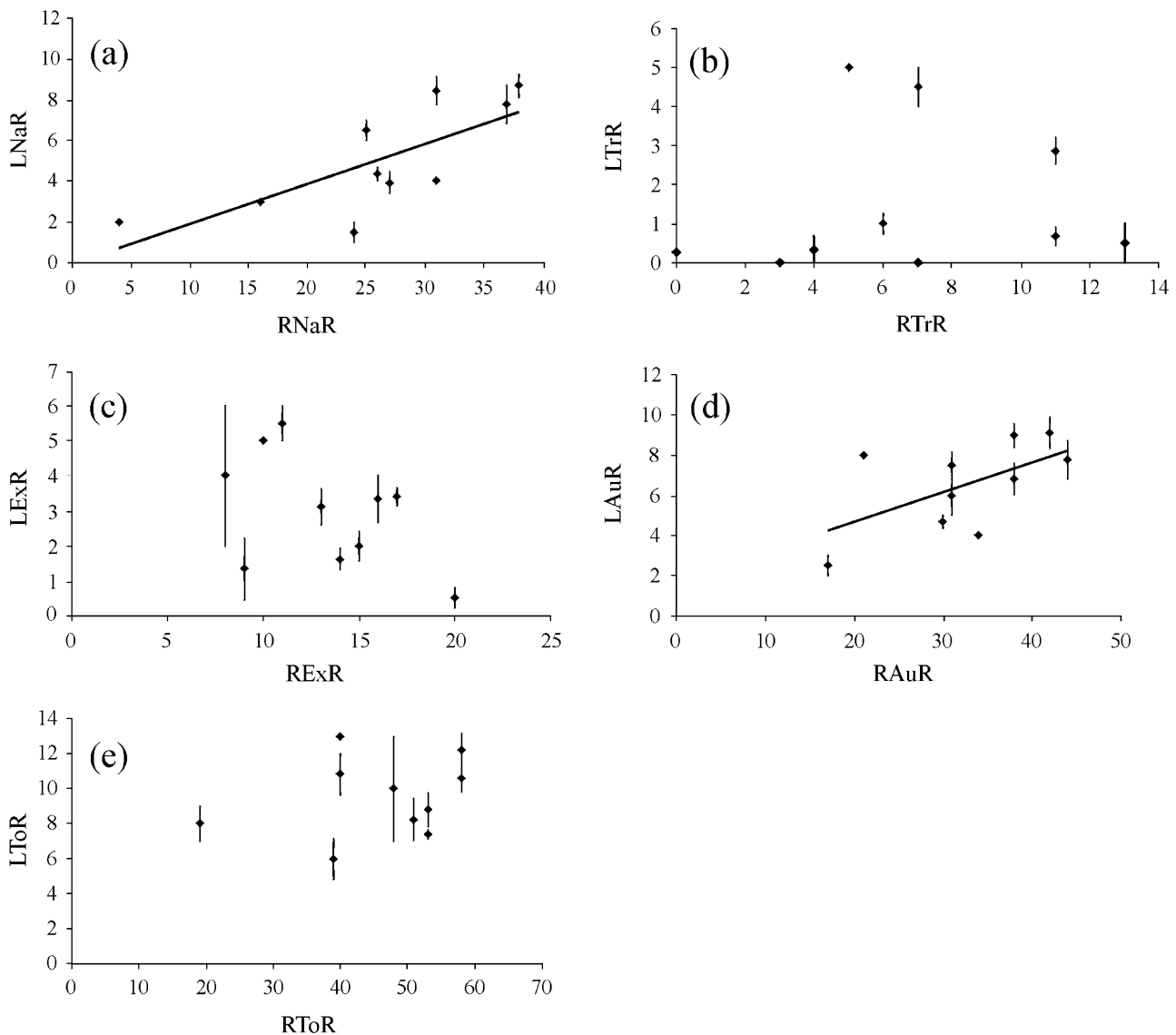


Figure 2 Relationship between regional and mean local species richness in each region. Bars represent standard errors. Regression lines were drawn only when the regression was significant at the 0.10 level. (a) Native richness ($n = 10$, $R = 0.741$, $P = 0.014$). (b) Translocated richness. (c) Exotic richness. (d) Autochthonous richness ($n = 10$, $R = 0.581$, $P = 0.078$). (e) Total richness. Natural and man-made lakes were pooled.

types. Bivariate correlations showed that the responses of LToR, LAuR and LNaR to the habitat variables were similar. They were positively correlated with lake area and maximum depth (Table 3). LExR and LTrR displayed a totally different pattern, only negatively related to altitude. It was noticeable that whatever the origin of the species, all the significant correlations with altitude were negative whereas those with depth and surface area were positive.

Local vs. regional influences

Plots of local vs. regional richness (native, translocated, autochthonous, exotic and total richness) are given in Fig. 2. Results from stepwise multiple-regression models developed to explain local species richness (native, translocated, autochthonous,

Table 3 Bivariate Pearson correlation coefficients between local native (LNaR), translocated (LTrR), exotic (LExR), autochthonous (LAuR) and total (LToR) species richness and lakes characteristics

	Altitude	log (Lake area)	log (Max depth)
LNaR	0.123	0.420***	0.414***
LTrR	-0.226*	0.217	0.124
LExR	-0.376***	0.092	-0.125
LAuR	0.020	0.542***	0.493***
LToR	-0.165	0.503***	0.357**

Natural and man-made lakes were pooled ($n = 76$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4 Results of stepwise multiple linear regression models of lakes species richness against regional richness and other independent variables. Lake area and depth were log-transformed. The regional richness entered is the one related to the local richness considered (the regional richness used as input for the LNaR model is RNaR, etc.). If the intercept of the unconstrained model was significantly positive we constrained the model through the origin and controlled for habitat effects by using the interaction terms (e.g. RToR' altitude) instead of direct terms as independent variables. R^2 values are not given for the constrained models because their value is artificially inflated. Table entries are regression coefficients

	Natural lakes ($n = 25$)					Man-made lakes ($n = 51$)				
	LNaR	LTrR	LAuR	LExR	LToR	LNaR	LTrR	LAuR	LExR	LToR
R^2	0.647	0.739	0.548			0.500	0.184	0.412		
Intercept	-12.1**	0.307	-0.005	—	—	-4.69**	0.359	-3.516	—	—
Regional richness	0.410**	0.116**	ns	ns	ns	0.218***	0.141**	0.168**	0.505**	0.295**
(Regional richness) ²	ns	ns	ns	ns	ns	ns	ns	ns	-0.022*	-0.004**
Log lake area	ns	ns	ns	0.018***	0.032***	0.896***	ns	1.000**	ns	0.018**
Altitude	ns	-0.002**	ns	-0.000*	ns	ns	ns	ns	ns	ns
Log max depth	1.21*	0.542**	2.104**	ns	ns	ns	ns	ns	ns	ns
LNaR	—	-0.116*	—	—	—	—	ns	—	—	—
LTrR	ns	—	—	—	—	ns	—	—	—	—
LExR	0.88**	ns	0.971**	—	—	ns	ns	ns	—	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant; variable not entered in model.

exotic or total) as a function of regional richness (native, translocated, autochthonous, exotic or total) and other independent variables are summarized in Table 4.

In the natural lakes, LNaR and LTrR were positively correlated to the appropriate regional richness variables. Controlling for RNaR, LNaR increased with log maximum depth and with the number of exotic species in the lake (LExR), while controlling for RTTrR, LTrR increased with log maximum depth, and decreased with altitude and with the number of native species (LNaR). Intercepts were either negative or not significantly different from zero, making it unnecessary to constrain the models to pass through the origin. LAuR was independent of regional richness and increased with log maximum depth and with the number of exotic species in the lake (LExR). LExR and LToR were both independent of the related regional richness variables, LExR increasing with log lake area and decreasing with elevation and LToR increasing only with log lake area. Note that, as intercepts of the last two models were both significantly greater than zero, we constrained regression lines to pass through the origin. LTrR and LNaR were negatively correlated whereas LExR was positively related to LNaR and to LAuR.

In the man-made lakes, LNaR, LTrR and LAuR were all positively correlated to the related regional richness variables. Controlling for RNaR, LNaR increased with log lake area. Controlling for RTTrR, LTrR was not related to any other independent variable. Controlling for RAuR, LAuR increased with log lake area. For both LExR and LToR, there was strong evidence of an asymptotic relationship between local and regional richness (Table 4). Note that, as the intercepts of the two models were both significantly greater than zero, we constrained regression lines to pass through the origin. Controlling for RTToR, LToR increased with log lake area.

DISCUSSION

Habitat-related patterns of species richness

Because the lakes are isolated from each other, our results can be interpreted in the context of island biogeography theory (MacArthur & Wilson, 1967; Barbour & Brown, 1974; Magnuson, 1976). Lake area and depth are indicators of within-lake space availability and habitat diversity. Their positive correlations with LNaR, LAuR and LToR are consistent with the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1967). Two major and nonexclusive explanations have been proposed to explain why more species exist in larger areas. The first, referred to as the area *per se* hypothesis (MacArthur & Wilson, 1967) considers species richness as a result of an equilibrium between immigration and extinction rates, which are both dependent on habitat size, i.e. the probability of extinction of a species increases as island size decreases, due to a decrease in total population size. The second one, referred to as the habitat diversity hypothesis (MacArthur & Wilson, 1967), suggests that larger areas contain a larger array of habitat configurations and food resources, thereby providing more niches and consequently favouring the coexistence of a large number of species (Williamson, 1988).

The negative correlation between altitude and richness in introduced species (measured by the variables LTrR and LExR) is more puzzling. However, the lakes located in the downstream parts of catchments are likely to experience the strongest anthropogenic stress because lowlands are the most densely populated areas in France and pollution fluxes tend to accumulate downstream. These conditions tend to increase, respectively, the probability of species introductions and the probability that

the introduced species get established due to environmental disturbances (Moyle & Light, 1996).

Definition of the regions and their species pools

Tests of community saturation based on plots of local vs. regional richness require samples taken from similar habitats at the local scale and assume that the whole regional pool could potentially colonize each sampling station if allowed by local biotic and abiotic conditions (Srivastava, 1999). This requires within-region connections of the sites allowing colonization migrations, which is largely true with our choice of hydrographic regions, although some of them pool coastal catchments. This division of the French territory displays reasonable within-region homogeneity, which is to a large extent explained by historical connections between catchments, particularly in downstream stretches during the latest ice ages (Keith, 1998). However, the connection between lakes is never that direct because it implies that species use rivers to migrate from one to the other. The likelihood of a fish species colonizing all the lakes within a region is therefore low, particularly since many dams have been built in the last decades.

Furthermore, the regional pool of species should be the pool of potential colonisers of the considered habitat, therefore excluding the species specialized to other types of habitat (Cornell & Lawton, 1992; Srivastava, 1999). In this context, our estimation of regional richness is likely to be slightly over-estimated because it encompasses purely riverine fishes. However, the distinction between purely riverine and purely lacustrine species is unclear, as attested by the presence in lakes of species usually considered as 'obligatory riverine species', e.g. by Penczak & Kruk (2000), which reflects the relatively low level of specialization of the western European fish fauna.

These considerations are related to the hypotheses underlying the interpretation of local-regional richness plots, but differ for native and introduced species because their spread, respectively, relies upon natural and human-mediated processes. The latter can be assumed to occur at a short time scale, a few decades, since most introductions were carried out since the 19th century (Persat & Keith, 1997), and are less likely to be disturbed by within-region alterations of the connectivity between lakes. The short time scale at which introductions have to be considered also tends to inflate the regional species pool faster (increase by one each time a new species is recorded at a single site) than the mean local richness, the delay corresponding to the time required for the new species to colonize the whole region.

Local vs. regional influences

Although analysing separately local-regional richness relationships for native, introduced and total richness is artificial (these three attributes belonging to a same community), this procedure provides insights into the processes contributing to structuring lacustrine fish communities.

The relationship between local and regional native richness for both natural and man-made lakes provided evidence of local

unsaturation of native species richness, and therefore of the dominance of regional factors over local ones in shaping natural fish communities. This does not mean that local abiotic effects were nonexistent, because log maximum depth or log lake area, two surrogates for habitat diversity (Magnuson, 1976; Eadie & Keast, 1984; Minns, 1989; Griffiths, 1997), also contributed significantly to the regression models (Table 4).

For both natural and man-made lakes, regional native richness accounted for more than two-thirds of the explained variation in local native richness (41% of 47% for natural lakes and 33% of 50% for man-made lakes), with the local variables log maximum depth or log lake area accounting for the remainder. The variation explained here by regional richness was much higher than observed by Griffiths (1997) for North American lacustrine fish communities (native regional richness accounted for 24% of 61% of the variation explained in local native richness). This result could be related to historical events. Western European fish communities have experienced drastic extinctions during the last Pleistocene ice-age (Moyle & Herbold, 1987; Matthews & Zimmerman, 1990; Oberdorff *et al.*, 1997). As a result, few congeneric species coexist at present in such communities compared to the situation in North America. If we assume that congeneric species have similar ecological niches, then they should be strong competitors, and competitive exclusion should occur more often among congeneric species than in more distantly related ones.

The hypothesis that regional richness is the key determinant of local richness was also supported in the case of translocated species for both natural and man-made lakes, as no sign of asymptotic relationships between local and regional translocated species richness was apparent in the models (Table 4). The influence of abiotic effects was demonstrated only for natural lakes by the inclusion of log maximum depth (positive effect) and elevation (negative effect) in the model. This last relationship could be related to a lower chance of introducing species in high elevation lakes or to an unsuitable environment for the establishment of these species (e.g. low temperature, typical of high elevation lakes, has been shown to influence negatively the success of introduced species (Baltz & Moyle, 1993)). Conversely, the hypothesis that regional richness is the key determinant of local richness was not supported for exotic species, as LExR was only dependent on abiotic factors in both natural and man-made lakes (Table 4).

When considering the number of autochthonous species (native and translocated species, LAuR) or the total number of species found (native, translocated and exotic species, LToR), slight differences were observed between natural and man-made lakes. With respect to natural lakes, whatever the measure of species richness (LAuR or LToR), no relationship appeared between local and regional richness. LAuR or LToR were, however, positively related to habitat diversity (measured by either lake area or maximum depth). This means that local factors dominate the regulation of these two measures of local diversity. On the contrary, the patterns of occurrence of autochthonous species (LAuR) in man-made lakes provided no evidence of saturation, while the asymptotic relationship found between

total local (LToR) and regional richness (RToR) suggested saturation of the community as a whole.

Effects of species introduction?

Lakes are islands of aquatic habitat separated by land barriers that inhibit colonization by fishes. Hence, because of their isolation, lakes and reservoirs provide good systems to assess the patterns and consequences of biological invasions on native communities. In our study, the species richness patterns for natural lakes indicated a regional control of native species while total richness would be controlled locally. If we admit that local extinctions of native species were negligible since introductions are essentially a recent phenomenon, the patterns of native species richness observed in our study reflect the preintroduction situation. Hence, such a pattern could result from an originally unsaturated community (regional control) being invaded by introduced species until the lakes' carrying capacity is reached (local control).

However, this hypothesis is supported neither by the positive correlation found between the local exotic and native species richness in natural lakes (which suggests little resistance of the native community to these distantly related invaders), nor by the published studies and reviews considering that all communities are susceptible to invasion by introduced species regardless of native species diversity (Moyle & Light, 1996; Williamson, 1996; Gido & Brown, 1999; Rathert *et al.*, 1999).

These apparent contradictions highlight the care required when drawing conclusions from local-regional richness relationships. It is reasonable to assume that most communities are neither totally saturated, nor proportional samples drawn from the regional species pool (Cornell & Lawton, 1992). The patterns observed in our study suggest such an intermediate situation.

CONCLUSION

Our results indicate that fish species richness in French natural and man-made lakes results from a combination of local, regional and anthropogenic influences. Species introductions can be regarded at the community level as an alteration of the balance between colonization and extinction rates. These practices have apparently contributed to saturate communities in these systems even if no clear negative effect on the survival of native species (i.e. species extinction) is detectable so far. We do not want to imply that biological invasions do not cause ecological changes like shifts in abundance and habitat distribution of native species, alteration of food webs, changes in ecosystem processes (Townsend, 1996), but rather that these effects cannot be detected from snapshot occurrence data because they proceed over longer time scales (Magnuson, 1976).

Setting up monitoring networks for lakes to meet the requirements of the European Water Framework Directive should allow better inference about these effects, but a precautionary principle should be the rule for it is now generally agreed that the establishment of a non-native species is an irreversible process and that importation of non-native species to many places

contributes to homogenize biodiversity at regional and global levels (McKinney, 2002).

ACKNOWLEDGEMENTS

We would like to thank the numerous persons and institutions who provided data for this study, Conseil Supérieur de la Pêche, Ecole Nationale Supérieure d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France. This work was funded by the Ministère de l'Ecologie et du Développement Durable. We are grateful to Bernard Hugué and an anonymous reviewer for helpful comments on earlier versions of the manuscript and to Xavier Irz for having improved the English.

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BIOSKETCHES

Pascal Irz has research interests in the patterns of fish species richness and community structure in relation to environmental and anthropogenic variables. Currently, he is carrying out a PhD project on assembly rules in lacustrine fish communities.

Christine Argillier is a fish researcher in Cemagref. Her research interests include population (particularly percids) and community ecology as well as behavioural topics, particularly in lacustrine environments.

Thierry Oberdorff works in community ecology for IRD. His research focuses on the role of the different spatial scales in the regulation of riverine fish communities. He is also interested in examining the consequences of anthropogenic effects on fish community structure and function.

P4: Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs?

Irz P., Odion M., Argillier C. & Pont D. (2006)

Aquatic Sciences, 68, 109-116

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Research Article

Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs?

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Received: 28 April 2005; revised manuscript accepted: 6 September 2005

Abstract. The European Water Framework Directive (WFD) aims at improving the ecological status of continental waters, including man-made water bodies. Thereby it raises the question of the reference conditions for reservoirs. A number of limnologists consider reservoirs as intermediate systems between lakes and rivers. Hence, the aim of this study is to contribute to the implementation of the WFD by comparing the fish communities across these three types of ecosystems. This was achieved using fish sampling data from 21 natural lakes, 50 reservoirs and 549 river stations. The lists of occurring species are very similar between lakes and reservoirs, and appear as a subset of the species occurring in rivers. Lakes and reservoirs are also very similar in terms of common and

rare species. Conversely, the comparison of community structures (summarised by correspondence analysis axes) supports the hypothesis of an intermediate position of reservoirs between lake and river systems. This latter result could reflect the effect of large-scale processes undergone by freshwater ecosystems whatever their type and the non-independence of water bodies within their catchments, particularly when considering the communities of highly mobile organisms like fishes. Although the major conservation concerns are about natural systems, artificial ones should also be considered in monitoring and assessment programs in order to allow efficient catchment-scale management policies.

Key words. Lentic system; lotic system; fish community; European Water Framework Directive; comparative analysis.

Introduction

The objective of the European Water Framework Directive (WFD) is to obtain the good ecological status of natural continental water bodies and the good “ecological potential” (EP) for artificial and heavily modified water bodies (European Community, 2000). Potentially, various methods can be implemented to define the maximum EP, how-

ever, the ECOSTAT working group proposed that “the maximum EP biological conditions should reflect, as far as possible, the biological conditions associated with the closest comparable natural water body type at reference conditions” (ECOSTAT, 2003). Accepting this position raises the question of how to choose the relevant natural hydrosystem type that will serve as a reference for reservoirs, which is a cross-ecosystem question. However, cross-ecosystem studies are not very common despite their interest in addressing the issue of generalisation in ecological patterns, mechanisms and theories (Pace, 1991). For example, cross-ecosystem studies provided a significant contribution to the debate on the relative strength of

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Published Online First: January 18, 2006

bottom-up vs. top-down controls of food chains (Chase, 2000; Pace et al., 1999; Shurin et al., 2002; Strong, 1992), on the response of ecosystems to disturbances (Fisher and Grimm, 1991) or on fisheries science and management (F.A.O., 1978). These kinds of studies also proved to be informative both on basic and applied issues when comparing freshwater ecosystem types (F.A.O., 1978; Ryder, 1978; Ryder and Pesendorfer, 1989).

Reservoirs are frequently termed artificial lakes and satisfy some of the definition criteria of lakes (Politou et al., 1993). Most of the major processes, i.e. internal mixing, nutrient uptake, primary production or predator-prey interactions, occur in both lakes and reservoirs (Thornton, 1990). However, in a review that contrasted the properties of natural lakes and reservoirs, Wetzel (1990) opposed a long list of ecological, hydrological, physico-chemical and morphological differences between these types of water bodies. Some limnologists also considered reservoirs as intermediate ecosystems between riverine and lacustrine environments (Gelwick and Matthews, 1990; Kimmel et al., 1990; Ryder, 1978) with regard to morphology and hydrology. Reservoirs can also be considered as having an intermediate status with regard to nutrient and organic matter supply (Kimmel et al., 1990).

Comparative ecological studies between rivers and reservoirs are not common in the scientific literature, maybe because they give rise to sampling issues. However, these systems are not so contrasted. River systems typically encompass both lentic and lotic waters and the upper zone of reservoirs is generally riverine (Thornton, 1990). In fact, the transition between typical riverine conditions and truly still waters takes place along a spatio-temporal continuum of hydraulic conditions. Therefore, conventional thresholds are used to define the geographical boundary between a reservoir and its tributaries or to classify the reaches of rivers influenced by a weir as lentic or lotic. However, ecological processes ignore these conventions and the issue of the “closest comparable natural water body” has to be addressed to assess reservoirs reference conditions for each of the biological elements taken into account in the WFD. Although the WFD considers reservoirs as parts of the “lake-type water bodies”, there is a risk that referring to lakes to assess the EP of reservoirs without considering alternatives could be a methodological mistake. Therefore, we investigated whether the analyses of fish community patterns in both lakes and rivers could be useful to assess the reference conditions for fish communities of reservoir systems. Thus, we developed a comparative study of the attributes of fish communities in these three types of systems. The hypothesis that reservoirs are intermediate systems between rivers and lakes, considered in a fish community perspective, leads to the hypothesis that they display intermediate patterns of 1. species occurrences 2. species commonness and rarity 3. fish community structure.

Materials and methods

The data set

The lakes and reservoirs data set was compiled from various sources (mostly unpublished study reports). In the absence of a national monitoring network, these studies addressed local concerns. Most of the surveys were carried out with gillnets but we also used fish censuses produced when the reservoirs were drained. Eventually, 50 reservoirs and 21 natural lakes were included. They range from sea level to 1100masl. Mountain lakes and reservoirs have been excluded from the analysis because they have been proven to have very different fish populations compared to lowland sites, mainly as a result of human-mediated introductions (Argillier et al., 2002). A more thorough description of the data set was made in previous papers (Argillier et al., 2002; Irz et al., 2004).

The 549 river stations data were extracted from the database held by the Conseil Supérieur de la Pêche, covering a period of 13 years of survey (1985 to 1998). All sites were sampled using electric fishing techniques during low flow periods. The size of each sampled site was sufficient to encompass complete sets of the local characteristic river habitat (generally >100m for wading sites and >500m for boat sites (Yoder and Smith, 1999)). Two main sampling strategies were used, depending on river size. When possible (river depth <0.7m), river reaches were sampled by wading (one passage). In large rivers, sampling was done by boat mainly in near shore areas. We only retained one fishing occasion per site. Sites belonging to the trout zone and sites characterized by the presence of only two species were excluded.

To limit the biases induced by the differences in sampling methods, fish communities were characterised by the presence/absence of the species. The river stations are well distributed throughout France, but the distribution of lakes and reservoirs is patchier (Figure 1). The main characteristics of the study sites display a strong heterogeneity (Table 1).

Sampling adequacy

One of the major concerns associated with comparisons of very different types of environments is the differences in sampling scheme. No single method allows an accurate fish sampling of both lentic and lotic systems, and it seems that the absence of the eel (*anguilla anguilla*) in both lakes and reservoirs is a consequence of the use of gillnets. The bitterling (*Rhodeus sericeus*) is also frequently too small to be effectively caught by gillnets unless they comprise very fine mesh (which was not the case in our data set, the lower limit generally being 10mm knot-to-knot).

However, it is quite commonly recognised that gillnetting is the most appropriate technique to sample fishes

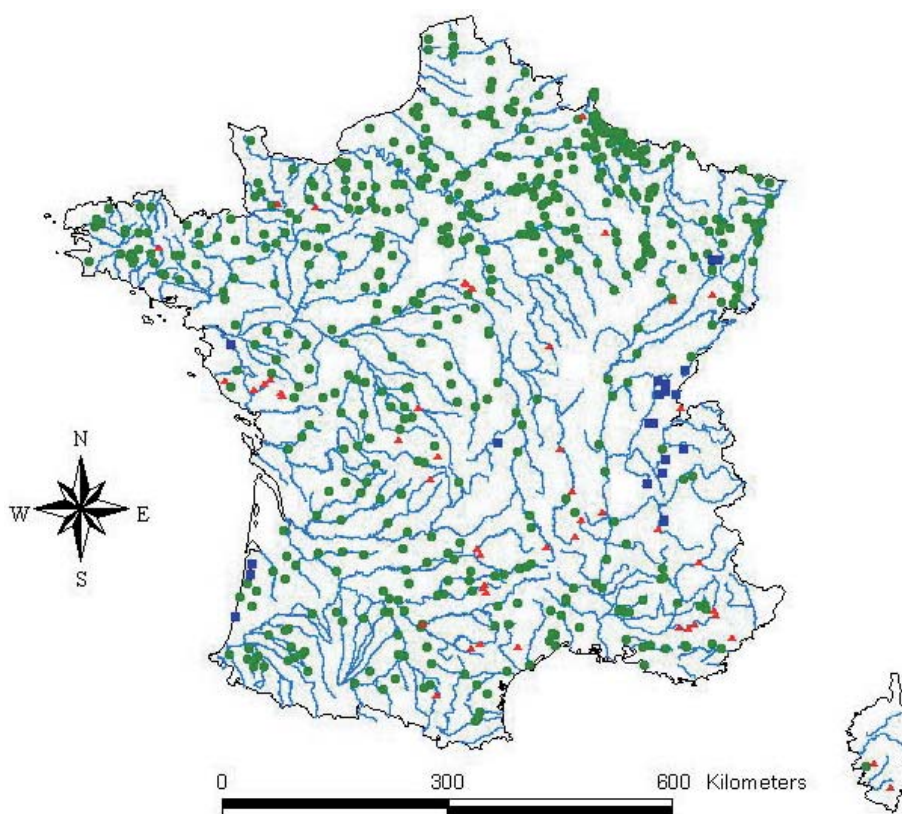


Figure 1. Location of the study sites on the French hydrographic network ■ natural lakes ▲ reservoirs ● river stations.

in lentic systems, as attested by the choice of the European Standardisation Committee to recommend a stand-

ardised gillnetting method to implement the WFD on lake-type water bodies (C.E.N., 2005), even though an extensive census of their species should also include complementary techniques in the shallows (US Environmental Protection Agency, 1998). Similarly, electrofishing is the most efficient technique for sampling fish in streams and rivers even if its efficiency decreases when river depth increases. Therefore, our cross-system comparison being based on appropriate techniques for each system type is likely to make sense despite the admitted sampling biases. Using a parallel with Pielou's (1977) consideration on the sampling biases in biogeographic studies, we could state that cross-ecosystem type comparative studies require the assumption that the signal-to-noise ratio of the data is high enough to ensure that, by appropriate statistical analysis, the signal may be recovered and correctly interpreted.

Table 1. Description of the study sites with the mean values, standard deviation and extreme values of the parameters.

	Parameter (unit)	Mean	S. D.	Max	Min
Lakes N = 21	Catchment area (km ²)	102	168	670	2
	Altitude (masl)	543	331	1,059	0
	Lake surface (ha)	1,199	2,079	6,500	7
	Maximum depth (m)	37	32	145	2.7
	Lake volume (Mm ³)	286	805	3,614	0.3
Reservoirs N = 50	Catchment area (km ²)	819	150	6,520	1
	Altitude (masl)	391	299	1,074	13
	Reservoir surface (ha)	334	565	3,200	4
	Maximum depth (m)	36	33	135	2
	Reservoir volume (Mm ³)	88	235	1,261	0.04
River st. N = 549	Catchment area (km ²)	2,135	7,354	68,000	2
	Altitude (masl)	155	142	935	2
	Slope (‰)	2.69	2.83	30	0
	Width (m)	18	34	350	1
	Mean air temperature (°C)	10.8	1.5	16	8

Analyses

The choice was made to use three different descriptors of lacustrine communities (list of occurring species, species occurrence rates and community structure) in order to obtain complementary views on fish community patterns (Samuels and Drake, 1997). The lists of occurring species were simply compared by distinguishing those that

were specific of a particular type of environment from those that were more widespread, and by calculating Jaccard's distances between the three types of systems based on the species occurrences.

In order to compare the patterns of rarity or commonness of species among the three types of systems, the relationship between the occurrence rates of the species in lakes, reservoirs and rivers were assessed using Spearman rank correlation. Cross-ecosystem similarities in the identity of the dominant and rare species are expected to produce positive correlations.

Then the fish occurrence matrices were analysed by means of Correspondence Analysis (CA) for each type of system. This ordination method allows a reduction of the dimensionality of the data set (Ter Braak, 1995). Hence, the first two CA axis of each analysis were considered as summaries of a primary and secondary between-site community structure. The six axes were then submitted to Spearman correlation analysis to assess to what extent

community structure was similar among system types. To limit the effects of rare species in the analyses, those with occurrence rates below 10 % were removed. All together 30 species were included in at least one of these analyses.

The mean species richnesses were compared among ecosystem type using ANOVA.

All statistical analyses were carried out with SPSS statistical package (SPSS Inc, 1999).

Results

Species occurrences and richnesses

The most common species (pike *Esox lucius*, roach *Rutilus rutilus*, perch *Perca fluviatilis* and tench *Tinca tinca*) are the same in lakes and reservoirs (Table 2). With occurrence rates over 75 %, these four species can be considered ubiquitous in lentic systems. Conversely, no single species attains such a rate in the river stations. The

Table 2. Occurrence rates of the fish species in natural lakes, reservoirs and river stations. Rates over 75 % are in bold.

Code	Common name	Scientific name	% occurrence lakes	% occurrence reservoirs	% occurrence rivers
ALBUAL	Bleak	<i>Alburnus alburnus</i>	33.3	40.0	32.2
ANGUAN	Eel	<i>Anguilla anguilla</i>	0	0	50.5
BARBFL	Barbel	<i>Barbus barbus</i>	0	18.0	32.4
RHODSE	Bitterling	<i>Rhodeus sericeus</i>	0	0	12.0
ABRASP	Bream	<i>Abramis sp.</i>	71.4	56.0	23.5
ESOXLU	Pike	<i>Esox lucius</i>	95.2	78.0	30.8
CYPRCA	Common carp	<i>Cyprinus carpio</i>	23.8	72.0	10.9
COTTGO	Bullhead	<i>Cottus gobio</i>	0	0	53.0
LEUCCE	European chub	<i>Leuciscus cephalus</i>	66.7	54.0	69.0
CORESP	Whitefish	<i>Coregonus sp.</i>	47.6	0	0
GASTAC	Three-spined stickleback	<i>Gasterosteus aculeatus</i>	0	0	15.5
PUNGPU	Ninespine stickleback	<i>Pungitius pungitius</i>	0	0	11.8
RUTIRU	Roach	<i>Rutilus rutilus</i>	100.0	96.0	60.8
GOBIGO	Gudgeon	<i>Gobio gobio</i>	28.6	30.0	72.9
GYMNCE	Ruffe	<i>Gymnocephalus cernuus</i>	28.6	26.0	9.1
CHONNA	Sneep	<i>Chondrostoma nasus</i>	0	0	13.5
BARBBA	Stone loach	<i>Barbatula barbatula</i>	0	0	69.9
LAMPEPL	Brook lamprey	<i>Lampetra planeri</i>	0	0	29.0
SALVAL	Arctic char	<i>Salvelinus alpinus</i>	19.0	2.0	0
AMEIME	Black bullhead	<i>Ameiurus melas</i>	9.5	24.0	7.5
PERCFL	Perch	<i>Perca fluviatilis</i>	95.2	96.0	42.1
LEPOGI	Pumpkinseed	<i>Lepomis gibbosus</i>	33.3	46.0	22.8
SCARER	Rudd	<i>Scardinius erythrophthalmus</i>	71.4	42.0	16.2
SANDLU	Pikeperch	<i>Sander lucioperca</i>	23.8	58.0	6.6
ALBUBI	Chub	<i>Alburnoïdes bipunctatus</i>	0	0	16.4
ONCOMY	Rainbow trout	<i>Oncorhynchus mykiss</i>	23.8	24.0	5.8
TINCTI	Tench	<i>Tinca tinca</i>	90.5	80.0	21.9
SALMTR	Common trout	<i>Salmo trutta</i>	52.4	38.0	58.1
PHOXPH	Eurasian minnow	<i>Phoxinus phoxinus</i>	0	0	62.8
LEUCLE	Dace	<i>Leuciscus leuciscus</i>	4.8	14.0	41.2

Table 3. Jaccard's distance matrix between the lists of species occurring in each of the three types of hydrosystems.

	lakes	reservoirs	rivers
lakes	0	0.10	0.43
reservoirs	0.10	0	0.38
rivers	0.43	0.38	0

Table 4. Spearman rank correlation between the occurrence rates of species (n = 30) in lakes, reservoirs and river stations. P-values are over the diagonal and correlation coefficients below.

	% lakes	% reservoirs	% rivers
% lakes		<0.001	0.709
% reservoirs	0.869		0.622
% rivers	0.071	0.094	

Table 5. Descriptive statistics of species richness in lakes, reservoirs and river stations.

	Nb	Mean	S.D.	Min	Max
Lakes	21	9.95	4.153	5	20
Reservoirs	50	10.02	3.248	4	16
Rivers	549	9.59	4.254	3	24

most widespread species in lotic systems are the gudgeon *Gobio gobio*, the European chub *Leuciscus cephalus* and the stone loach *Barbatula barbatula*. Ten species are river-specific (eel, bitterling, bullhead *Cottus gobio*, three-spined stickleback *Gasterosteus aculeatus*, nine-spine stickleback *Pungitius pungitius*, sneep *Chondrostoma nasus*, stone loach, brook lamprey *Lampetra planeri*, chub *Alburnoïdes bipunctatus* and Eurasian minnow *Phoxinus phoxinus*) while only the whitefish *Coregonus sp.* is lake-specific in this data set (present in 47.6% of the lakes). All the species found in reservoirs are also present in either or both lakes and rivers. On the basis of Jaccard's index, the lists of occurring species are much more similar between lakes and reservoirs than between lentic systems and rivers (Table 3). The 0.10 distance between lakes and reservoirs (Table 3) indicates that 90% of the species are common between these types of systems.

The correlation analysis of the occurrence rates of the species among system types (Table 4) confirms that the species that are widespread in lakes are also widespread in reservoirs but that the occurrence rate of species in lotic systems was independent of that in lentic ones.

Therefore, it is clear that more species occur in rivers (28) than in lentic systems (20) although this might be biased due to a higher number of the former than of the latter in our data set, and that both types of lentic systems display very similar patterns of species occurrences.

However, there is no significant difference in the mean local species richness among ecosystem types (ANOVA, $p = 0.736$; Table 5).

Community structure

The first axis (primary structure) of the CA carried out on reservoirs displays an opposition between the arctic char *Salvelinus alpinus* and a group composed of the black bullhead *Ameiurus melas*, ruffe *Gymnocephalus cernuus* and pumpkinseed *Lepomis gibbosus* on the first axis. The secondary structure opposes the dace *Leuciscus leuciscus* to the black bullhead and the arctic char.

The analysis on river stations opposes the brook lamprey, brown trout *Salmo trutta*, ninespine stickleback to the bitterling and bream *Abramis sp.* (Table 6). The second axis (secondary structure) opposes the ninespine stickleback and rudd *Scardinius erythrophthalmus* to the chub, barbel *Barbus barbus* and sneep.

In lakes, the primary structure opposes the black bullhead to the whitefish while the second axis opposes the dace to a group of species such as the ruffe, rudd, and pikeperch *Sander lucioperca*.

The correlations between the species scores on the axis of the three analyses above can be interpreted in terms of cross-ecosystem similarity in the community structures (the sign of the coefficients has no meaning because CA axes are not oriented). The first axis of reservoirs was significantly correlated with all four axes of rivers and lakes analyses (Table 7), the strongest correlation being with the first CA axis of lakes. There is also a strong correlation between the second axis of lakes and rivers.

Discussion

Cross-ecosystems comparisons

Our initial hypothesis was that the fish communities of reservoirs would display intermediate patterns between those of lakes and river stations with respect to 1. species occurrences 2. species commonness and rarity 3. fish community structure. Considering the first two points, reservoir fish communities are clearly more similar to the communities of natural lakes than to those of river stations. The lists of species dwelling in the two types of lentic systems are almost identical and clearly divergent from that of rivers. Apart from the two lake specialists (*Salvelinus alpinus* and *Coregonus sp.*), the list of lentic species is a subset of the lotic species list, which is likely to result from historical influences. The western European fish fauna has been quite depauperated since the last ice age drove many species to local extinction. At the scale of a large catchment (i.e., with sufficient latitudinal and/or altitudinal extension), a population of a river species can respond to climatic variations through an adaptation of its

Table 6. Species scores on the first two axes of the CA of fish assemblages performed separately for river stations (F1rivers and F2rivers), lakes and reservoirs. Species codes refer to Table 2.

Code	F1 rivers	F2 rivers	F1 lakes	F2 lakes	F1 reservoirs	F2 reservoirs
ALBUAL	0.70	-0.19	-0.51	0.74	0.19	-0.63
ANGUAN	-0.06	0.22				
BARBFL	0.39	-0.74			1.16	0.00
RHODSE	0.92	-0.08				
ABRASP	0.92	0.45	-0.15	-0.14	-0.36	-0.49
ESOXLU	0.42	0.19	0.15	-0.23	-0.24	0.12
CYPRCA	0.71	0.62	-0.77	-0.06	-0.31	0.20
COTTGO	-0.79	0.16				
LEUCCE	0.16	-0.18	0.38	0.23	0.58	-0.28
CORESP			0.70	0.28		
GASTAC	-0.51	-0.15				
PUNGPU	-0.90	1.12				
RUTIRU	0.37	0.07	0.18	-0.26	-0.01	0.18
GOBIGO	0.04	-0.15	0.16	0.83	1.09	0.24
GYMNCE			-1.04	-0.48	-0.58	-0.28
CHONNA	0.65	-0.74				
BARBBA	-0.39	-0.15				
LAMPEPL	-1.17	0.45				
SALVAL			-0.02	0.94	2.39	0.58
AMEIME			-1.82	0.05	-0.88	0.66
PERCFL	0.51	0.24	0.30	-0.26	-0.04	0.13
LEPOGI	0.67	0.42	-0.68	0.23	-0.50	0.23
SCARER	0.88	0.96	0.08	-0.32	-0.09	-0.08
SANDLU			-1.32	-0.35	-0.39	-0.37
ALBUBI	0.27	-0.98				
ONCOMY			-0.74	0.58	0.97	0.40
TINCTI	0.72	0.66	0.21	-0.16	-0.05	0.31
SALMTR	-0.99	0.05	0.38	0.35	0.94	-0.12
PHOXPH	-0.50	-0.28				
LEUCLE	0.19	-0.39	-0.55	1.69	-0.20	-1.46

Table 7. Spearman rank correlations between the species scores in the CA of fishes occurrences in river stations, lakes and reservoirs. P-values are above the diagonal and correlation coefficients below (*significant at the 0.05 level; **significant at the 0.01 level). The sign of the coefficients has no meaning because CA axes are not oriented. The analysis includes only the species that are common between the two types of systems compared, i. e. for lakes and rivers, n = 13; for lakes and reservoirs, n = 18 and for rivers and reservoirs n = 14.

	F1 rivers	F2 rivers	F1 lakes	F2 lakes	F1 reservoirs	F2 reservoirs
F1rivers		0.42	0.10	0.09	0.02	0.81
F2rivers	0.17		0.66	0.01	0.02	0.10
F1lakes	-0.48	-0.14		0.65	0.01	0.83
F2lakes	-0.48	-0.70**	0.11		0.02	0.59
F1reservoirs	-0.63*	-0.63*	0.63**	0.53*		0.52
F2reservoirs	0.07	0.46	-0.05	0.14	0.16	

geographic range (Gaston, 2003), for example by reaching refugial zones. Conversely, lakes are frequently regarded as biogeographic islands due to their relative isolation from each other (Barbour and Brown, 1974; Magnuson, 1976; Magnuson et al., 1998). Thus, typical

lacustrine species have restricted means to escape an environment becoming less and less favourable. Therefore, it appears reasonable to assume that lacustrine species, if they existed in Western Europe before the last ice age, have undergone higher extinction rates than riverine ones.

Furthermore, the post-glacial westward re-colonisation of fishes from the Danubian refugial zones occurred through the hydrographic network, which means that even for those lentic species that maintained populations in refugial zones, re-colonisation through this unfavourable network of flowing waters was unlikely.

The primary structure of reservoir fish communities displays similarities with all four axes of the analysis carried out on rivers and lakes, which supports our initial hypothesis. Drawing conclusions would have been easier with clear correspondences with either and not both the primary or secondary structure of lakes and rivers (e.g. the reservoirs primary structure corresponds to the lakes secondary structure). However, this rather confused pattern of interrelationships between the community structures could reflect the effects of large-scale phenomena on the fish communities. The response to large-scale environmental gradients (e.g. temperature) or the cross-catchments variations in species pools is likely to generate similar patterns whatever the type of ecosystem.

The secondary community structure of reservoirs was correlated with neither lakes' nor rivers' CA axes, thereby indicating a different pattern or an absence of pattern (e.g. this might be due to stochastic events such as human-mediated species introductions or unpredictable water level fluctuations).

Conversely, the secondary structure of fish communities in the two types of natural systems was quite similar, thereby suggesting common underlying processes. Although opposed in terms of hydrology, lakes and rivers share a common natural origin that may account for this similarity. When compared to reservoirs that are "recent" systems (on an ecological time scale) undergoing rapid aging processes (Kubecka, 1993; Popp et al., 1996; Thouvenot et al., 2000), natural systems may be considered as "mature" systems. This means that a number of processes underlying community structure, such as competitive interactions or colonisation events, may not have operated long enough to generate community patterns in reservoirs. Consequently, the observation of natural systems is of no help in analysing the secondary structure of reservoirs' fish communities.

The fact that the patterns in fish community structure are not so contrasted between the three types of ecosystems could further reveal that lakes, rivers and reservoirs are not independent from each other. They are all components of catchments and interconnected in a network. The catchment corresponds to the natural borders within which freshwater fish populations express their dynamics. Several of the species that were found in lakes and reservoirs are considered as typically riverine and do not reproduce in these systems (Penczak and Kruk, 2000). Hence, considering stream reaches, lakes or reservoirs as isolated from each other does not take into consideration the high mobility of fishes compared to most other fresh-

water organisms, particularly in the Western European context in which the majority of the fishes, even those dwelling lentic systems, are of lotic origin.

Conclusions

The initial hypothesis that reservoirs were intermediate environments between natural lakes and rivers was only partially supported by the results obtained in our study. We highlighted both differences and similarities in the patterns of fish communities among ecosystem types. The conclusions drawn on the basis of species occurrences, commonness and rarity, and community structure were quite different, thereby confirming the complementarity of these descriptors of the communities (that are also likely to respond differently to anthropogenic stresses). To some extent, this is also the spirit of the WFD that states that several attributes of fish communities must be taken into consideration for the assessment of the ecological status of water bodies. Using continuous descriptors of the hydraulic conditions (e.g. water velocity, Froude number) is certainly a perspective that should allow the simultaneous consideration of a wide array of hydrosystems regardless their type.

The present study carried out on fish does not mean that the other biological compartments follow equivalent rules, but suggests that the *a priori* choice of natural lakes as references for reservoirs may be questionable.

Despite the close deadlines scheduled in the implementation of the WFD, the studies aiming at proposing reference conditions for reservoirs are rare as most efforts have been concentrated on natural environments that represent major conservation concerns. However, reservoirs also represent important environments particularly in southern Europe (in France, around 90% of the lake-type water bodies over 50ha are artificial) that should not be neglected if one wishes an efficient catchment-scale management policy.

Acknowledgments

We would like to thank the numerous persons and institutions who provided data for this study, Conseil Supérieur de la Pêche for the major part of the dataset, and also Ecole Nationale Supérieure d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France. Nicolas Poulet, Jean-François Holley and Emmanuel Poncet provided useful comments on the draft. Our research program on the scientific developments for the implementation of the WFD on lentic systems is supported by the French "Ministère de l'Ecologie et du Développement Durable".

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P5: Partitioning the variability in fish metrics into environmental and anthropogenic components for the bioassessment of Northeast U.S.A. lakes and reservoirs

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Ce manuscrit sera complété pour :

- *mieux décrire les sites d'études,*
- *évaluer l'impact des espèces introduites sur les résultats,*
- *intégrer une réflexion sur le choix des traits et la façon de calculer les métriques,*
- *intégrer les résultats d'une étude méthodologique qui a montré que les méthodes d'analyses (modèles linéaires, GLM) influençaient peu les résultats.*

Partitioning the variability in fish metrics into environmental and anthropogenic components for the bioassessment of Northeast U.S.A. lakes and reservoirs

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Running title: Fish metrics for lakes and reservoirs

Keywords: Biological monitoring, lentic systems, impoundment, impact, variance partitioning, functional guilds, land use, index of biotic integrity.

7096 words including title page, abstract, references, tables and figures.

Abstract

1. Attempts to develop fish-based bioassessment tools are far less numerous on lentic than on lotic systems. Two major difficulties arise in such work: (i) choosing the relevant variables to describe the biotic, environmental and anthropogenic data sets and (ii) 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 and reservoirs of northeast USA.
2. Fish surveys, environmental features (ENV) and catchment-scale descriptors of anthropogenic stresses (ANT) were collected for 113 natural lakes and 58 reservoirs.
3. Fish metrics were calculated as percentages of species belonging to reproductive, trophic, and tolerance guilds and regressed against ENV and ANT variables. The variation in each metric was partitioned into environmental and anthropogenic components.
4. The response of the metrics to perturbations was clearly different between natural lakes and reservoirs. In lakes, metrics displayed clear response to urbanisation pressure, mainly for reproductive guilds based metrics. In reservoirs, intolerant and benthophageous species proportions metrics exhibited responses to urbanisation and agricultural pressures respectively.
5. *Synthesis and applications.* Fish communities appear valuable for the bioassessment of both lakes and reservoirs; however, they display different responses to anthropogenic stressors and hence require the development of distinct evaluation tools.

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 the socio-economic development. The idea that the alteration of ecosystems' functioning could strongly affect the human uses of these systems widened the stakes in environmental conservation (Baron *et al.*, 2002). Of 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 as a prerequisite to 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 U.S.A.). 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 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” (Karr & Dudley, 1981). Although this is an ecosystem-level definition, most studies assessing ecological integrity rely upon community-, guild- or population-level indicators.

Attempts to develop fish-based Indices of Biotic Integrity (IBIs) for the bioassessment of lentic systems are far less numerous than on running waters (Dionne & Karr, 1992; Hughes *et al.*, 1992; Minns *et al.*, 1994; Jennings *et al.*, 1995; Jennings *et al.*, 1999; Whittier, 1999; Appelberg *et al.*, 2000; Drake & Pereira, 2002). Most of these studies were only preliminary even if some assessed the response of individual fish metrics to anthropogenic stresses undergone by lakes such as acidification (Appelberg *et al.*, 2000), eutrophication (Jennings *et al.*, 1999) or land use (Drake & Pereira, 2002). However, a major difficulty in identifying which bioassessment metrics perform best (those that clearly respond to anthropogenic pressures) is that these metrics generally also display natural patterns of variation (Karr *et al.*, 1986; Karr, 1999; Smogor & Angermeier, 1999; Oberdorff *et al.*, 2002). Therefore, it is necessary to adjust the metrics to account for this natural variability before analysing their relationship with anthropogenic stresses, which has not or only partially (i.e. adjusting metrics to a single environmental gradient) been done in the previous studies dealing with standing waters.

The question of the bioassessment of reservoirs is becoming more topical, as dam building continues at the global scale (Dynesius & Nilsson, 1994; Nilsson *et al.*, 2005). In some regions, reservoirs represent a major component of the aquatic ecosystem (e.g., in France, around 350 of the 400 lentic freshwater bodies over 50ha are reservoirs). These systems frequently undergo rapid alteration processes (e.g. siltation, eutrophication, biological invasions) that eventually could compromise the services and commodities they provide. Because they are entirely artificial environments, “natural reference condition” has no meaning (USEPA, 1998) and the concept of biotic integrity is not directly transposable to

reservoirs. However, the development of tools to support decision making is as necessary to ensure the sustainability of their water and biological resources as it is for natural lakes.

Thus, the aims of the present study are (i) to assess the response of northeast USA lake and reservoir fish metrics to anthropogenic pressures when environmental variability is controlled for and (ii) to compare the responses of these metrics between the two types of ecosystems in order to evaluate to what extent natural lakes and reservoir ecosystems could be considered in a same way from an ecological monitoring point of view. Because good quality data on lentic fish communities are lacking in southern Europe, we believe this study of Northeast USA lakes 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 northeastern U.S. lakes by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) (Baker *et al.*, 1997). The lakes were selected using a probability design to be representative of regional conditions (Larsen *et al.*, 1994). Fish surveys were carried out in summer using gill nets, trap nets, minnow traps, and beach seines (Baker *et al.* 1997). Data for all gear were combined. 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. The level of sampling effort was determined by lake size and ranged from one to 10 sets of each passive gear and up to six seining sites. Fish were identified to species and counted.

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

Ten traits were derived from the community guilds: four from the trophic guilds (piscivorous, invertivorous, omnivorous and benthivorous, see table 2), four from the reproductive guilds (litho-psammophilous, phytophilous, guarder and diadromous, see table 3) and two from the tolerance guilds (tolerant and intolerant). Using species' migratory and parental care characteristics is not common in IBI metrics but we hypothesised that these traits, being

important features of the species life-history strategies, might display responses to anthropogenic disturbances (Winemiller & Rose, 1992).

Metrics were then expressed as proportions of species (i.e., number of species sharing a trait divided by the total number of species in the sample). The total number of guild-based metrics was therefore 10, to which the total species richness metric was added (Table 4). 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 estimates for fish in deep and heterogeneous environments, such as lakes and reservoirs, always gives rise to sampling issues (Jackson & Harvey, 1997).

Catchment-scale measures of land use and anthropogenic pressures were obtained from digitised maps. The assemblage and habitat data analysed here are available at the EMAP website (<http://www.epa.gov/emap/html/data/surfwatr/data/nelakes>).

Analytical procedure

The procedure was designed (i) to analyse the relationship between the fish communities and the environmental and anthropogenic features of the lakes and (ii) to partial out 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 5) and the correlation among them required factor analysis to reduce dimensionality and avoid collinearity. This was achieved by means standardised principal component analysis (PCA). The principal components (PCs) are independent from each other and summarise 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 anthropogenic pressures related to urbanisation were highly correlated (both for lakes and reservoirs), therefore, they were synthesised 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 whereas the percentage of land occupied by mining activities (MINE_TOT) was encoded as a binary (presence / absence) variable, because most values were null, and entered in the regression as an independent factor.

Each fish metric was transformed to $\arcsine\sqrt{X}$ and regressed against the environmental and anthropogenic variables in multiple linear regressions (MLR). This transformation is

classically recommended for percentage variables (Sokal & Rohlf, 1994). The significance of the models was assessed using F-test.

Variance partitioning was then carried out for each fish metric following the four steps recommended by (Legendre & 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^2_1 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^2_3 measured [a]+[b]+[c].
- Step 4: Each component was obtained by subtraction: [a]= $R^2_3-R^2_2$; [b]= $R^2_1+R^2_2-R^2_3$; [c]= $R^2_3-R^2_1$; [d]= $1-R^2_3$.

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 & Legendre, 1998).

All analyses were computed with R software (Ihaka & Gentleman, 1996) and carried out separately for natural lakes (including “augmented lakes”, i.e. lakes that existed before European settlement that have been deepened by >30%) and reservoirs because a preliminary analysis had shown that both environmental and land use variables differed between these two types of systems. Seepage lakes and quarries were uncommon in this region and were omitted from these. Natural lakes and reservoirs with a total species richness of three or less were also omitted because IBI metrics have little chance to be relevant for species depauperate sites (Fausch *et al.*, 1990). The final data set included 113 natural lakes and 58 reservoirs. As some of the sites had been surveyed on more than one occasion, and in order to avoid sampling biases, we only included in the analysis the first sampling visit.

Results

Analysis of the environmental variables

The PCA carried out on the environmental variables (Table 6) showed that the variables related to the lakes’ size were strongly correlated and contributed to the first environmental PC (env1) for both natural lakes and reservoirs. The second axis (env2) was also similar between the two types of lakes. It summarised the geographical location of the lakes, with the

variables related to the altitude and straight-line distance to the sea. Axis 3 (env3) was different between natural lakes and reservoirs. It carried the rainfall regime for the former and the retention time for the latter, but their eigenvalues were rather low (corresponding to 13% and 12% of the total variance respectively).

Response of fish metrics to environmental and anthropogenic influences

For natural lakes, four of the eleven candidate fish metrics displayed a response to anthropogenic land-use pressures (Table 7). The only type of pressure significantly contributing to the models was Urb_PCA, indicating the predominance of catchment urbanisation as an impacting force. Lakes with urbanised catchments displayed a decrease in the percentage of diadromous species (%_Sp_Diad) and an increase in the proportion of phytophilous (%_Sp_Phyto), guarder (%_Sp_Guarder) and piscivorous (%_Sp_Pisc) species. Apart from %_Sp_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 anthropogenic pressures. The main natural factor contribution to the models was the lake size (env1). The strongest response to anthropogenic pressure was the increase in %_Sp_Guarder, with 29% of the variance attributed to the anthropogenic variables, then %_Sp_Phyto with 12% and %_Sp_Diad with 10%. Three of the four models displaying response to anthropogenic pressures were related to the reproductive requirements, combined with a single trophic structure metric (%_Sp_Pisc).

For the reservoirs, only two of the eleven metrics were significantly related to the anthropogenic pressures. The proportion of benthivorous (%_Sp_Benth) increased with agricultural land use and that of intolerant species (%_Sp_Intol) decreased with the urbanisation pressure. The proportion of the variance attributed to “pure” anthropogenic effects was respectively 6% to 14%. Only the %_Sp_Benth model included significant environmental coefficients, increasing with reservoir size.

Mines are uncommon in the region, so it was not surprising that the presence of mining activities in the catchments did not appear as a major stressor for the fish communities.

Discussion

Choice of the metrics

Candidate metrics based on trophic, reproductive and tolerance guilds responded to anthropogenic pressures, but species richness did not. The absence of clear impact on species richness 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.*, 2004b), to a decrease due to the extirpation of habitat sensitive taxa (Corbacho & Sanchez, 2001). It is also clear that lacustrine species richness is strongly influenced by zoogeographic factors not controlled for in our analysis (Griffiths, 1997; Irz *et al.*, 2004a). However, this metric is one of the most frequently included in IBIs (Hughes & Oberdorff, 1999; Belpaire *et al.*, 2000). Including non-responsive metrics in an index means increasing the noise in the data and hence alters its ability to detect or assess the impact of anthropogenic 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 & Hughes 2001) are unlikely to be optimised in terms of indicator properties.

The reproduction-based metrics were those that most frequently significantly contributed to the models although they are not commonly included in IBIs (Karr *et al.*, 1986; Karr, 1991; Hughes & Oberdorff, 1999). The availability of suitable spawning habitats is certainly one of the major factors driving the fish (and guilds) species distributions in freshwater systems. These results indicate that the alteration of these habitats is likely to be responsible for major impacts on lentic fish communities.

The trophic structure of the fish communities also displayed relationships with the anthropogenic pressures. This was consistent with the frequent inclusion of trophic metrics in IBIs (Hughes & Oberdorff, 1999; Belpaire *et al.*, 2000) and has been previously suggested with a different analytical procedure on a sub-sample of the present data set (Whittier, 1999), and on other lentic systems (Jennings *et al.*, 1999; Drake & Pereira, 2002). This was expected considering the relative temporal stability of lentic systems as compared to lotic ones. Environmental stability is generally considered as promoting within-community interactions (competition, predation) and consequently gives rise to trophically structured communities whereas the physical stress exerted on stream fish communities as a result of hydrological variability is frequently considered as maintaining less interactive communities (Hugueny &

Paugy, 1995; Grossman *et al.*, 1998; Oberdorff *et al.*, 1998). Thus, on a conceptual basis, the trophic structure of lentic fish communities was expected to reflect their human-mediated alterations. However, it is possible that the tolerant species obscure the response of communities to human pressures, which has led some authors to omit these taxa for the calculation of trophic-based metrics (Angermeier *et al.*, 2000).

The tolerance metrics did not display a clear response to anthropogenic pressures, apart from %_Sp_Intol on reservoirs. Most of the fish-based IBIs include tolerance metrics (Hughes & Oberdorff, 1999; Belpaire *et al.*, 2000) that frequently exhibit clear relationship with the pressures. In our study, the choice was made to use the fish species tolerance rating according to (Halliwell *et al.*, 1999) rather than according to (Whittier & Hughes, 1998; Whittier, 1999). Although these latter studies were dedicated to the fish communities of our study area lakes, 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 the 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 some particular type of environment (e.g. at the edges of its distribution area (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 anthropogenic stresses and to analyse the response of tolerance metrics to the same stresses would have led to a circular reasoning. Experimental tests of sensitivity to specific stresses would ensure the independence between the assessment of the 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.

Although various studies have reported adverse ecological, histological, pathological or physiological effects of mining effluents on lake fish communities (Wong *et al.*, 1999; Moiseenko & Kudryavtseva, 2001; Holopainen *et al.*, 2003; Tkatcheva *et al.*, 2004), on this set of lakes and reservoirs, the presence of mining activities in the catchments did not appear as a major stressor for the fish communities (as we described it). This may reflect the fact that point-source pollutions have too local effects to be correctly assessed by broad-scale studies.

Comparison between natural lakes and reservoirs

The present results can also contribute to the development of bioassessment tools for reservoirs, and more generally for artificial water bodies. This is particularly topical in Europe due to the progressive implementation of the Water Framework Directive (WFD) that aims at obtaining good ecological status of natural continental water bodies and good « ecological

potential » for artificial water bodies (European Community, 2000). Several approaches could be developed to define good ecological potential for each reservoir, and it has been tempting to consider natural water bodies as references for artificial ones (ECOSTAT, 2003; Irz *et al.*, in press). However, it is clear from the results presented here that such an approach is questionable. Although natural lakes and reservoirs both meet the generic definition of lakes, the response of their fish communities to anthropogenic stresses was clearly distinct in the present study. Most of the major processes, for example internal mixing, nutrient uptake, primary production or predator-prey interactions, occur in both lakes and reservoirs (Thornton, 1990). However, in a review that contrasted the properties of natural lakes and reservoirs, (Wetzel, 1990) presented a long list of ecological, hydrological, physico-chemical and morphological differences between these types of water bodies. For example, the living communities dwelling reservoirs, having to deal with frequent and erratic disturbances, are generally dominated by organisms with broad eco-physiological tolerance (Wetzel, 1990). Many of the other contrasts were confirmed by a study on the sites included in the present study (Whittier *et al.*, 2002). Hence, it is not surprising that reservoir fish communities exhibit responses to land-use disturbances that are different from that of natural lakes. It is also true that in the data set we used, the urban land use is more important in the catchments of natural lakes than in that of reservoirs (Whittier *et al.*, 2002). This might be the reason for the predominance of Urb_PCA in the lakes' metrics models as well as of the differences among ecosystem type in the lists of metrics significantly responding to the pressures.

Last but not least, introduced fish species are more frequent in reservoirs than in natural lakes (Whittier *et al.*, 2002). The contribution of these introduced species to the variations in the metrics is certainly important due to their particular biological traits (e.g. they are frequently piscivorous species) and to their impacts on the native prey species is generally important (Whittier *et al.*, 1997).

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 & Schluter, 1993; Oberdorff, 1999). However, if the processes structuring living communities range from local to global, then conservation strategies need to take these scale-issues into account (Turner, in press). Thus, it is important to develop large-scale tools for the assessment of the ecological integrity of ecosystems and for their restoration.

The spatial scale is also important when considering the assessment of anthropogenic pressures. The functioning of freshwater ecosystems is tightly dependant upon the catchment from which they receive most of their inputs (Baron *et al.*, 2002), but also upon their connectivity with the downstream river network from which they receive most of the colonist species and upon local human uses. In our study, only the catchment was considered. Thus, the metrics that display no link with the anthropogenic pressures at the catchment scale in our study could respond to other local pressures such as hydroelectricity production, power boating, and flood control, as well as broad-scale pressures.

Conclusion

The pioneering works on IBIs have been carried out at limited spatial scale in order to mitigate the “uncontrolled” larger-scale processes. However, appropriate statistical methods have proved that the natural variability in the bioassessment tools could be accounted for, thereby allowing working at multiple basins and ecoregions scales (Oberdorff *et al.*, 2002; Pont *et al.*, in press). Regression models and variance partitioning of the community metrics proved to be efficient techniques to deal with such difficulties and to quantify the relative effects of environmental and anthropogenic sets of variables. This opens new perspectives for the development of assessment tools for lentic systems in lake-poor regions, such as southern Europe, in which 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 anthropogenic stresses.

Acknowledgements

Nicolas Poulet provided constructive comments on the initial manuscript. Emmanuel Poncet was of great help for the statistical analysis and programming. This study was funded by Cemagref through its Etat Ecologique Action and by the French Ministère de l’Ecologie et du Développement Durable. The authors are grateful to the US EPA for making the EMAP data set available. Although the data on Northeast USA lakes have been funded wholly or in part by the U.S. Environmental Protection Agency through its EMAP Surface Waters Program, it has not been subjected to Agency review, and therefore does not necessarily reflect the views of the Agency and no official endorsement of conclusions should be inferred.

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Legends

Table 1: Assignment of the fish species into trophic, reproductive and tolerance guilds. The codes refer respectively to tables 2 and 3 for the trophic guilds and reproductive guilds. Tolerance guilds are from Halliwell et al. 1999. I: intolerant, MT: intermediate tolerance, T: tolerant.

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

Table 3: Correspondence between reproductive guilds and the modalities used to derive the metrics.

Table 4: Description of the fish metrics.

Table 5: Environmental and anthropogenic variables included in the analysis.

Table 6: Principal Components Analysis carried out on the environmental variables. Table entries are the variables scores on the first three axis of the PCA. Those loading most heavily on each PC are in bold.

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

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 & Legendre (1998).

Table 1

Species	Trophic guild	repro guild	Tolerance	Species	Trophic guild	repro guild	Tolerance
<i>Acantharchus pomotis</i>	CI	B.2.5	MT	<i>Lota lota</i>	BI	A.1.2	MT
<i>Alosa pseudoharengus</i>	KI	A.1.4	MT	<i>Luxilus cornutus</i>	GF	A.2.3	MT
<i>Ambloplites rupestris</i>	IC	B.2.2	MT	<i>Margariscus margarita</i>	GF	A.1.3	MT
<i>Ameiurus catus</i>	TC	B.2.7	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	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	T	<i>Moxostoma valenciennesi</i>	BI	A.1.3	I
<i>Aphredoderus sayanus</i>	CI	C.1.4	MT	<i>Notemigonus crysoleucas</i>	GF	A.1.5	5
<i>Aplodinotus grunniens</i>	GF	A.1.1	MT	<i>Notropis bifrenatus</i>	CI	A.1.5	I
<i>Carassius auratus</i>	BI	A.1.5	T	<i>Notropis heterodon</i>	CI	A.1.5	I
<i>Carpoides cyprinus</i>	GF	A.1.2	T	<i>Notropis heterolepis</i>	BI	A.1.5	I
<i>Catostomus catostomus</i>	BI	A.1.2	I	<i>Notropis hudsonius</i>	BI	A.1.2	MT
<i>Catostomus commersoni</i>	GF	A.1.2	T	<i>Notropis rubellus</i>	CI	A.2.3	I
<i>Coregonus artedi</i>	KI	A.1.1	I	<i>Notropis volucellus</i>	GF	A.1.5	MT
<i>Coregonus clupeaformis</i>	BI	A.1.2	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	I
<i>Cyprinus carpio</i>	BG	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>Enneacanthus chaetodon</i>	CI	B.2.2	I	<i>Phoxinus eos</i>	GF	A.1.5	MT
<i>Enneacanthus gloriosus</i>	CI	B.2.2	I	<i>Phoxinus neogaeus</i>	IN	A.1.4	MT
<i>Enneacanthus obesus</i>	CI	B.2.2	I	<i>Pimephales notatus</i>	GF	B.2.7	T
<i>Erimyzon oblongus</i>	GF	A.1.2	I	<i>Pimephales promelas</i>	GF	B.2.7	T
<i>Esox lucius</i>	TC	A.1.5	I	<i>Pomoxis annularis</i>	IC	B.2.5	T
<i>Esox niger</i>	TC	A.1.5	MT	<i>Pomoxis nigromaculatus</i>	IC	B.2.5	MT
<i>Etheostoma fusiforme</i>	BI	A.1.5	I	<i>Pungitius pungitius</i>	CI	B.2.4	MT
<i>Etheostoma olmstedi</i>	BI	B.2.7	MT	<i>Rhinichthys atratulus</i>	BI	A.1.2	T
<i>Exoglossum maxillingua</i>	BI	B.2.3	I	<i>Rhinichthys cataractae</i>	BI	A.1.2	MT
<i>Fundulus diaphanus</i>	CI	A.1.5	T	<i>Salmo salar</i>	IC	A.2.3	I
<i>Fundulus heteroclitus</i>	GF	A.1.4	T	<i>Salmo trutta</i>	IC	A.2.3	I
<i>Gasterosteus aculeatus</i>	CI	B.2.4	MT	<i>Salvelinus alpinus</i>	IC	A.2.3	I
<i>Hybognathus regius</i>	BH	A.1.4	I	<i>Salvelinus fontinalis</i>	CI	A.2.3	I
<i>Ictalurus punctatus</i>	IC	B.2.7	MT	<i>Salvelinus namaycush</i>	IC	A.2.3	I
<i>Labidesthes sicculus</i>	CI	A.1.4	I	<i>Scardinius erythrophthalmus</i>	IH	A.1.4	T
<i>Lepisosteus osseus</i>	TC	A.1.4	MT	<i>Semotilus atromaculatus</i>	IC	A.2.3	T
<i>Lepomis auritus</i>	CI	B.2.3	MT	<i>Semotilus corporalis</i>	IC	A.2.3	MT
<i>Lepomis gibbosus</i>	IC	B.2.2	MT	<i>Sander vitreus</i>	TC	A.1.2	MT
<i>Lepomis macrochirus</i>	GF	B.2.2	T	<i>Umbra limi</i>	GF	B.1.4	T
<i>Lepomis microlophus</i>	BI	B.2.2	MT				

Table 2

Trophic guild	Description	Piscivore	Invertivore	Omnivore	Benthic feeder
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

Table 3

Guild	Description	Guarder	Litho- psammophilous	Phyto- philous
A.1.1	Nonguarders - Open substratum spawners - Pelagophils	0	0	0
A.1.2	Nonguarders - Open substratum spawners - Lithopelagophils	0	1	0
A.1.3	Nonguarders - Open substratum spawners - Lithophils	0	1	0
A.1.4	Nonguarders - Open substratum spawners - Phytolithophils	0	1	1
A.1.5	Nonguarders - Open substratum spawners - Phytophils	0	0	1
A.2.3	Nonguarders - Brood hiders - Lithophils	0	1	0
A.2.4	Nonguarders - Brood hiders - Speleophils	0	1	0
B.1.4	Guarders - Substratum choosers - Phytophils	1	0	1
B.2.2	Guarders - Nest spawners - Polyphils	1	1	1
B.2.3	Guarders - Nest spawners - Lithophils	1	1	0
B.2.4	Guarders - Nest spawners - Ariadnophils	1	1	1
B.2.5	Guarders - Nest spawners - Phytophils	1	0	1
B.2.7	Guarders - Nest spawners - Speleophils	1	1	0
C.1.4	Bearers - External bearers - Gill-chamber brooders	1	0	0

Table 4

Metric name	Description
SpRichness	Number of species in the sample
%_Sp_LithPsam	Percentage of lithophilous or psammophilous species
%_Sp_Phyto	Percentage of phytophilous species
%_Sp_Guarder	Percentage of nest guarder species
%_Sp_Diad	Percentage of long-range diadromous species
%_Sp_Pisc	Percentage of piscivorous species
%_Sp_Inv	Percentage of invertivorous species
%_Sp_Omn	Percentage of omnivorous species
%_Sp_Benth	Percentage of benthivorous species
%_Sp_Tol	Percentage of species tolerant to environmental variations
%_Sp_Intol	Percentage of species intolerant to environmental variations

Table 5

	Variable	Description	
Environmental variables	AREA_WS	Area of the catchment (ha)	
	AV_DEP	Estimated mean depth (m)	
	ELEV	Lake altitude (m)	
	HI_PT	High point of catchment (m)	
	KM_SEA	Distance from the ocean (km)	
	LKVOL2M3	Estimated lake volume (m ³)	
	LK_HA	Lake surface area (ha)	
	LTROFF_M	Long-term average annual runoff (m)	
	PRECIP_M	Long-term average precipitation (m)	
	RETENT	Estimated water retention time for lakes (years)	
	SHR_LTH	Length of shoreline including islands (m)	
Anthropogenic variables	urbanisation variables	URB_TOT	% catchment urban (nonresidential + residential)
		HOUDENKM	Housing unit density (housing/km ²)
		POPDENKM	Population density (persons/km ²)
		RD_DEN	Road density (m/ha)
		AG_TOT	% catchment agricultural
		MINE_TOT	% catchment strip mine/quarry/gravel pit

Table 6

	Natural lakes			Reservoirs		
	env1	env2	env3	env1	env2	env3
Inertia	41%	26%	13%	46%	21%	12%
AREA_WS	0.80	-0.01	-0.38	0.71	-0.05	-0.44
AV_DEP	0.78	-0.04	0.14	0.89	-0.03	0.21
ELEV	0.04	0.85	0.46	0.38	0.77	0.15
HI_PT	0.42	0.79	0.27	0.59	0.72	-0.08
KM_SEA	0.17	0.91	0.14	0.30	0.83	-0.04
LKVOL2M3	0.99	-0.10	-0.05	0.96	-0.15	0.17
LK_HA	0.95	-0.10	-0.14	0.93	-0.23	0.12
LTROFF_M	0.16	-0.50	0.63	0.59	0.00	-0.54
PRECIP_M	0.01	-0.64	0.60	0.30	-0.46	-0.50
RETENT	0.53	-0.14	0.39	0.45	-0.30	0.69
SHR_LTH	0.92	-0.14	-0.10	0.86	-0.31	0.01

Table 7

		intercept	Urb_PCA	AG_TOT	MINE_TOT	env1	env2	env3	F	sig.	var env	var ant	var com	unexpl
Env.PCs interpretation						Size	Altitude	Runoff						
							Dist. Sea	Precipitation						
Natural lakes	%_Sp_Phyto	0.831***	0.051***	-0.101	0.044	-0.033***	-0.009	-0.034*	8.7	<0.001	10.50	11.52	11.01	66.96
N=113	%_Sp_Guarder	0.595***	0.085***	-0.059	0.036	0.006	0.008	-0.000	9.8	<0.001	0.48	29.02	6.28	64.22
	%_Sp_Diad	0.285***	-0.048***	0.173	0.048	0.024**	-0.065***	0.014	7.6	<0.001	26.09	9.52	-5.65	70.03
	%_Sp_Pisc	0.762***	0.047**	-0.103	0.015	0.024*	-0.029*	-0.003	5.4	<0.001	7.13	7.85	8.41	76.62
Env.PCs interpretation						Size	Altitude	Retention						
							Dist. Sea	time						
Reservoirs	%_Sp_Benth	0.034	0.009	0.128*	0.03	0.033***	0.029	-0.012	4.3	0.001	21.21	6.43	6.05	66.32
N=58	%_Sp_Intol	0.174***	-0.048**	-0.043	0.114	0.016	-0.019	0.003	3.2	0.01	3.55	14.10	9.69	72.66

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

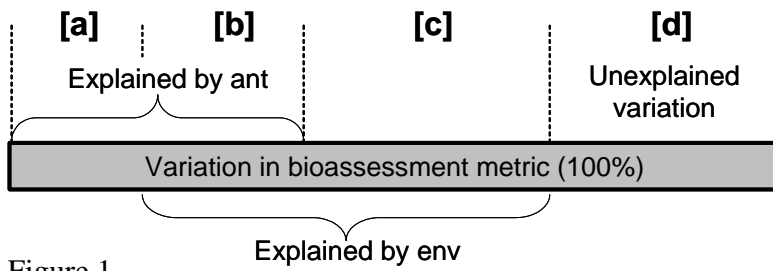


Figure 1

P6: Fish community convergence along environmental gradients in lakes of France and Northeast U.S.A.

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Fish community convergence along environmental gradients in lakes of France and Northeast U.S.A.

Running title: Convergence of lake fish communities

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Abstract

Community convergence occurs when distinct communities experiencing similar habitat conditions become more similar than their ancestors. Convergence in different contexts suggests that contemporary environmental conditions represent a strong selective pressure towards community properties whereas it is not expected if phylogenetic inertia and historical contingencies make natural selection a second order driving force.

The aim of the present study was to assess whether 8 traits of fish communities (species richness, 3 reproductive traits and 4 trophic traits) respond similarly to environmental gradients, and consequently displayed convergence, between the lentic systems of NEUSA and France

The data set encompassed fish surveys of 75 French and 168 NEUSA lakes, the assignment of species into reproductive and trophic guilds and environmental variables characterising the lakes and their catchments. The analytical procedure was adapted from the recommendations of Schluter (1986).

The comparison of the regional pools of lacustrine fishes indicated that NEUSA was about twice as speciose as France. This was mostly due to higher species turnover across lakes although NEUSA lakes were consistently more speciose than French ones for a given surface area. Warmer environments were consistently inhabited by more phytophilous and guarder species than colder ones. Hence there was convergence in community reproductive traits. Conversely, there was no sign of convergence in the trophic structure of lacustrine fish communities across regions.

The availability of spawning substrates is a major determinant of fish community composition in the lakes of the temperate regions of the northern hemisphere. It is likely related to temperature conditions and therefore our results suggest that fish communities could be affected in their composition in the event of global warming. The absence of convergence in community trophic features may reflect the consistency of the relative abundance of trophic guilds across environmental gradients in France. It may also indicate that the species guild assignment is inappropriate in a communities dominated by generalist feeders.

Phylogenetic constraints, past events such as the diversification of the North American fish fauna, the selective extinctions during Pleistocene glaciations and the subsequent recolonisations, by their influences on the regional species pools, contribute to explain the

contemporary patterns of fish communities of north temperate regions.

Keywords: Fish community, lake, community convergence, ecological guilds, species richness, environmental gradients, species-area relationship, intercontinental comparison.

INTRODUCTION

Community convergence occurs when distinct communities experiencing similar habitat conditions become more similar than their ancestors (Orians & Paine, 1983). The search for such convergence across regions has stimulated community ecologists since the end of the 60's (MacArthur & Levins, 1967; Cody, 1968, 1973; Fuentes, 1976; Cody & Mooney, 1978). Convergence studies test clear and contrasted hypotheses: convergence in different phylogenetic contexts suggests that contemporary environmental conditions represent a strong selective pressure towards community properties (Winemiller, 1991; Losos *et al.*, 1998). Conversely, no convergence should be observed if phylogenetic inertia and historical contingencies make natural selection a second order driving force (Price *et al.*, 2000; Verdu *et al.*, 2002; but see Stephens & Wiens, 2004). Thus, making the hypothesis of convergence across biota relates to the deterministic view that community features can be predicted from the environment. Although there are major uncertainties in identifying and quantifying the appropriate habitat features that represent selective forces on biotic communities (Poff, 1997), convergence testing is a powerful method to assess the generality of some patterns observed locally and hopefully of the processes causing these patterns.

Several difficulties arise when studying community convergence. While convergence at the species level can be identified directly when fossil records are available to assess whether species in different regions have evolved to be more similar than their ancestors, characteristics of the ancestral communities are generally not known when examining community convergence (Schluter, 1986). Furthermore, some community attributes may display convergence while some others may not (Samuels & Drake, 1997; Fukami *et al.*, 2005). Last, choosing the appropriate methodology to test community convergence is not straightforward. Similarity among communities occupying similar habitats does not necessarily imply convergence, nor need differences in community attributes preclude it (Schluter, 1986; Schluter & Ricklefs, 1993). For example, two communities may be highly dissimilar and yet have converged when compared to the differences between their ancestors (Schluter & Ricklefs, 1993).

Freshwater fish communities seem to present several advantages in order to address the topic of intercontinental ecological convergence for at least three reasons. First, they encompass a

large number of taxa, around 10,000 true freshwater fish species (Nelson, 1994), occurring over the vast majority of the continental hydrographic networks. They colonised all the freshwater bodies but those isolated by dispersal barriers, such as mountain lakes, or those undergoing extremely stressful abiotic conditions such as periodic dry-outs or long-term ice cover inducing oxygen depletion. Second, and certainly contributing to explain their being widespread, they evolved into a broad array of life history strategies (Winemiller & Rose, 1992; Vila-Gispert *et al.*, 2002) and ecological features. Thus, there is sufficient variation in these traits for natural selection to act upon as a response to environmental conditions, including biotic interactions. Third, at least in temperate regions, their ecological requirements, habitat and other life history features are reasonably well documented (Lamouroux *et al.*, 2002).

Although the organisation of local contemporary communities results from the combination of local and regional processes, and consequently are bounded by some limits set by historical and biogeographical contexts (Ricklefs & Schluter, 1993), several patterns in the response of freshwater fish communities to the environment have been consistently identified across continents. For example, the dependence of richness upon the area surveyed (species-area relationships, SARs) has been quantified for many ecological groups including fish (see Rosenzweig, 1995; Gaston & Spicer, 2004 for reviews), at a variety of scales and for various freshwater ecosystem types (Barbour & Brown, 1974; Eadie *et al.*, 1986; Rahel, 1986; Angermeier & Schlosser, 1989; Oberdorff *et al.*, 1995; Griffiths, 1997; Matthews & Robison, 1998). Riverine fish communities of various continents also show consistent patterns of species additions and trophic structure along longitudinal gradients at the basin scale (Huet, 1949; Schlosser, 1982). Hydraulics, substrate characteristics or geomorphology appear to strongly constraint the life history, behavioural, habitat or trophic traits of riverine fish communities regardless of the region (Lamouroux *et al.*, 2002; Goldstein & Meador, 2004). Other attributes of fish communities structure, such as the abundance of habitat specialists or reproductive guilds, display consistent patterns of response to environmental gradients and anthropogenic stressors, as attested by the development of regionally adapted indices (IBIs) using these guilds for the fish-based assessment of various types of streams and rivers on different continents (see Hughes & Oberdorff, 1999; Karr & Chu, 2000; Roset *et al.*, in press for reviews).

Intercontinental comparisons of lake fish communities have seldom been carried out. The two ones we are aware of compared those of small forest lakes of Wisconsin and Finland (Tonn

et al., 1990; Magnuson *et al.*, 1998). Communities were described using species richness and species assemblages as community descriptors. Therefore, it appears that the functional attributes of fish communities have never been compared across continents.

Hence, the general objective of the present paper is to test whether functional traits of the lacustrine fish communities from Northeast USA (NEUSA) and France display convergence. We hypothesised that species richness and proportions of trophic and reproductive guilds would (i) respond to the same environmental gradients, (ii) that these responses would be similarly oriented between NEUSA and French lentic systems and (iii) that these responses would be quantitatively equivalent between regions.

MATERIEL AND METHODS

Throughout this article, we refer to natural lakes for lakes of natural origin (although some might have been deepened by human actions), to reservoirs for lentic systems created artificially by the damming of a valley, and to the generic term of lakes for both types. Although this study compares the attributes of fish communities between lake sets located in different continents, they are far from representative of the lakes of each continent. Therefore, the differences between these two lake sets are referred to as regional effects rather than as continental effects.

The data set

The data set encompasses the results of fish surveys, the assignment of species into reproductive and trophic guilds and environmental variables characterising the lakes and their catchments. For both French and NEUSA data sets, lakes with species richness below four were omitted from the data because they were unlikely to contribute meaningfully to community-level inferences. The total data set comprises 75 French and 168 NEUSA lakes, including 51 and 58 reservoirs respectively.

Fish survey data

Fish data of French lakes and reservoirs originate from various sources (research institutes, universities, consultants and administrative authorities). These sites have not been specifically selected to be representative of the heterogeneity among French lakes. However, they represent a broad array of environmental conditions that we consider covering most of the variability observed on French natural lakes and reservoirs. The lakes have been sampled

using gillnets series with mesh sizes ranging from 10 to 60 mm, but there was no standardised sampling strategy. We also included data obtained by collecting fish during reservoir draining operations. Further information on data collection is available from previous studies (Argillier *et al.*, 2002b; Irz *et al.*, 2002; Irz *et al.*, 2004a).

The NEUSA sites were chosen as a random draw from the census of NEUSA lentic systems (Larsen *et al.*, 1994). The fish surveys have been carried out from 1991 to 1995 according to the EMAP-surface waters monitoring programme (Baker *et al.*, 1997). Thus, the samples included catches from gillnets, fyke nets, beach seines and electrofishing. As French data did not include an equivalent set of fishing gear, and due to the low efficiency of gillnets above 10mm mesh size on the young-of-the-year (YOY), we excluded the YOY from the NEUSA data. Restricting the analyses to the gillnet catches would have provided more comparable data between regions but the catches of the different gears had been pooled, preventing us from distinguishing those of gillnets. Consequently, it is clear that part of the between-region differences in community attributes can be due to the heterogeneity in sampling methods. Such problems are almost inherent to broad scale studies (Blackburn & Gaston, 1998, 2004). Therefore, carrying out such studies require assuming that the signal-to-noise ratio of the data is high enough to ensure that, by appropriate statistical analysis, the signal may be recovered and correct generalisations derived (Pielou, 1977). The few intercontinental comparisons of lake fish community patterns published so far also had to deal with sampling inconsistency (Tonn *et al.*, 1990; Magnuson *et al.*, 1998).

Environmental parameters

Numerous environmental parameters were available to characterise local habitat (Figure 1). Temperature data were obtained at the lake centroid from a 10' latitude/longitude data set of mean monthly surface climate over global land areas (New *et al.*, 2002). Three variables were derived from the raw data: the mean annual air temperature (T_m) obtained by averaging the monthly values and the minimum and maximum mean monthly air temperature (T_{min} and T_{max} respectively). Elevation (Elev), area of the catchment (AreaWS), shoreline development (Shore) and lake area (Lkha) were determined by digitising topographical maps while mean depth was obtained during the surveys. These variables have been precisely described in previous studies (Argillier *et al.*, 2002b; Irz *et al.*, 2002; Whittier *et al.*, 2002; Irz *et al.*, 2004a). For graphical display and analyses, temperature data were kept raw, elevation was square-root transformed and the other variables were log-transformed.

Strong correlations appeared among the environmental parameters (Table 1). Two groups of variables could be distinguished: the first was related to air temperature, including elevation, while the second encompassed the attributes of lake size (shoreline length, mean depth, area of the catchment, lake volume). Hence, we chose mean annual air temperature (T_m) at the lake centroid and water body surface area (Lkha) as weakly correlated habitat descriptors.

These environmental parameters are likely to influence the composition of the community in two distinct ways. Temperature is known to strongly affect patterns of fish communities (Rathert *et al.*, 1999) because it is one of the major dimensions of fish species ecophysiological requirements (Matthews, 1998), thereby related to the geographical distribution of individual species (Shuter *et al.*, 1980; Lelek, 1987; Shuter & Post, 1990). This parameter is also related to a broad range of other environmental parameters such as the water oxygen content (Matthews, 1998) and reflects an important aspect of the energy availability within ecosystems (Lennon *et al.*, 2000; Evans *et al.*, 2004, 2005). Lake area had to be considered because the area of the sampled system is one of the most commonly recognised determinants of species richness in general (SARs, see (Magurran, 1988; Rosenzweig, 1995) for reviews) and in lakes in particular (Barbour & Brown, 1974; Griffiths, 1997; Irz *et al.*, 2002; Irz *et al.*, 2004a). Furthermore, lake area can be considered as a variable summarising various aspects of lake size (habitat diversity, stability) and connectivity (catchment area, see Table 1).

Species biological traits

Species were assigned to reproductive guilds according to Balon (1975) for French species and to (Simon, 1999b) for NEUSA ones. The latter study extended the scope of the former to a larger array of North American species and in some cases updated the genuine classification according to more recent findings on the ecology of species. These classifications were based on the species early development stages, spawning substrates and reproductive behaviour.

The classification of species into trophic guilds was based on Bruslé and Quignard (2001) and Keith and Allardi (2001) for France and according to literature survey for NEUSA (Whittier, 1999). *Noturus insignis* was considered benthic invertivore as the other *Noturus* species listed in (Simon, 1999a).

Community metrics

When comparing community structures, the scope of the inference is restricted to the least

common denominator of community information (Samuels & Drake, 1997). Therefore, although comparative analysis of density, or abundance data, would have been highly valuable, the French census data were too heterogeneous to allow the assessment of such quantitative variables. Therefore, we limited our investigations to community attributes, or metrics, that could be derived from species presence / absence data.

Fish survey data and species traits were combined to obtain variables corresponding to community reproductive (CRT) and trophic traits (CTT) in terms of proportions of the total species richness belonging to functional guilds (e.g. Phyto was calculated for each lake as the ratio of the number of phytophilous species to the species richness). As many species can spawn on various substrates and feed on several items, we initially considered two ways for deriving the metrics (Table 2). The first one was a strict encoding (e.g. Phyto_strict is the proportion of species that need macrophytes to spawn) and the second one corresponded to the species ability (e.g. Phyto is the proportion of species that are able to spawn on macrophytes). Therefore, the former is a subset of the latter. However, it appeared that the two sets of metrics were strongly correlated (Table 3), so we removed those derived from the strict encoding for the analyses. For example, Inv and Pisc_strict were almost complementary because few species feed exclusively on items including neither fish nor macroinvertebrates. Thus, interpreting variations for Inv is similar to interpreting those for Pisc_strict.

The metric Herb (Herbivores) was also removed because it was redundant with Omn (Omnivores). Despite this selection, some correlations remained among metrics, reflecting the limited number of combinations in ecological traits among species and the non-independence of reproductive and trophic traits. These correlations were between Pisc and Guarder and between Pisc and Benth for both natural lakes and reservoirs, and between Benth and Guarder in reservoirs (Table 3).

Analytical procedure

The analytical procedure was designed to assess whether lacustrine fish communities on the two continents displayed convergence in terms of species richness, CRT and CTT composition. An indirect methodology has been proposed to detect community convergence if data are available from local communities dwelling contrasted habitats (Schluter, 1986). This methodology relies upon the partitioning in the variance in community attributes into a habitat component (common between regions), a regional component (differences between regional groups that persist regardless of habitat), to which an interaction component habitat x region

was added as an indicator of between-region quantitative difference in responses to habitat conditions (Lamouroux *et al.*, 2002).

Most of such cross-region studies published so far have either compared regional species pools (assuming that environmental conditions were similar across regions) or contrasted several habitat types within regions (thereby assuming that sites in different regions matched by habitat types were identical) to infer potential common patterns in community organisation. However, such assumptions are usually controversial. Hence, we chose to characterise the habitats quantitatively using environmental gradients. The analyses have been processed separately for natural lakes and reservoirs because there was no *a priori* reason to hypothesise that their fish communities respond similarly to environmental gradients (Irz *et al.*, in press). However, when the separate models for a given metric exhibited similar trends, both lake types were pooled to obtain final models.

Comparison of the regional species pools

Differences between the traits of the regional pools were assessed using chi-squared tests between regions and species binary traits. This was not strictly rigorous since the species pools were not totally independent (indeed, 11/111 species were present in both regions), nevertheless we provided significant p-values as indications.

In order to assess whether differences in regional richness arose from differences in the numbers of sites between regions or indicated differences in diversity distributional patterns, we constructed species accumulation curves. Such curves are plots of the cumulative number of species discovered, SR(n), within a defined area, as a function of some measure n of the effort needed to find them (Colwell & Coddington, 1994). In our case, n was the number of lakes included in the sample and we plotted the mean cumulative number of species found in 100 random draws of lakes as a function of the number of lakes using Estimates software (Colwell, 1997).

Convergence assessment

The analytical procedure was summarised in Figure 2. In the different steps, we modelled species richness and community metrics in different ways. For species richness, we used linear models on the log-transformed species richness. For the community metrics, we used generalised linear models (GLM), with binomial error distributions and a *logit* link function. This kind of model presents the following advantages over linear models to analyse the

response of proportion data: (i) it does not assume the constancy of the variance, but instead models it using the binomial function (ii) it weights proportions by the number of observations (1/2 is given less weight than 500/1000), (iii) it constrains the response variable between 0 and 1.

In order to quantify the variability accounted for by the models, we used the pseudo-R-squared (Crawley, 2005) calculated as:

$$R^2 = 1 - (\text{Residual deviance}) / (\text{Null deviance}).$$

All the analyses were performed with the free software R 2.2.1 (R Development Core Team, 2005).

We followed a hierarchical analytical procedure including five steps.

Step 1: To identify the metrics significantly influenced by environmental gradients, species richness, CTT and CRT were modelled, for each lake type and region, as a function of Lkha and Tm. If the coefficients were significant for the same independent variable, we proceeded to step 2. If the coefficients were significant in only one region, there was no convergence (case 5, see Figure 2). If coefficient were significant neither for NEUSA nor for French lakes, we simply tested whether the metrics differed on average between regions (Analysis of variance (ANOVA) for species richness and analysis of deviance for the other community traits). If they did, there was between-region dissimilarity (case 7, see Figure 2) and similarity (case 6) otherwise.

Step 2: To test whether the metrics responded in the same direction to a given independent variable in the two regions, we examined the sign of the significant coefficients obtained in step 1. Similar signs between continents indicated at least qualitative convergence (cases 1 to 3) and we proceeded to step 3. Conversely, opposite signs indicated an absence of convergence (case 4; never met in our data).

Step 3: To detect quantitative differences in the responses between regions, we performed an analysis of covariance (ANCOVA) with "Region" as factor. This step was carried out only for those "metrics × lake type" combinations for which the coefficients' signs indicated a common direction of response between regions. The significance of the slopes difference indicated that the convergence was only qualitative (case 3).

Step 4: When slopes did not significantly differ in step 3, the interaction term from the ANCOVA was removed to test for significant differences between intercepts. Significant

difference indicated convergence in the intensity of the response to the environmental gradient, despite an overall regional dissimilarity (case 2). The non-significance of both indicated convergence and an absence of regional dissimilarity (case 1).

Step 5: If both lake types corresponded to the same case in Figure 2, in order to broaden the extent of our conclusions, we pooled the data of both lake types and rebuilt the model with lake type as factor (with possible interactions with the other terms). Non-significant terms were removed step-by-step to obtain the final model. This allowed detecting differences in response according to region, lake type or both of them.

In step 1, a hierarchical partitioning procedure was implemented in order to identify the environmental gradient most influential on local community attributes (Chevan & Sutherland, 1991) thanks to a modification of the "hier.part" R package (MacNally & Walsh, 2004). This procedure allows the assessment of the independent contribution of each explanatory variable to the modelled variance. To assess the contribution of one particular variable, it implies processing all the possible models that do not include the variable of interest, then adding it and calculating the mean improvement of the goodness-of-fit (here the pseudo R-squared) attributable to this variable.

Steps 2 to 5 were carried out separately for the responses to Tm and Lkha because none of the metrics appeared to simultaneously respond to both variables in both regions.

RESULTS

Comparability of the lakes between regions

On average, the French natural lakes and reservoirs are slightly warmer, but they clearly experience less annual temperature range and less harsh winter conditions than NEUSA ones (Figure 1). One of the difficulties in convergence studies is that the environment is never totally similar across regions (Orians & Paine, 1983). Our data are no exceptions to this rule. However, despite these differences, all the environmental variables overlap across regions and their standard deviations have the same order of magnitude (apart from depth). Therefore, we considered that the two sets of lakes were similar enough to provide meaningful comparisons of the responses of fish communities to habitat conditions.

Overall comparison of regional lacustrine fish fauna

The number of species occurring in NEUSA lakes was 83 vs. 39 in French lakes (Table 4).

NEUSA natural lakes are about twice as speciose as French ones, regardless of the differences in number of sites sampled (Figure 3). This difference is slightly lower for on reservoirs, but a random draw of 51 reservoirs in NEUSA on average contains 51.6 species as compared to 36 observed in French ones.

The distribution of species across families (Table 4) revealed that 13 families were exclusively found in NEUSA (e.g. Catostomidae, Clupeidae, Cyprinodontidae and Gasterosteidae) while 4 were only found in France (e.g. Balitoridae, Mugilidae, Poeciliidae and Siluridae). The Cyprinids were by far the most speciose family in both regions, encompassing half the total species in France. The Centrarchids were the second most speciose family in NEUSA. The two species belonging to this family and recorded in the French data set (*Lepomis gibbosus* and *Micropterus salmoides*) have been introduced from North America. In France, 10/14 families were represented by a single species. This ratio was 12/22 in NEUSA. The numbers of lithopsammophiles, phytophiles, invertivores and omnivores in NEUSA are about twice those in France (Table 4), therefore their proportional importance did not differ across regions (Chi-squared test, $p > 0.7$). Conversely, NEUSA lakes sheltered a disproportionately low proportion of benthic feeders ($p = 0.01$) and a high proportion of guards and piscivores ($p = 0.12$ and 0.29 respectively), although the latter two were not significant at the 0.05 level.

Response of metrics to habitat variables within region

Fifteen out of sixteen metrics (corresponding to 8 metrics x 2 lake types) were significantly explained by at least one habitat variable on the NEUSA data, but only 6/16 on the French data (Table 5).

Species richness

Species richness (SR) was positively related to the water body surface area (Lkha) regardless the type of lake or region (Table 5). The independent contribution of Lkha to explain the variation in SR (p_{Lkha}) ranged from 30 to around 50% and was strongest in NEUSA. SR also increased significantly with mean annual air temperature (T_m) in the NEUSA natural lakes and reservoirs.

Community functional traits

Nine out of twelve CRT models were significant. The proportion of litho-psammophilous

species (LithPsam) was not significantly related to the environment except for NEUSA natural lakes where it decreased with Tm and increased with Lkha. Phyto increased with Tm regardless the type of lake or region and decreased with Lkha in French reservoirs and NEUSA natural lakes. Surprisingly, in both regions Guarder responded (negatively) to Lkha in reservoirs (despite a Tm effect in NEUSA) and exclusively (positively) to Tm in natural lakes. Altogether, Tm significantly entered eight models and Lkha five.

All the CTT responded to habitat variables in NEUSA, but none did in France (Table 5). For the former region, Pisc decreased with Lkha in reservoirs and increased with Tm in natural lakes; Inv decreased with Lkha on reservoirs and with Tm in natural lakes; and, regardless of the lake type, Omn decreased with Lkha while Benth decreased with Tm and increased with Lkha. Consequently, lake area was the main independent variable explaining CTT (significant in 6/8 NEUSA models), particularly in reservoirs.

In NEUSA water bodies, the models were consistent among lake types for Omn and Benth. The models that were not significant in French reservoirs (LithPsam and all the CTT) were not either in natural lakes. For the other community traits, some differences appeared between lake types; however, there was no case of opposite significant response to an environmental gradient between lake types.

When averaged over lake types and continents, the respective contributions of Tm (p_Tm) and Lkha (p_Lkha) to CRT are 21% and 8% respectively while they contributed to 5% and 11% to CTT. Hence, the temperature regime appeared to strongly influence fish community reproductive structure while trophic structure was (but to a lesser extent) related to the lake size.

When averaged over lake types and community traits, the respective contributions of Tm and Lkha to community attributes in French lakes were 11% and 8% respectively while they contributed to 15% and 10% in NEUSA lakes. This indicated that the models fitted on NEUSA water bodies accounted for a greater part of the variability in community traits than those fitted on French data.

When averaged over continents and community traits, Tm and Lkha respectively explained 7% and 11% of the variation in reservoir community traits compared to 20% and 8% in natural lakes. Therefore, temperature appeared mostly influential in natural lakes.

Between-regions comparison

The analysis of deviance comparing the proportions of LithPsam in reservoirs (the only metric that displayed no response to habitat variables) versus regions showed that the proportions of species belonging to this reproductive guild did not differ between regions ($P=0.995$). This pattern corresponds to case 6 in Figure 2.

The community traits that were significantly related to the same habitat variables in water bodies of NEUSA and France were the same for natural lakes and reservoirs and displayed the same direction of response between continents (Table 5). Consequently, they were submitted to ANCOVA.

For species richness, ANCOVAs revealed no significant slope difference neither between lake types nor between regions on the pooled data set (natural lakes and reservoirs of both regions) (Figure 4 and Table 6). However, the intercepts differed significantly, indicating that, for a given area, NEUSA water bodies were more speciose than French ones ($P<0.001$) and that reservoirs were more speciose than natural lakes ($P=0.029$). Hence, the SAR observed indicated both convergence and regional dissimilarities (case 2 in Figure 2).

The other three metrics submitted to ANCOVA were CRT metrics (Table 6). A single model could be fitted for Phyto (Figure 5A), with no differences neither in slopes nor in intercepts across regions or lake types ($R^2=0.45$, case 1). This metric was therefore the only one displaying convergence and regional similarity. Guarder only differed in intercepts between regions in its response to T_m in natural lakes (Figure 5B) and Lkha in reservoirs, thereby indicating convergence despite overall regional dissimilarities (case 2).

DISCUSSION

The aim of the present study was to assess whether 8 traits of fish communities (species richness, 3 reproductive traits and 4 trophic traits) responded similarly to environmental gradients, and thus displayed convergence, between the lentic systems of NEUSA and France. A single one (Phyto), regardless of the lake type, conformed to case 1 (Figure 2), that of convergence with no significant regional dissimilarity (Table 7). Species richness and Guarder (in both lake types) corresponded to case 2, convergence despite regional dissimilarity. In sum, convergence was detected in 6 out of 16 "traits x lake type" combinations and was restricted to SR and CRT. Species richness variability was mainly due to lake size whereas CRT exhibited clear response to mean annual air temperature.

Among the 10 traits that displayed no convergence, only LithPsam in reservoirs indicated no

overall regional dissimilarity (case 6). The nine other "traits x lake type" combinations (LithPsam in natural lakes and the CTT for both lake types) exhibited response to the environmental gradients only in NEUSA. They corresponded to case 5. Cases 3, 4 and 7 were never observed. In sum, there was no sign of convergence in the trophic structure of lacustrine fish communities across regions.

Regional species pools

The comparison of the regional pools of lacustrine fishes indicated that NEUSA was about twice as speciose as France, which is comparable to the earlier comparison between the lake fish communities of Wisconsin and Finland (Tonn *et al.*, 1990). This difference is not a peculiarity of lentic systems and had already been shown comparing the rivers of Poland and Ontario (Mahon, 1984). Indeed, the stream fish faunas of Western Europe and of North America west of the Rocky mountains are more similar to each other than either does from that of eastern North America, both in terms of richness and in terms of ecological features (Moyle & Herbold, 1987). The main taxonomic differences between regions come from the presence of Centrarchidae, Catostomidae and Ictaluridae and the diversification of small Percidae (darters) and Cyprinidae (minnows) in North America, which explains its higher species richness. These taxonomic differences also contribute to overall differences in the traits of the regional fauna such as the higher proportions of piscivores and guarders in NEUSA lakes than in French ones. The palearctic and nearctic continents separated after the Atlantic opening during the mid-Cretaceous (Brown & Lomolino, 1998). Despite some later connections between these land masses across the Bering strait, allowing some biotic exchanges (Brown & Lomolino, 1998), freshwater fish faunas, restricted to the area of their basins, evolved separately (except from some modifications of the hydrographic network or some exceptional connections on the occasion of extreme hydrologic events). Furthermore, the fish fauna of temperate zones of the northern hemisphere suffered severe extinctions during the Pleistocene glaciations (Mahon, 1984; Moyle & Herbold, 1987; Banarescu, 1989). To avoid going extinct during important climatic fluctuations, living species can either adapt to these environmental fluctuations or modify their geographic range to track appropriate habitat conditions (Gaston, 2003). Freshwater fishes are particularly prone to extinction in such situations because their possibilities to "escape" environmental harshness are limited to the range of conditions within their catchments (catchment limits being barriers to dispersal). The differences in climatic conditions between the two study regions during glacial periods (harsher in Europe) as well as in the layout of their hydrographic networks certainly

explain most of the differences between the regional faunas.

Species-area relationships (SARs)

The slope of the log-log SAR obtained on our data sets (0.153) is less than that observed on small forest lakes (0.32 in Wisconsin and 0.34 in Finland). This study (Tonn *et al.*, 1990) included much smaller lakes than ours and the slope of the SAR may differ between small and large lakes (Griffiths, 1997).

Our results revealed convergence in species richness (SR) between lacustrine fish communities of NEUSA and France. Despite a significant increase in species richness with temperature detected in NEUSA natural lakes, it remains that lake area appears as a major determinant of local richness, quantitatively consistent across lake types and regions. SARs are one of the few general laws of ecology (May, 1975; Rosenzweig, 1995; Lawton, 1999) and have been observed for lacustrine fish of various regions of North America (Tonn & Magnuson, 1982; Eadie *et al.*, 1986; Rago & Wiener, 1986; Matuszek & Beggs, 1988; Minns, 1989; Mandrak, 1995; Chapleau *et al.*, 1997; Griffiths, 1997; Magnuson *et al.*, 1998; Matthews, 1998; Allen *et al.*, 1999; Whittier & Kincaid, 1999) and France (Irz *et al.*, 2002; Irz *et al.*, 2004a). Earlier studies comparing lake fish communities of Wisconsin and Finland had already identified such convergence in SARs (Tonn *et al.*, 1990; Magnuson *et al.*, 1998).

At least four hypotheses have been proposed to account for the SARs in lake systems. (i) Larger lakes could be more speciose simply because they contain more individuals than small ones. It has been shown that for a set of individuals belonging to species following the classical log-normal species abundance distribution and distributed randomly across a given surface, the individuals contained in successively larger areas tended to belong to a higher number of species (Coleman, 1981; Coleman *et al.*, 1982). (ii) It has been suggested that this relationship could be a consequence of the lesser environmental (physico-chemical) stability of small lakes as compared to large ones. Such temporal fluctuations in habitat conditions could increase local extinction risks (Jackson *et al.*, 2001). (iii) The “habitat diversity hypothesis” (Williams, 1943; MacArthur & Wilson, 1967; Diamond, 1975) suggests that the heterogeneity of the habitat (and consequently the diversity of available food resources) increases with the size of the area, thus offering a large number of available niches and consequently favouring the coexistence of a larger number of species (Williamson, 1988). (iv) The SAR could reflect the outcome of an equilibrium between stochastic extinction and colonisation events (MacArthur & Wilson, 1967). In the theory of island biogeography, the

rates of colonisation depend on the degree of isolation of the islands (i.e. distance to the mainland) and the rates of extinction are size-dependent. Then, the equilibrium richness increases with island area and decreases with island isolation. Indeed, lake ecosystems share a number of common features with islands (Barbour & Brown, 1974; Magnuson, 1976; Browne, 1981; Eadie *et al.*, 1986; Magnuson *et al.*, 1998). They are isolated from each other and colonisation events are rare because connections between lakes are mainly through flowing waters that limit dispersal for limnophilous fishes.

In the first hypothesis, Lkha would determine the number of individuals in the lake that would eventually determine the number of species. Hence, if we assume that the samples obtained from the fish surveys are representative subsets of the distribution of the individuals across species at the lake scale, this hypothesis should lead to stronger correlations between Lkha and the number of individuals in the samples (NIS) and between NIS and SR than directly between Lkha and SR (Angermeier & Schlosser, 1989). This is not the case in NEUSA lakes (Table 8), so this hypothesis is not likely to explain the observed SAR at least in this region (the number of individuals in the samples was not considered in our comparative study because it was not available for most of the French lakes).

The three other hypotheses are not mutually exclusive. Except for the great lakes, and due to their geologically ephemeral nature (Matthews, 1998), lakes are not speciation spots. So, the number of species they shelter is the outcome of colonisation and local extinctions. The last three hypotheses eventually represent different processes influencing species richness through their action on the rates of colonisation or extinction. Therefore, they can be represented in the framework proposed in Figure 6. Assessing the relative importance of the different pathways through which lake area influences lake species richness would require acquiring data on the level of isolation and an assessment of the within-lakes habitat diversity as well as the monitoring of the physico-chemical properties of waters. Although such data are not currently available, some inferences related to the second and third hypotheses above (stability and habitat diversity) can be obtained by comparing natural lakes and reservoirs. Reservoirs typically undergo unpredictable water level fluctuations and stratification regimes (Wetzel, 1990), which led some authors to consider them as intermediates between lake and river ecosystems (Ryder, 1978; Gelwick & Matthews, 1990; Kimmel *et al.*, 1990). They are generally very homogeneous as compared to natural lakes. Although the inflow from the main tributaries creates a gradient of hydraulic and substrate conditions, and hence some diversity of habitat, water level fluctuations due to water withdrawals frequently hamper the

development of macrophytic vegetation (one of the main spawning and refuge habitat for fishes), cause erosion of the banks and subsequent clogging of coarse substrates, and tend to homogenise water physical and chemical properties throughout the water column (Wetzel, 1990). According to these two hypotheses, unpredictable environmental fluctuations and poor habitat diversity in reservoirs should limit the number of species in these systems as compared to natural lakes, which contradicts our results. However, these considerations are not sufficient to discard these hypotheses in that the comparison between the two lake types should be carried out “all else being equal”, which is obviously not the case. Indeed, reservoirs statistically have larger catchment areas, for a given lake area, than natural lakes ($\log(\text{AreaWS})=0.96+1.80\log(\text{Lkha})$ and $\log(\text{AreaWS})=1.14+1.38\log(\text{Lkha})$ respectively). If we consider that catchment area is a surrogate for the pool of potential colonisers, and that the higher the inflow, the higher the upstream connectivity, reservoirs are likely to experience higher colonisation rates from the upstream than natural lakes. Conversely, colonisation from downstream is generally limited due to the presence of dams seldom equipped with fish passes. Therefore, the direct comparison across systems is not sufficient to infer the mechanisms responsible for the SAR. It remains that the residuals of the SAR are significantly correlated to the lakes' catchment area (AreaWS) in both natural lakes and reservoirs ($p<0.001$) of NEUSA, which suggests that although extinction variables have in some occasions been proved to explain most of the variation in lakes species richness (Magnuson *et al.*, 1998), connectivity with the river networks also contributes to the patterns in species richness. In French water bodies, this relation was not significant. However, there was little chance the independent effect of one or the other variable could be detected due to the strong correlation between Lkha and AreaWS ($r=0.83$ in natural lakes and 0.73 in reservoirs).

The island biogeography theory only considers the pool of colonisers and the local communities in terms of species numbers (MacArthur & Wilson, 1967). However, their ability to colonise new localities and their susceptibility to extinction are direct functions of their life-history, ecological, behavioural and physiological traits (Poff, 1997). For example, only those species with individuals able to swim fast-flowing riffles have the potential to reach the upstream parts of river basins. It is also clear that the habitat features of lakes act as a filter excluding those species of the regional pool that require unavailable substrates to spawn. This is why the bolded signs in Figure 6 are considered dependent upon the regional species pool.

Indeed, species richness patterns most likely result from the interplay between all these processes as shown in Figure 6. Attempts to quantify their relative importance appear more relevant than binary approaches testing the significance of one or the other, but require data not yet available.

Scale and species richness

Different spatial scales can be considered when analysing patterns of species richness (Whittaker, 1972). The regional richness (gamma diversity) can be estimated by several methods, but if we consider it as the cumulated amount of species occurring in the localities in the regions compared, NEUSA natural lakes are about twice as speciose as French ones.

In a given region, gamma diversity can be expressed as the sum of the mean local (alpha) diversity and of the turnover (beta) diversity (Loreau, 2000). So, the higher gamma diversity in NEUSA lakes as compared to French ones could be due to higher mean alpha diversity, higher gamma diversity or both. In the model corresponding to Figure 4, the intercept difference between NEUSA and France is 0.197 (Table 6) on a log-log scale. This means that for a given surface area, the local species richness in a NEUSA lake is $e^{0.197} = 1.22$ times that of a French lake. Hence, the higher alpha diversity in NEUSA lakes is far from explaining the two-fold difference in gamma diversity and therefore beta diversity is higher in NEUSA. The comparison of the small forest lakes of Finland and Wisconsin (Tonn *et al.*, 1990) had already identified superior beta diversity in North America. The relationship between alpha, beta and gamma diversity has in numerous occasions been analysed to infer saturation of local communities (Cornell, 1985b, a; Hugueny & Paugy, 1995; Oberdorff *et al.*, 1998). The proportionality between the three has been considered indicative of unsaturated communities. Conversely, the independence of alpha over gamma diversity or the tendency of ceiling of the former for high values of the latter would indicate that local conditions tend to set a limit to the number of species that can coexist within local communities. However, great care is needed to interpret such patterns (Lawton, 1999; Srivastava, 1999; Hillebrand & Blenckner, 2002; Mouquet *et al.*, 2003; He *et al.*, 2005; Hillebrand, 2005; Shurin & Srivastava, 2005).

Although comparing two regions has a limited power to detect the shape of a local-regional species richness plot and NEUSA are only 20% more speciose than French ones despite a species pool twice as speciose. Therefore we are far from proportionality between local and regional richnesses. However, for such analytical approaches to allow meaningful inferences upon the relative importance of local versus regions processes in determining local species

richness, it is important that the regional species be precisely assessed as the pool of potential colonisers of individual lakes (Srivastava, 1999). In our study, this regional pool is clearly overestimated because both the NEUSA and the French regions encompass several basins. This is likely to explain why the results obtained here partially seem to contradict those obtained in earlier studies in France on almost the same set of lakes (Irz *et al.*, 2004a) and in North America on different data (Griffiths, 1997), both indicating proportionality between local and regional species richness for the native fishes, a result blurred when introduced species were included in the analyses. Consequently, an important part of the beta diversity may be attributed to the between-basin turnover in species. The basin is an intermediate spatial scale that should be considered to obtain more comprehensive inferences on the patterns of distribution of fish diversity relating broad regions and local biota (Tonn, 1990).

Reproductive traits of lake fish communities

Most reproductive traits of fish communities appeared very consistent in their responses to the environment across regions and lake types. Although the development of IBIs, generally including CRT, in a broad array of regions and ecosystem types, suggested some kind of generality in the response of these traits to environmental gradients and anthropogenic stressors, convergence in CRT as identified here has never, to our knowledge, been shown. A comparative study between the fish communities of the Rhône river catchment (France) and of Virginia (USA) has shown some convergence in the response of life-history traits to hydraulic conditions (e.g. body length, longevity and fecundity, see Lamouroux *et al.*, 2002), but these conclusions did not consider reproductive habitat requirements.

The convergence in the response of reproductive habitat requirements to temperature shows that warmer lakes are consistently inhabited by more phytophiles (and therefore less strictly lithopsammophilous species) than colder ones. This indicates a turnover in species reproductive substrates along a temperature gradient and consequently suggests that some of the correlates of temperature are related to the availability of spawning substrates. For example it can be hypothesised that warmer waters allow more primary productivity both by macrophytes (thereby providing adequate substrates for phytophiles) and by phytoplankton. Strong productivity could lead to the accumulation of organic matter and consequently the clogging of the mineral substrates required for lithopsammophiles to reproduce.

Our results show that, in natural lakes, the increase in the proportion of guarder species with temperature is a pattern consistent across regions. Three primary life history strategies,

representing the endpoints of a trilateral continuum, have been identified in North American fishes (Winemiller & Rose, 1992) and could be applied in a variety of regions and ecosystem types (Vila-Gispert *et al.*, 2002). In this framework, parental care is associated with a suite of traits classically considered indicative of a *K*-strategy (Pianka, 1970) and called "equilibrium strategy" (Winemiller & Rose, 1992). This strategy is likely to be an adaptation to stable, resource-limited and competitive environments (Pianka, 1972).

Although we have no data or means of evaluating resource availability or competition intensity, the lakes located in the coldest regions are also those experiencing the strongest environmental fluctuations. First, mean annual air temperature (T_m) is strongly negatively correlated to the annual temperature range calculated as the difference between T_{max} and T_{min} (Pearson correlation, $r=-0.87$ and -0.80 respectively for NEUSA and French natural lakes). Secondly, these cold lakes undergo longer periods of ice cover that frequently induce oxygen depletion. As water oxygen content and temperature regime are important dimensions of the ecophysiological requirements of fishes (Matthews, 1998), their variability is likely to exert sufficient pressure on fishes to constrain their life history strategies.

Furthermore, warmer lakes tend to be located in the downstream parts of the basins and hence connected to larger rivers that are more stable than small streams. Dispersal between the lakes and the adjacent riverine systems may therefore also contribute to explain the presence of guarders in warmer lakes. Therefore, the observed increase in Guarder with T_m meets the expectations of Winemiller and Rose (1992).

However, we also noticed that the proportion of guarders in reservoirs decreased with lake size that can be considered as a surrogate for environmental stability (Jackson *et al.*, 2001), which seems to contradict the upon framework.

These results deserve to be considered within the context of current global change. The predicted increase in average global air temperature is about 4°C within the coming half century (Boer *et al.*, 1992). The models fitted here suggest that the community reproductive traits could strongly respond to such warming (Figure 7). The communities of the coldest lakes could be those most affected in such a scenario.

Trophic traits of fish communities in lakes

Unrelated fish species happen to evolve similar morphological adaptations to their main food resources or feeding habitats (Winemiller *et al.*, 1995; Hugueny & Pouilly, 1999). However, the trophic models obtained here were only statistically significant for NEUSA lakes, even

though the ones obtained for French lacustrine water bodies generally displayed similar tendencies (Table 5). In NEUSA, Lkha was the main variable contributing to explain the variability of CTT in reservoirs while both Tm and Lkha significantly the variations in CTT in natural lakes. Tm is likely related to the amount of food resource available within each lake (although primary productivity might be more explained by nutrients) while lake area could, to some extent, reflect the diversity of the available food items.

These results put forward that the constraints driving convergent morphological evolution at the species level do not transfer at the community level for lacustrine fishes in the temperate regions of the northern hemisphere. At least three non-exclusive factors could explain this absence of convergence.

First, apart from the great lakes, lentic systems generally support very few specialist species due to their geologically ephemeral nature (Matthews, 1998). This is also true for reservoirs that are inhabited mainly by generalists due to the temporal fluctuations induced by hydraulic management practices such as electricity production (Fernando & Holcik, 1991). Indeed, most of these species are rather opportunistic feeders and our CTT, based on their classification into trophic guilds, may not accurately reflect the trophic structure of the fish communities. On some more accurate data sets including abundance estimations and individual measurements, it may be more informative to use individual-level guild assignment that could account for the frequent diet shifts fish species undergo along their ontogenic development.

Secondly, trophic structure appears constant across environmental gradients in French lakes. Strong trophic constraints on communities may lead to guild proportionality, i.e. a proportional representation of the different guilds that is constant between communities (Cohen, 1977; Jeffries & Lawton, 1985). If that was the case, convergence as we considered it here was not to be expected and the consistency of the trophic structure of communities across regions should be searched using other methods such as null models (Connor & Simberloff, 1979; Gotelli & Graves, 1996) developed to identify assembly rules (Diamond, 1975; Weiher & Keddy, 2001).

Third, the absence of convergence may reflect the strong constraints that historical and biogeographical processes have set upon local contemporary fish communities in Western Europe. It has already been shown for Mammals that trophic characteristics of species in a given region were strongly influenced by regional and phylogenetic history, and largely by the characteristics of species that initially colonised these regions (Kelt *et al.*, 1996). The

extinctions of the Pleistocene (Moyle & Herbold, 1987; Banarescu, 1989) were not only massive, but certainly also selective upon species traits. Western Europe underwent the most severe climatic conditions during the glaciations and had few catchments that could serve as refuges for freshwater species (Reyjol *et al.*, in press). Thus, the filtering of the ancestral taxocenes has certainly been even more constraining in Europe and those species that are found at present in this temperate region are strongly selected subsets of the species pools prior to the glaciations in which generalists are overrepresented.

Phylogeny

Although the pool of species dwelling NEUSA and French lakes are clearly distinct with only 10% of fishes occurring in both regions, they can not be considered independent in that they share 9 families. Such non-independence may have important consequences in community ecology (Webb *et al.*, 2002) due to niche conservatism (Wiens & Graham, 2005). Indeed, depending on the level of phylogenetic homogeneity across regions, similarity in ecological requirements between closely related species may explain most of the patterns identified in our study. For example, if families were restricted in distribution to a single region, we could expect any of the cases displayed in Figure 2 due to idiosyncratic family-level niche requirements. If similar families were present in both regions, we could expect case 6 if the environmental gradient did not correspond to a niche dimension influencing species distribution, or case 1 due to the equivalent sorting of families along environmental gradients across regions. Such sorting is well documented for river Salmonids that are known to occur in cold waters both in France (Huet, 1949; Illies & Botosaneanu, 1963) and in USA (Rahel & Hubert, 1991; Torgersen *et al.*, in press). This family is both very homogenous in terms of reproductive requirements (lithophilous and nest spawners) and clearly distinct from the others. Therefore, the response of CRT to temperature may be strongly related to the distribution of Salmonids along the temperature gradient. However, the response of Phyto and Guarder to temperature remains highly significant on the subset of lakes that do not shelter any Salmonids species ($P = 4.19e-10$ and $1.61e-07$, respectively). This shows the robustness of the relationship that can not be explained solely by the distribution of this family. However, the slope of the relationship is steeper in lakes with Salmonids. Therefore, the overall response of CRT to temperature is likely attributable to the combined effects of niche conservatism within families that are shared between regions and of community processes.

While some families with holarctic distributions may contribute to explain the convergence,

those that are restricted to a single region can explain some of the differences the traits of species pools. For example, in North America, the Centrarchidae and Ictaluridae are two families of freshwater fishes of which most species inhabit still waters. They are predators with advanced styles of reproduction (nesting and guarding) that are uncommon in the European fish fauna (Mahon, 1984).

Potential developments

Throughout this article, lake habitat conditions have been summarised using only two variables: lake surface area and mean annual temperature. The choice of environmental parameters constraining community features is essential to the search of convergence. The absence of response in CTT in French lakes may result from inappropriate environmental gradients. For example, water quality variables directly related to primary productivity, but unavailable on the French lakes, may have revealed different patterns. In a context of increasing anthropogenic stress exerted on freshwater ecosystems, measurements of several types of such stresses may also be useful for convergence assessment and for the development of the scientific knowledge necessary to design efficient bioassessment tools using lake fish communities. Our results further indicate some very consistent responses of community attributes to environmental gradients, which highlights the need for controlling effects of natural variability on fish metrics when developing broad scale bioassessment tools.

The widespread introduction of fish species in lakes frequently leads to the establishment of new species in both study regions (Whittier & Kincaid, 1999; Argillier *et al.*, 2002a; Irz *et al.*, 2004a; Irz *et al.*, 2004b). This constitutes a disturbance in community composition that certainly perturbs both species richness and community functional attributes. This was not considered in our study. Obviously, carrying out such a study exclusively using data on lakes without introduced species would have been preferable, but such sites are rare and almost restricted to small natural lakes. Omitting the introduced species from the analyses would not have solved this problem because it would have meant working on a subset of the actual communities and therefore would have been difficult to interpret. Apart from a few Salmonids in both regions or the pike *Esox lucius* in France that are maintained artificially through stocking, most of the introduced species successfully established populations in lakes, thereby showing that the local environmental conditions suit their requirements.

This study revealed some patterns consistent across regions. However, phylogenetic constraints, past events such as the diversification of the North American fish fauna, the

selective extinctions during the Pleistocene glaciations and the subsequent recolonisations, by their influences on the regional species pools, contribute to explain the contemporary patterns of fish communities of north temperate regions.

Whether due to community-level processes or to the similar sorting of families along a temperature gradient, the distributional patterns observed here suggest that the reproductive attributes of fish communities are likely to be altered in the event of global warming.

Acknowledgements

We would like to thank the numerous persons and institutions who provided data for this study, particularly Conseil Supérieur de la Pêche, Ecole Nationale Supérieure d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France for French lakes. Jean-François Holley and Cédric Lanoiselée are greatly acknowledged for database and GIS handling. Nicolas Poulet provided constructive comments on the draft. Although the data collection on Northeast USA lakes has been funded wholly or in part by the U.S. Environmental Protection Agency through its EMAP Surface Waters Program, it has not been subjected to Agency review, and therefore does not necessarily reflect the views of the Agency and no official endorsement of conclusions should be inferred.

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LEGENDS

Figure 1: Box-plot representations of the features of the lakes of France (FR) and NEUSA (US). T_m = Mean annual air temperature, °C; T_{min} = Minimum monthly air temperature, °C; T_{max} = Maximum monthly air temperature, °C; Elev = square root(altitude above sea level, m); AreaWS = log(catchment area, ha); Lkha = log(lake area, ha); Shore = log(Shoreline length, m); AvDep = log(mean depth, m).

Figure 2: Summary of the conceptual framework and the analytical procedure implemented to test for between-regions similarities in the attribute (M) of fish communities. In order to gain clarity, the only environmental variable considered was lake area (Lkha) but the actual procedure was similar for temperature (T_m).

Figure 3: Rarefaction curves indicating the cumulated number of species found in random draws of water bodies differing in number.

Figure 4: Log-log scatterplot of species richness (SR) vs. lake area (Lkha) for the natural lakes (NL) and reservoirs (Res) of NEUSA (US) and France (FR) with regression lines.

Figure 5: Examples of relationships between community reproductive traits and mean annual temperature (T_m). (A) Phyto (percentage of phytophiles, *logit* scale) with a single model fitted for both regions and both lake types. (B) Guarder (percentage of the species that spawn in a nest and guard it, *logit* scale) with different trend curves fitted for natural lakes (NL) and reservoirs of NEUSA (US) and France (FR). Trends assessed using GLM with binomial error distribution and logit link function.

Figure 6: Synoptic of the various processes potentially contributing to the increase in fish species richness with lake size. The signs indicate the direction of the effects. The shaded signs are those influenced by the regional species pool.

Figure 7: Modelled response of Phyto (in both lake types and regions) and Guarder in reservoirs (Res: reservoirs; FR: France; US: Unites States) to a 4°C increase in mean annual air temperature as a function of current mean annual air temperature.

Table 1: Pearson correlation coefficients between environmental variables including lakes of NEUSA (above the diagonal) and France (below the diagonal). Values over 0.4 are in bold and are highly significant ($P < 0.001$). Tm = Mean annual air temperature, °C; Tmin = Minimum monthly air temperature, °C; Tmax = Maximum monthly air temperature, °C; Elev = square root(altitude above sea level, m); AreaWS = log(catchment area, ha); Lkha = log(lake area, ha); Shore = log(Shoreline length, m); AvDep = log(mean depth, m).

Table 2: List of the reproductive and trophic traits considered to derive community metrics.

Table 3: Pearson correlation coefficients between fish metrics including lakes and reservoirs of NEUSA (above the diagonal) and France (below the diagonal). See Table 2 for metrics names.

Table 4: Distribution of the fish species sampled from NEUSA (US) and French (FR) across families and functional guilds. *exclusively composed of exotic species.

Table 5: Summary of models of fish metrics in reservoirs (Res) and natural lakes (NL) in France (FR) and in North-East USA (US) vs. mean annual air temperature (Tm) and lake area (Lkha). Species richness (SR) models are multiple regressions. Functional metrics models are GLM with binomial distribution errors (link function: logit). Table entries are model coefficients, independent contributions of independent variables to the adjusted R-squared (p_Tm and p_Lkha), residual deviance (Dev.), and model significance (Sig.). * significant at 0.05 level, ** significant at 0.01 level, *** significant at 0.001 level. See table 3 for metrics names.

Table 6: Summary of final models of species richness (SR, linear models) and proportions of species (generalised linear models, distribution error: binomial, link function: logit) belonging to reproductive guilds vs. Lake area (Lkha) or temperature (Tm) . LakeType: natural lake (NL) or reservoir (Res). Dev: residual deviance of the model. df: residual degree of freedom, R²: pseudo-R-squared. * significant at 0.05 level, ** significant at 0.01 level, *** significant at 0.001 level. See table 3 for metrics names.

Table 7: Summary of the convergence tests referring to the cases displayed in Figure 2 for natural lakes (NL) and reservoirs (Res). The environmental gradients used to assess convergence are indicates (Lkha: lake area, Tm: mean annual air temperature). See Table 1 for metrics abbreviations.

Table 8: Pearson correlation coefficients between the log of the lake area (Lkha), number of individuals sampled (NIS) and species richness (SR) obtained for Northeast USA natural lakes and reservoirs. * significant at 0.05 level, ** significant at 0.01 level, *** significant at 0.001 level.

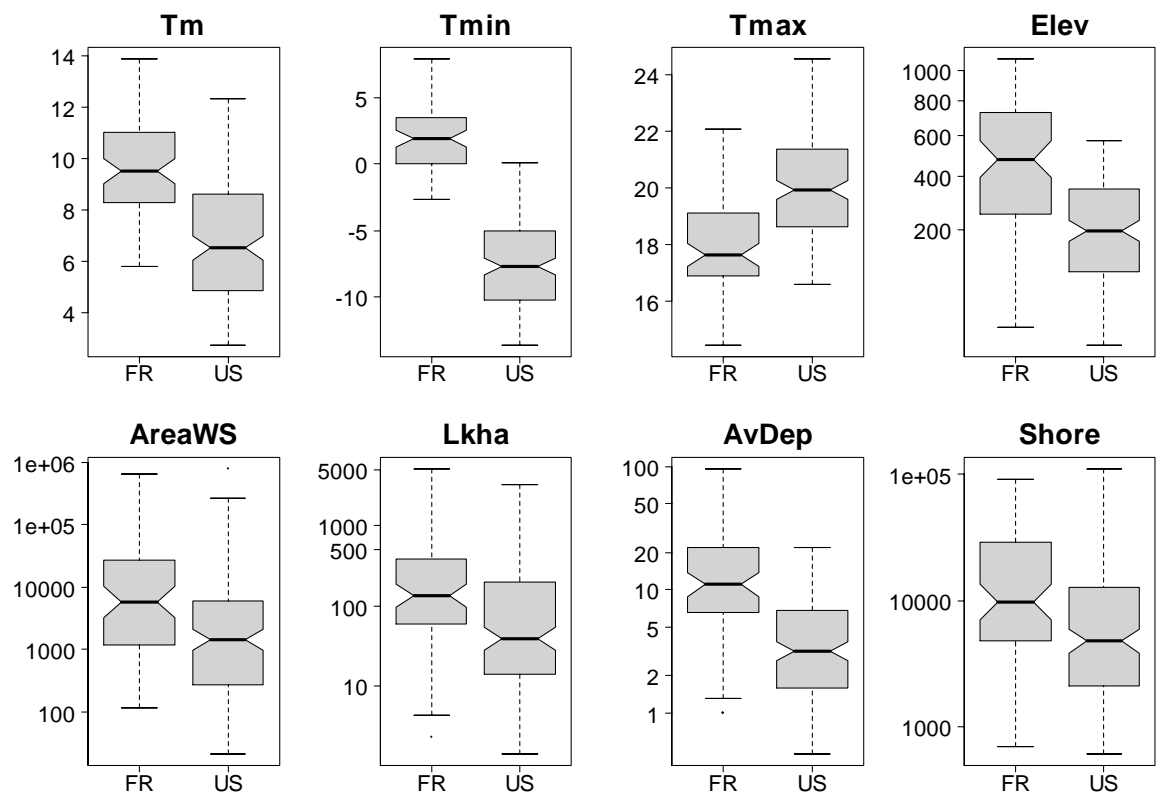


Figure 1

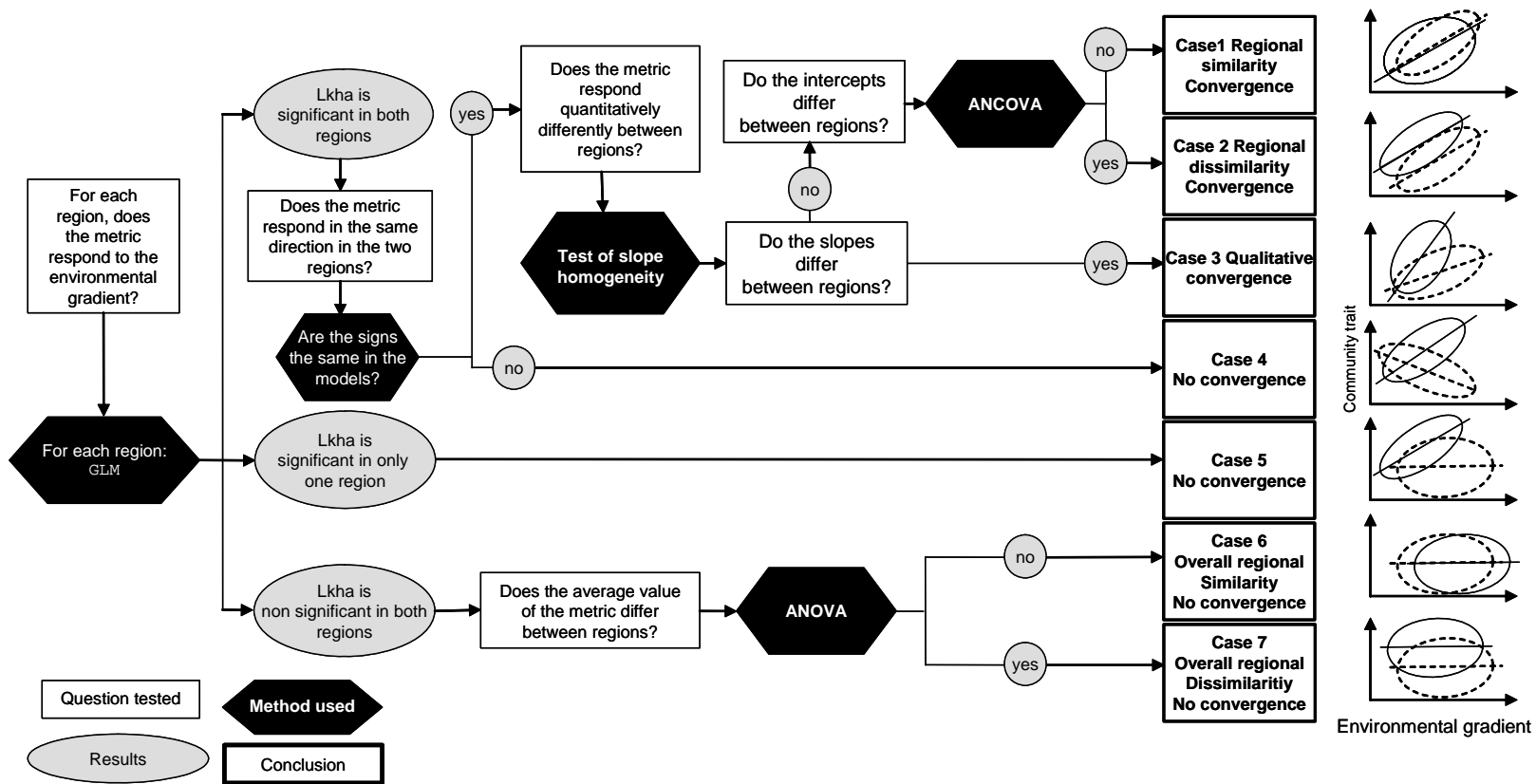


Figure 2

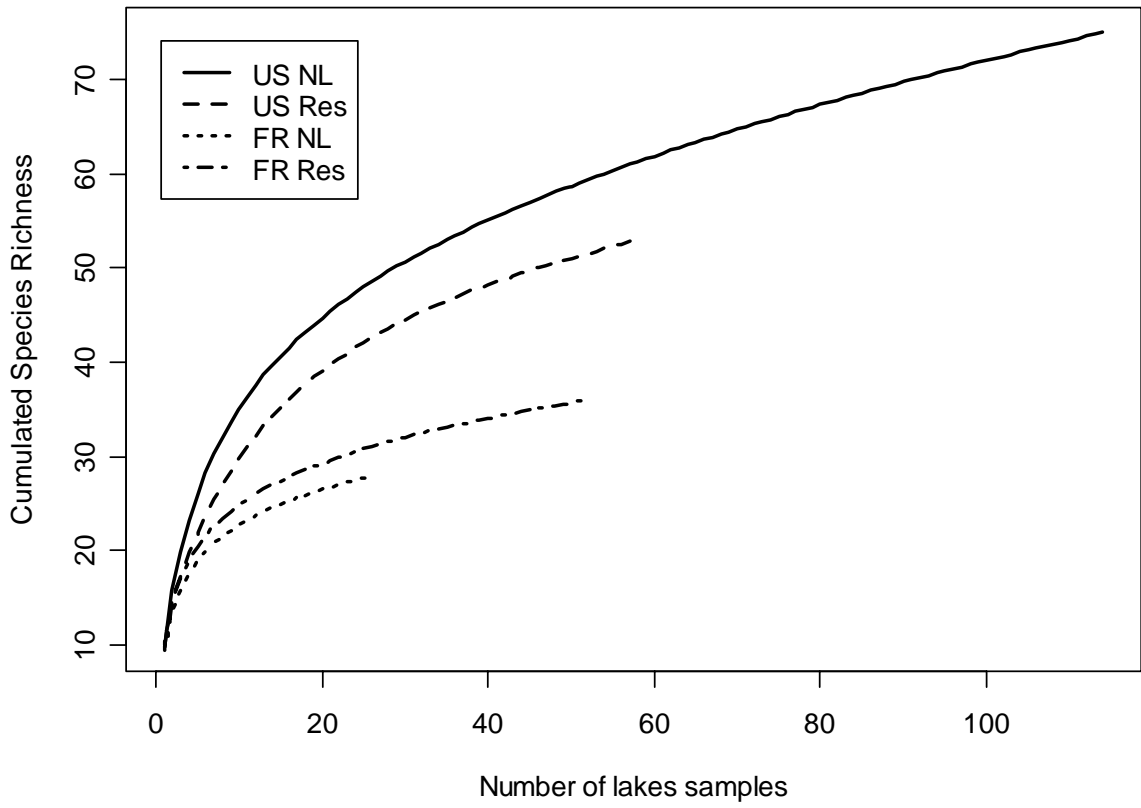


Figure 3

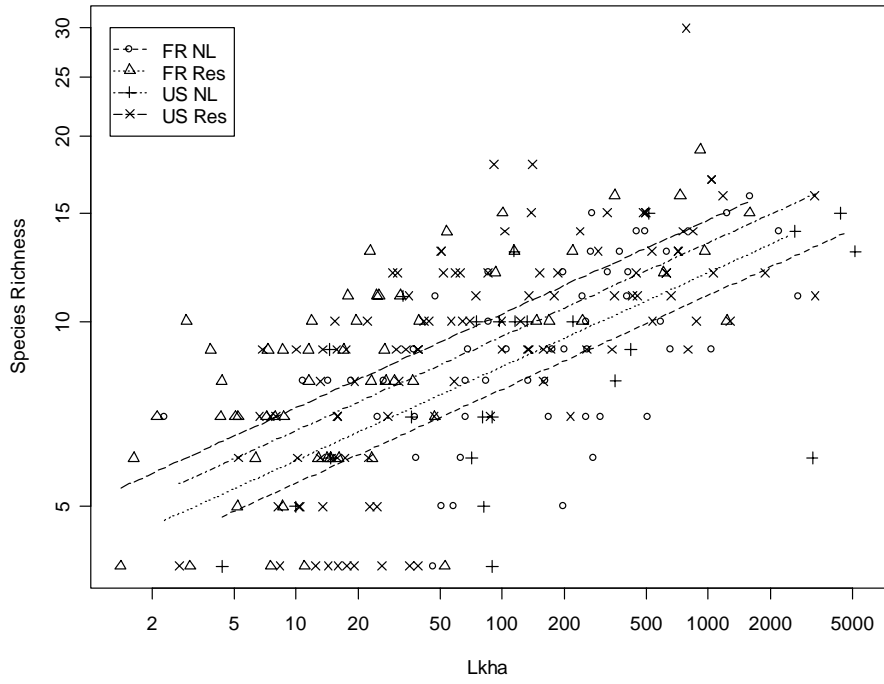


Figure 4

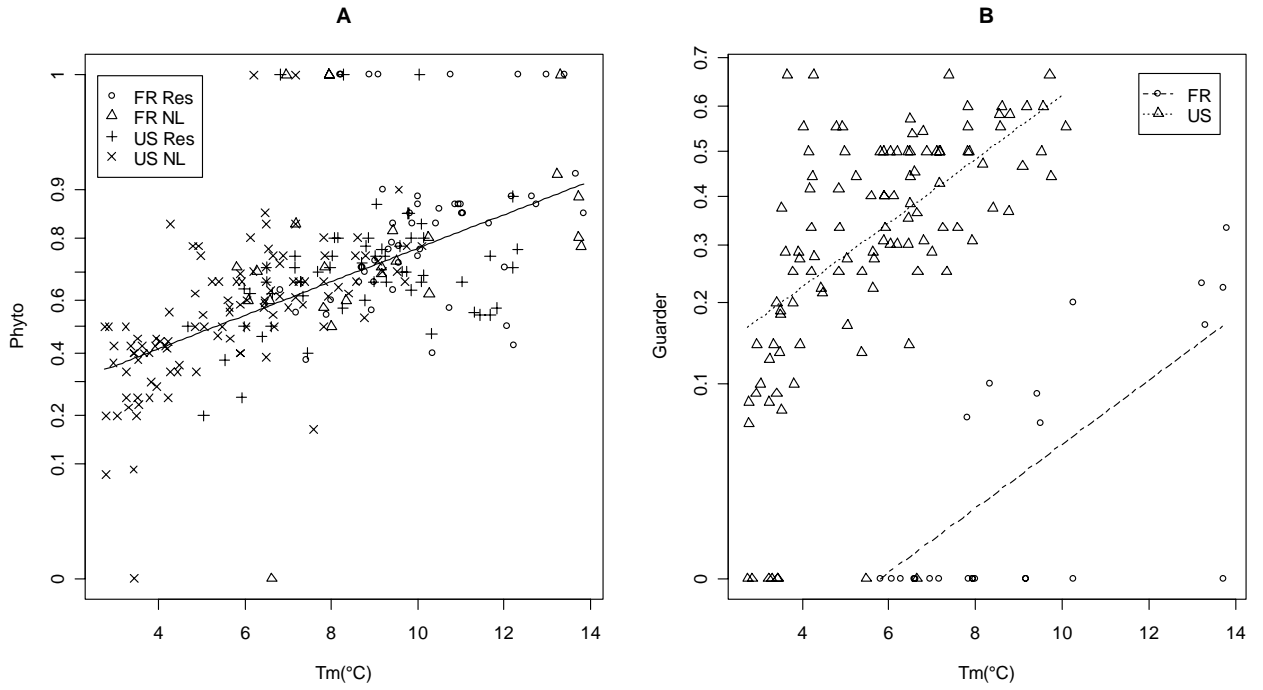


Figure 5

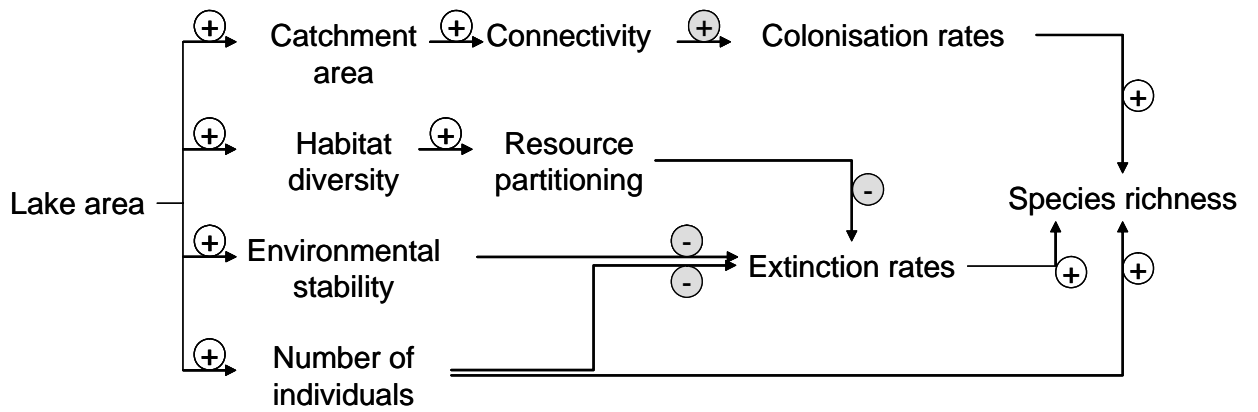


Figure 6

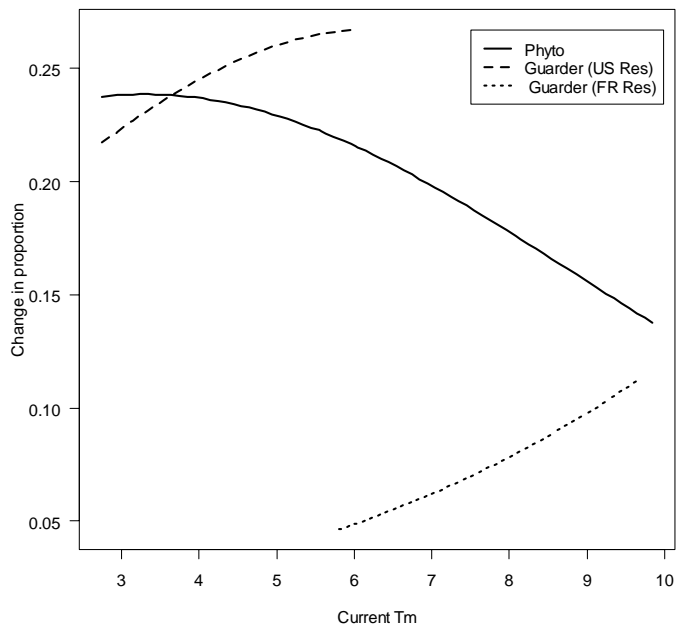


Figure 7

	Tm	Tmin	Tmax	Elev	AreaWS	Lkha	Shore	AvDep
Tm		0.992	0.978	-0.672	-0.137	-0.344	-0.231	-0.214
Tmin	0.956		0.946	-0.631	-0.127	-0.329	-0.211	-0.201
Tmax	0.925	0.819		-0.737	-0.142	-0.342	-0.241	-0.227
Elev	-0.790	-0.759	-0.633		-0.102	0.098	0.026	0.127
AreaWS	0.138	0.164	0.149	-0.012		0.697	0.729	0.441
Lkha	0.000	0.006	0.036	0.090	0.716		0.948	0.681
Shore	0.059	0.091	0.091	0.092	0.851	0.909		0.604
AvDep	-0.243	-0.220	-0.123	0.456	0.485	0.633	0.588	

Table 1

	Trait code	Description
Reproductive traits	LithPsam	Lithopsammophilous: can reproduce on mineral substrates
	LithPsam_strict	Strictly lithopsammophilous: need mineral substrates to reproduce
	Phyto	Phytophilous: can reproduce on vegetal substrates
	Phyto_strict	Strictly phytophilous: need vegetal substrates to reproduce
	Guarder	Guarders: Exhibit parental care of the nests
Trophic traits	Pisc	Piscivorous: Feed on fish at least partially when adults
	Pisc_strict	Strictly piscivorous: Feed exclusively on fish when adults
	Inv	Invertivorous: Feed at least partially on invertebrates
	Inv_strict	Strictly invertivorous: Feed exclusively on invertebrates
	Herb	Herbivorous: Feed on vegetal items
	Herb_strict*	Strictly herbivorous: Feed exclusively on vegetal items
	Omn	Omnivorous: Feed on both animal and vegetal items
	Benth	Benthophageous: Feed mainly on benthic items
	Benth_strict	Strictly benthophageous: Feed exclusively on benthic items

Table 2

	log(SR)	LithPsam	LithPsam_strict	Phyto	Phyto_strict	Guarder	Pisc	Pisc_strict	Inv	Inv_strict	Herb	Omn	Benth	Benth_strict
log(SR)		0.162	0.198	-0.214	-0.203	-0.119	-0.185	-0.047	0.042	0.213	-0.070	-0.077	0.128	0.140
LithPsam	0.125		0.223	-0.150	-0.856	-0.029	-0.019	-0.203	0.176	-0.065	0.132	0.109	0.012	-0.018
LithPsam_strict	0.127	0.377		-0.908	-0.209	-0.008	0.051	-0.278	0.240	0.082	0.068	0.040	-0.078	0.032
Phyto	-0.129	-0.310	-0.905		0.208	-0.014	-0.065	0.266	-0.232	-0.085	-0.028	0.000	0.096	-0.013
Phyto_strict	-0.163	-0.829	-0.343	0.345		0.006	0.007	0.200	-0.176	0.053	-0.098	-0.076	0.017	0.054
Guarder	0.079	-0.068	-0.242	0.236	0.039		0.648	-0.165	0.181	-0.449	0.034	0.047	-0.637	-0.598
Pisc	-0.093	-0.116	-0.099	0.072	0.073	0.475		-0.076	0.087	-0.711	0.135	0.148	-0.716	-0.723
Pisc_strict	-0.078	-0.221	-0.444	0.438	0.212	0.268	0.247		-0.949	-0.035	-0.074	-0.048	0.111	0.042
Inv	0.073	0.219	0.440	-0.435	-0.210	-0.270	-0.245	-0.996		0.024	0.066	0.074	-0.125	-0.066
Inv_strict	0.178	0.130	0.254	-0.231	-0.098	-0.361	-0.817	-0.371	0.366		-0.340	-0.350	0.644	0.770
Herb	-0.265	0.038	0.033	0.013	0.056	-0.150	0.037	-0.125	0.125	-0.139		0.964	-0.156	-0.241
Omn	-0.269	0.037	0.031	0.014	0.056	-0.150	0.039	-0.125	0.127	-0.141	0.998		-0.168	-0.258
Benth	0.184	0.191	0.026	-0.009	-0.170	-0.276	-0.539	-0.160	0.156	0.418	0.049	0.047		0.846
Benth_strict	0.236	0.135	0.090	-0.075	-0.103	-0.284	-0.551	-0.179	0.176	0.489	-0.062	-0.065	0.871	

Table 3

Region	FR	US
Family		
Amiidae		1
Anguillidae	1	1
Aphredoderidae		1
Atherinidae		1
Balitoridae	1	
Blenniidae	1	
Catostomidae		6
Centrarchidae	2*	13
Clupeidae		2
Cobitidae	1	1
Cyprinidae	19	24
Cyprinodontidae		2
Esocidae	1	2
Gasterosteidae		3
Ictaluridae	1*	6
Lepisosteidae		1
Lotidae	1	1
Mugilidae	1	
Osmeridae		1
Percichthyidae		1
Percidae	3	5
Percopsidae		1
Poecilidae	1*	
Salmonidae	5	8
Sciaenidae		1
Siluridae	1	
Umbridae		1
Functional guild		
Lithopsammophiles	29	63
Phytophiles	20	38
Guarder	8	30
Piscivores	15	42
Invertivores	36	74
Omnivores	10	18
Benthic feeders	17	19

Table 4

Lake type	Metric	Region	Intercept	Tm	Lkha	p_Tm	p_Lkha	Dev.	Sig.
Reservoirs									
FR: n=51	log(SR)	FR	1.561 ***	0.000	0.124 ***	0.7	29.3	----	***
		US: n=58	US	1.221 ***	0.045 *	0.160 ***	2.8	49.0	----
	LithPsam	FR	0.669	0.003	0.096	0.2	7.2	19.296	
		US	1.678 **	-0.085	0.073	9.3	6.5	27.596	
	Phyto	FR	0.242	0.190 **	-0.172 *	12.7	8.8	57.275	***
		US	-0.233	0.136 **	-0.077	15.2	5.8	47.894	**
	Guarder	FR	-1.727	0.117	-0.273 **	5.4	14.7	48.581	**
		US	-0.998 *	0.173 ***	-0.112 *	29.5	13.6	31.489	***
	Pisc	FR	0.388	-0.013	-0.021	0.2	0.3	24.008	
		US	4.079 ***	-0.094	-0.296 ***	1.0	16.8	73.914	***
	Inv	FR	2.610 *	-0.073	0.001	3.3	0.1	24.212	
		US	2.458 **	0.076	-0.211 **	3.8	16.5	36.700	**
	Omn	FR	-1.119	0.003	0.118	0.4	12.4	20.316	
		US	0.473	-0.035	-0.198 ***	0.8	39.6	21.627	***
	Benth	FR	-0.983	0.034	-0.002	1.2	0.1	28.406	
		US	-2.089 *	-0.219 *	0.235 *	8.82	9.21	52.513	**
Natural lakes									
FR: n=24	log(SR)	FR	1.548 ***	-0.004	0.123 **	0.6	32.9	----	**
		US: n=110	US	1.042 ***	0.059 ***	0.189 ***	5.6	50.3	----
	LithPsam	FR	0.469	0.142	-0.062	20.2	1.2	12.058	
		US	1.423 ***	-0.131 ***	0.112 *	17.8	10.2	59.825	***
	Phyto	FR	-0.395	0.211 **	-0.095	22.2	1.4	27.987	*
		US	-1.041	0.290 ***	-0.102 *	45.2	7.7	86.381	***
	Guarder	FR	-7.921	0.393 ***	0.224	46.3	17.5	11.061	***
		US	-2.062	0.256 ***	-0.018	35.2	1.5	105.580	***
	Pisc	FR	-0.115	0.043	-0.043	5.4	2.6	7.995	
		US	1.249 **	0.141 **	-0.094	7.4	3.1	150.965	***
	Inv	FR	2.432 **	-0.028	-0.027	1.9	1.2	6.578	
		US	3.473 ***	-0.213 ***	0.002	14.7	0.4	99.561	***
	Omn	FR	-0.424	0.078	-0.120	19.5	28.7	3.548	
		US	0.362	-0.062	-0.149 ***	2.7	15.2	64.658	***
	Benth	FR	-1.905 **	0.047	0.121	7.9	20.2	9.541	
		US	-2.886	-0.154 *	0.192 *	5.4	5.9	105.615	***

Table 5

Metric	Lake type	Difference in intercept		Difference in intercept		log(Lkha)	Tm	Deviance	Df	R ²
		(Region=US)	(Lake Type=Res)	(Region=US)	(Lake Type=Res)					
Log(SR)	Res + NL	1.346 ***	0.197 ***	0.085 *	0.153 ***	---	---	---	239	0.436
Guarder	Res	-5.251 ***	2.991 ***	---	0.274 ***	---	---	121.89	131	0.555
Guarder	NL	-0.971 ***	1.736 ***	---	---	-0.181 ***	---	98.079	106	0.673
Phyto	Res + NL	-1.291 ***	---	---	---	0.243 ***	---	245.6	241	0.454

Table 6

	log(SR)		LithPsam		Phyto		Guarder		Pisc		Inv		Omn		Benth	
	Nat	Res	Nat	Res	Nat	Res	Nat	Res	Nat	Res	Nat	Res	Nat	Res	Nat	Res
1					Tm	Tm										
2	Lkha	Lkha					Tm	Lkha								
3																
4																
5			X						X	X	X	X	X	X	X	X
6																
7				X												

Table 7

	Lkha vs NIS	NIS vs SR	SR vs Lkha
Natural lakes	0.382 ***	0.291 ***	0.656 ***
Reservoirs	0.536 ***	0.341 **	0.59 ***

Table 8

Titre: Approche comparative des communautés piscicoles lacustres.

RESUME

L'objectif de cette thèse est de préciser les patrons de variabilité des communautés piscicoles entre les plans d'eau en vue de contribuer à la compréhension des mécanismes qui en sont responsables, qu'ils soient naturels ou conséquences des activités de l'Homme. Cette approche macroécologique des peuplements en France et dans le nord-est des Etats-Unis a montré des patrons d'addition et de remplacement d'espèces en fonction des caractéristiques abiotiques locales et de la position géographique des plans d'eau. Le rôle structurant des interactions biotiques est moins évident. Les introductions d'espèces modifient radicalement la relation entre richesses locales et régionales alors que l'occupation agricole et urbaine des bassins versants entraîne des modifications de la structure en guildes des communautés. La convergence observée dans la réponse des communautés aux conditions climatiques et à la taille du plan d'eau montre que la disponibilité des habitats de reproduction exerce une contrainte forte sur les communautés locales et autorise quelques inférences sur les conséquences du changement climatique global. L'étude des règles d'assemblage et une réflexion relative au fonctionnement de métacommunautés à l'échelle des bassins versants offrent des perspectives sur les plans scientifique et appliqués.

Mots-clé: Macroécologie, lac, retenue artificielle, communauté piscicole, facteurs environnementaux, interactions interspécifiques, impacts, espèces introduites, convergence, guildes.

Title: Comparative approach of lacustrine fish communities.

SUMMARY

The objective of this thesis was to investigate fish community patterns in the lakes of France and northeast USA in order to infer the underlying processes. This was achieved using a macroecological approach. Fish communities displayed patterns of addition and replacement of species along environmental gradients related to the lakes' local features and geographic location. The structuring role of biotic interactions was not demonstrated. Human-mediated species introductions clearly perturb the relation of local vs. regional species richnesses. Land use in the lakes' catchments appears to modify guild community structure. The response of community structure along gradients of temperature and lake size displayed convergence between the lakes of France and northeast USA, thereby indicating that the availability of spawning substrates exerts a strong constraint on local communities. These results allow inferring the potential effect of global warming on lake fish communities. Complementary studies of assembly rules and metacommunity processes should be fruitful for both basic and applied ecology.

Keywords: macroecology, lake, reservoir, fish community, environmental factors, interspecific interactions, impacts, non-native species, convergence, guilds.

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