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par

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Outils de diagnose structurelle et fonctionnelle pour la bioévaluation de la qualité des sédiments associés à la présence de barrages. Approche intégrée de la population au processus écosystémique.

Soutenue le **3 Juillet 2012** devant la commission d'examen :

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« Les espèces qui survivent ne sont pas les espèces les plus fortes, ni les plus intelligentes, mais celles qui s'adaptent le mieux aux changements »

Charles Darwin *(1809-1882)*

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Chapitre I

Introduction générale

1. Les sédiments aquatiques : problématique qualitative et quantitative

1.1. Les sédiments : composante essentielle de l'intégrité des écosystèmes aquatiques

Dans sa définition la plus stricte et générale, un sédiment est une particule minérale ou organique de taille variable : des sédiments fins constituant la charge solide en suspension jusqu' aux sédiments plus grossiers, constituant la charge de fond des rivières. Ce travail de recherche se focalise volontairement sur les sédiments comme définit par le groupe de travail sur l'analyse et le suivi des substances prioritaires (AMPS) de la Directive Cadre européenne sur l'Eau (DCE), à savoir : « **matériel particulaire tel que le sable, le limon, les argiles ou la matière organique qui a été déposé sur le fond des masses d'eau et qui est susceptible d'être transporté par l'eau** » (Stronkhorst *et al.*, 2004).

Les sédiments des cours d'eau ont une **origine extrinsèque** associée aux dépôts atmosphériques des poussières et particules érodées transportées par le vent, à l'érosion des minéraux et matériaux organiques des sols du bassin versant, et une **origine intrinsèque**, associée à l'érosion des berges et des plaines alluviales, à l'apport des affluents et à la resuspension des sédiments des rivières suite aux variations d'écoulement (Taylor et Owens, 2009). L'hydromorphologie naturelle des rivières maintient **un équilibre dynamique** entre sa charge solide et sa charge liquide par des mécanismes d'érosion, de transport et de dépôt (Brils, 2008). Cette hydrodynamique sédimentaire participe à la genèse de la **diversité des habitats** aquatiques et permet d'offrir des conditions favorables à une large **diversité d'organismes** estimée dans les sédiments de la surface du globe à plus de 100 000 espèces d'invertébrés benthiques, 10 000 espèces d'algues et 20 000 espèces de protozoaires et de bactéries (Palmer *et al.*, 2000).

Les sédiments exercent un contrôle fondamental sur le comportement hydrologique et géomorphologique des rivières. En outre, les sédiments et le biota qu'ils abritent ont **un rôle fonctionnel majeur** associé aux transformations biogéochimiques, au maintien de la qualité de l'eau, au processus de décomposition de la matière organique et à la production primaire. Par exemple, les processus microbiens qui prennent place dans les sédiments permettent le

bon fonctionnement des cycles nutritifs, primordiaux pour l'ensemble de la colonne d'eau. Les macroinvertébrés, compartiment également essentiel au bon fonctionnement biogéochimique des sédiments, utilisent ces substrats pour déposer et incuber leurs œufs, pour s'alimenter (Minshall, 1984), comme refuge contre la prédation (Brusven et Rose, 1981), les perturbations physiques (Dole-Olivier *et al.*, 1997; Gayraud *et al.*, 2000) et les évènements extrêmes de sécheresse (Fenoglio *et al.*, 2006). En outre, l'activité de la macrofaune bioturbatrice est essentielle pour favoriser la minéralisation de la matière organique accumulée dans les sédiments et permettre un bon fonctionnement des cycles du carbone, de l'azote et du phosphore notamment. En plus de leur rôle fondamental dans le fonctionnement hydrologique et géomorphologique des rivières, les sédiments aquatiques constituent des apports de limons fertiles en périodes de crues et d'inondation, essentiels au fonctionnement des plaines alluviales (Förstner et Salomons, 2010).

1.2. Enjeux écologiques associés à une double problématique

Il est largement admis que la problématique hydrosédimentaire est double. **Quantitative**, d'une part, résultante de l'occupation et des activités du bassin versant et des nombreuses **perturbations hydromorphologiques** des cours d'eau telle que la construction d'obstacles à l'écoulement naturelle des eaux et, **qualitative** d'autre part, associée principalement au **pouvoir adsorbant** des particules fines sédimentaires **des polluants** de la colonne d'eau.

1.2.1. Les sédiments, déséquilibres quantitatifs

Dépendants de l'occupation du bassin versant et des modifications hydromorphologiques des cours d'eau, l'excès ou au contraire le déficit en sédiments ont de graves conséquences sur l'intégrité des écosystèmes aquatiques. De nombreuses études ont montré que les flux de sédiments fins dans les rivières ont fortement augmenté dans le monde. Ces flux ont été associés à l'augmentation de l'érosion des sols suite aux **transformations des bassins versants** par les activités humaines telles que la déforestation, l'agriculture, la construction et les activités d'extraction de minerais (Wolman et Schick, 1967; Trimble, 1983;Dearing *et al.*, 1987; Walling, 1996; Foster et Lees, 1999; Owens *et al.*, 2005). Outre la modification des bassins versants, les **altérations hydromorphologiques** du linéaire des cours d'eau favorisent également l'apport et la rétention des sédiments fins. L'altération des habitats riverains

(plaines alluviales, ripisylve) a été identifiée comme principal facteur de contrôle de l'érosion des sols (De Baets *et al.*, 2011) et des berges (Eaton et Giles, 2009). La végétation dans le lit mineur des rivières influence aussi fortement les dépôts et la stabilisation du lit. Par exemple, des études récentes ont montré que les macrophytes et le periphyton sont importants dans le contrôle des dépôts et de la remise en suspension des sédiments (Wharton *et al.*, 2006; Heppell *et al.*, 2009; Jones *et al.*, 2011; Owens et Xu, 2011; Salant, 2011).

La présence d'obstacles à l'écoulement, tels que les seuils et les barrages, modifie également le transport sédimentaire et induit **une forte rétention des sédiments** dans les réservoirs. Le rapport de la Commission Mondiale des Barrages (2000) souligne l'étendue des interventions humaines sur les écosystèmes aquatiques par la construction de 45 000 barrages d'une hauteur supérieure à 15 mètres qui fragmentent plus de 60% des rivières dans le monde, et modifient de ce fait les flux sédimentaires. Vörösmarty (2003) estime par exemple que les réservoirs stockent environ 25 à 30% des flux totaux de sédiments vers les océans. En plus de ces grands barrages, de nombreux barrages de plus petites tailles et des seuils fragmentent le linéaire des cours d'eau pour la production d'hydroélectricité, la régulation du régime des eaux ou encore l'irrigation. En France, en plus des 700 barrages supérieurs à 5 mètres, 60 000 seuils et petits barrages (inférieurs à 5 mètres) ont été référencés (Fig.1), dont seulement 30% auraient un usage économique avéré (Malavoi *et al.*, 2011).

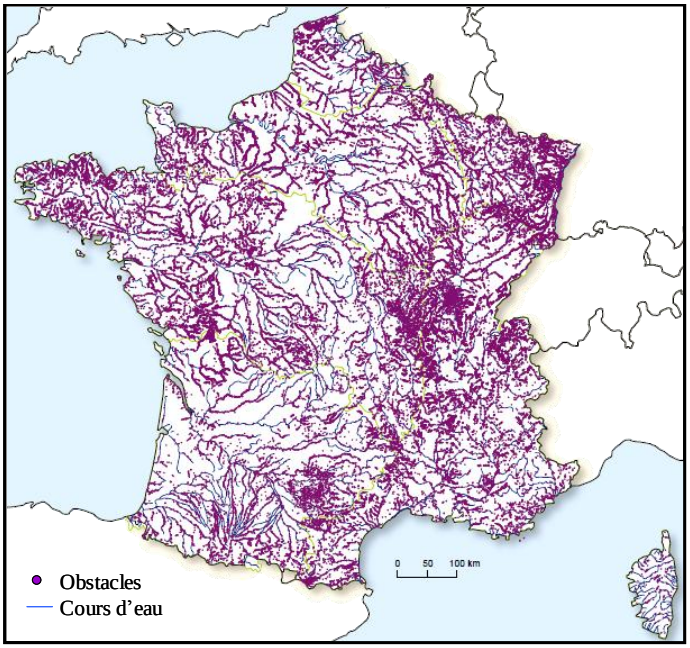

Fig.1.Référentiels des obstacles à l'écoulement (ROE) – Source : Onema

Ces apports excessifs de sédiments fins ont été reconnus comme **une limite majeure de l'amélioration écologique** des écosystèmes aquatiques (Larson *et al.*, 2001) et ont été identifiés comme une des principales **causes d'échec de la restauration des rivières** (Feld *et al.*, 2011). Les effets néfastes sur le biota d'un dépôt excessif en sédiments fins sont relativement bien documentés. Par exemple, l'augmentation de la turbidité réduit la production primaire et la perception visuelle des prédateurs (Davies-Colley *et al.*, 1992; Davies-Colley et Smith, 2001). Le colmatage modifie la structure du substrat et les habitats benthiques (Schälchli, 1992; Rehg *et al.*, 2005) et altère les échanges à l'interface eau-sédiment (Turnpenny et Williams, 1980; Richards et Bacon, 1994; Larsen *et al.*, 2011). Outre les effets négatifs associés aux dépôts, la remise en suspension des sédiments fins a également de nombreux effets adverses sur le biota. Pour les macroinvertébrés, par exemple, de tels effets peuvent être l'augmentation des taux de dérive (Rosenberg et Wiens, 1978) et la réduction de la diversité et des densités des populations (Nuttall et Bielby, 1973; Gray et Ward, 1982; Quinn *et al.*, 1992; Shaw et Richardson, 2001; Bilotta et Brazier, 2008). Pour les poissons, il a été rapporté une augmentation de la mortalité des alevins, des œufs et des juvéniles (Newcomb et Flagg, 1983; Reynolds *et al.*, 1988), une réduction de la croissance (Shaw et Richardson, 2001) et des dommages physiques sur les branchies (Lake et Hinch, 1999). De plus, lorsque ces sédiments en suspension ont un fort contenu organique, leur décomposition peut réduire les niveaux en oxygène dissous dans l'eau et induire des conditions d'anoxie délétères pour la faune aquatique (Ryan, 1991).

En interrompant la **continuité écologique** et de ce fait le transport des sédiments, la présence de barrages induit en aval un **déficit** en sédiments. Tout comme son excès, le déficit en sédiment altère également le fonctionnement hydromorphologique et écologique des rivières. La faible charge en sédiments en aval des barrages (« hungry water ») peut conduire à une incision du chenal, à l'érosion des berges et à une modification de la composition granulométrique du lit (Kondolf, 1997). Ces phénomènes d'érosion traduisent la recherche d'un nouvel équilibre entre charge liquide et solide et sont souvent responsables de la détérioration d'ouvrages d'art tels que les ponts. En perturbant les flux sédimentaires, la présence de barrage affecte également la distribution des nutriments et des particules organiques, la chimie de l'eau (Crowder et Diplas, 2000), la composition et la disponibilité des habitats (Hart et Finelli, 1999). Or, les pertes d'habitat et de ressources alimentaires se traduisent communément par une forte diminution de la richesse en invertébrés (Dewson *et al.*, 2007; Morley *et al.*, 2008). D'une manière générale, la perte de connectivité associée à la

présence de barrage affecte tous les compartiments biologiques (Petts, 1984), particulièrement les poissons en limitant la migration des organismes amphihalins mais également holobiotiques (Ovidio et Philippart, 2002; Ovidio *et al.*, 2007).

1.2.2. Les sédiments : puits et sources de contamination

Il est très largement admis que les sédiments agissent comme **un réservoir et un vecteur** des pollutions anthropogéniques, et qu'à ce titre la question de leur qualité physico-chimique est cruciale. En effet, les sédiments ont une **forte capacité d'adsorption des polluants** tels que les métaux et les hydrocarbures (Cairns *et al.*, 1984) qui se lient préférentiellement aux particules fines (Estebe *et al.*, 1997). Généralement le stockage des contaminants dans les sédiments se produit dans les zones de dépôts du chenal des rivières et dans les plaines alluviales (Taylor et Owens, 2009). En favorisant la rétention des sédiments, les réservoirs constituent des zones privilégiées d'accumulation de contaminants, reflétant l'historique des pollutions issues des bassins versants. Malgré l'augmentation de la réglementation pour réduire les rejets polluants et l'amélioration de la qualité de l'eau, l'**héritage du passé** est encore présent dans les sédiments stockés derrière les barrages mais également dans le fond du chenal des rivières, dans les plaines alluviales, les lacs et les estuaires.

De ce fait, la contamination des sédiments est souvent plus forte que celle de l'ensemble de la colonne d'eau (Chapman, 1992; Piol *et al.*, 2006). Ces sédiments constituent **un risque latent**, non seulement à une échelle locale (dans les réservoirs par exemple), mais aussi pour les écosystèmes en aval. Les contaminants stockés peuvent être **remobilisés dans la colonne d'eau** à diverses occasions, entre autres lors de modifications des conditions physico-chimiques locales (Lafont *et al.*, 2007). Les sédiments eux-mêmes peuvent être **transportés en aval** à l'occasion de vidange ou d'effacements de barrages, provoquant des **perturbations physiques** (comme le colmatage des espaces interstitiels) **et chimiques** (Larsson, 1985; Asare *et al.*, 2000; Coulthard et Macklin, 2003). A ce titre, la contamination des sédiments menace l'intégrité écologique de nombreux hydrosystèmes (Neal *et al.*, 2005; Sheppard, 2005; Norris *et al.*, 2007; Johnston et Roberts, 2009).

Les contaminants stockés, s'ils sont biodisponibles, exercent, outre une toxicité aiguë, des **réponses chroniques et sublétales** conduisant à la modification des assemblages biologiques

et notamment à la disparition des macroinvertébrés sensibles et, à travers leur accumulation, à la détérioration des espèces situées à des niveaux trophiques supérieurs (Field et Pitt, 1990; Beyer *et al.*, 2000; Viganò *et al.*, 2002; Yi *et al.*, 2008). Outre les impacts des dépôts, la remise en suspension de ces sédiments contaminés pose un sérieux risque pour les écosystèmes aquatiques. La fraction la plus fine des sédiments, qui accumule la plus grande quantité de contaminants du fait d'un plus grand rapport surface/volume et d'une plus grande disponibilité en sites d'adsorption, est également la fraction la plus facilement et durablement remise en suspension. La remise en suspension des sédiments induit des modifications chimiques des sédiments telles que l'augmentation du potentiel redox et la diminution du pH qui ont tendance à augmenter la biodisponibilité des métaux (Simpson *et al.*, 1998). La remise en suspension des sédiments a été identifiée comme un **vecteur majeur du transport des contaminants**, pouvant induire une toxicité par voie aqueuse (contaminants relargués par les particules sédimentaires) ou par ingestion des particules sédimentaires (Bonnet *et al.*, 2000; Hill *et al.*, 2009).

1.2.3. Facteurs de stress multiple associés aux barrages

Les aspects quantitatifs et qualitatifs interviennent souvent conjointement. La plupart des écosystèmes aquatiques sont affectés par une multitude de perturbations lesquelles peuvent induire des **impacts cumulés et synergiques** (Owens *et al.*, 2010). L'évaluation et la compréhension des réponses des écosystèmes aux multiples facteurs de stress représentent un enjeu primordial pour une gestion durable de la ressource en eau mais également pour prédire l'impact des changements globaux.

La présence de barrages illustre ce **contexte de perturbations multiples**, dans la mesure où ils induisent des **perturbations physiques et chimiques** lors de l'accumulation de sédiments contaminés. Ce contexte de stress multiples peut être résumé (i) dans les réservoirs par la contrainte physique associée à la conversion des habitats lotiques en habitats lentiques, à la perte de l'hétérogénéité des habitats due à une forte sédimentation et à la rupture de la continuité écologique limitant la dispersion des organismes, alors soumis à un stress toxique persistant ; (ii) pour les écosystèmes en aval par les perturbations hydromorphologiques, la remise en suspension des sédiments contaminés et la détérioration de la qualité de l'eau, induites par la présence du barrage. Malgré ce contexte de perturbations multiples, les impacts

des perturbations physiques et chimiques associés à la présence de barrage sur les écosystèmes aquatiques sont généralement **évalués indépendamment** (Chapman, 2007; Burton et Johnston, 2010).

1.3. Enjeux réglementaires et sociétaux

La Directive Cadre Européenne sur l'eau (DCE) impose à l'ensemble des états membres de l'Union Européenne d'atteindre le « **bon état écologique** » pour au moins les deux tiers des masses d'eau naturelles d'ici l'horizon 2015. Pour répondre à cet objectif herculéen, elle impose la mise en place de méthodologies de diagnostic, de suivi et de restauration. Le bon état écologique d'une masse d'eau est défini sur la base des éléments biologiques (diatomées, macroinvertébrés, macrophytes, poissons), chimiques et hydromorphologiques. Parmi ces éléments de qualité, il ne figure **aucun paramètre directement relié au fonctionnement des écosystèmes** (processus écosystémiques).

Bien qu'il soit clair que la qualité des sédiments puisse entraver la réalisation des objectifs communautaires, **la DCE ne traite pas spécifiquement de ce compartiment**. Une récente prise de conscience du Parlement Européen (amendement de 2008) suggère aux pays membres de l'Union Européenne d'opter pour l'application de normes de qualité environnementale basées sur les concentrations en polluants dans les sédiments et/ou dans le biota plutôt que dans l'eau. Pour autant, à l'heure actuelle il n'existe **aucune vue d'ensemble** sur l'évaluation de la qualité des sédiments par les Etats membres ; chaque pays développe ses propres lignes directrices quant à la qualité des sédiments (Sediment Quality Guideline) et ses propres stratégies de suivi (Ahlf *et al.*, 2002; EPA, 2002) conduisant à **un manque d'uniformité** des méthodes d'échantillonnage, des techniques analytiques et dans la définition des seuils de qualité.

La prise en compte des **retenues au fil de l'eau** en tant qu'écosystèmes qu'il convient d'évaluer et de restaurer est également une des **grandes omissions de la DCE** dans la mesure où le « bon état écologique » ne concerne pas ce type de masse d'eau. En effet, la DCE distingue trois types de masse d'eau : les masses d'eaux naturelles (lacs et tronçons naturels des rivières), les masses d'eaux artificielles (canaux, gravières…) et les **masses d'eaux**

fortement modifiées, catégorie dans laquelle seraient inclues les retenues au fil de l'eau. Les Etats membres peuvent désigner une masse d'eau comme artificielle ou fortement modifiée lorsque la restauration de ses caractéristiques hydromorphologiques requise pour la réalisation du bon état écologique, aurait des effets néfastes sur (i) la navigation incluant les installations portuaires ou les activités récréatives, (ii) les activités associées au stockage pour l'approvisionnement en eau potable, la **production d'hydroélectricité** ou l'irrigation, (iii) la **régulation des régimes hydriques** pour la protection contre les crues ou (iv) tout autre utilisation qui soutient le développement des activités humaines. En 2005, les Etats membres ont procédé à une première désignation au terme de laquelle environ 15% des masses d'eau de surface ont été identifiées comme fortement modifiées et 4% comme artificielles. Cette situation varie considérablement entre les Etats membres. Par exemple, la Belgique, la République Tchèque, les Pays-Bas et la Slovaquie ont désigné 40% de leurs masses d'eau de surface comme fortement modifiées.

Pour ces masses d'eau, le bon état écologique est remplacé par le « **bon potentiel écologique** » pour lequel aucune définition précise n'est fournie. Les éléments à intégrer dans l'évaluation du potentiel écologique sont définis comme ceux applicables à la catégorie des masses d'eaux naturelles la plus apparentée à la masse d'eau considérée. En d'autres termes, les éléments de qualité qui devraient être évalués concernant les retenues au fil de l'eau devraient être les mêmes que ceux intégrés dans l'évaluation de l'état écologique des rivières. A l'instar de l'évaluation du « bon fonctionnement » des écosystèmes, le bon potentiel écologique des masses d'eau fortement modifiées et artificielles n'a été évalué dans aucun des Etats membres, probablement en raison des imprécisions de la Directive. Cette absence d'un réel suivi de la qualité des retenues au fil de l'eau pose le problème majeur des modalités de **restauration de la continuité écologique**.

Le **retrait des barrages** est par essence, une méthode efficace de restauration de la continuité écologique des rivières. En France, la loi Grenelle (issue du Grenelle de l'environnement – loi du 2 juillet 2010) s'est engagée à restaurer cette continuité écologique à travers la constitution d'une **trame bleue**. Cependant, associé au relargage des sédiments, contaminés ou non, stockés dans les barrages, le retrait des barrages représente un **risque écotoxique potentiel** pour les écosystèmes en aval. Il reste donc de nombreux efforts à conduire pour atteindre l'objectif de la DCE. Parmi ces efforts, il apparaît essentiel : (i) de considérer les écosystèmes

retenues d'un point de vue écologique et non plus uniquement économique, (ii) de **développer des méthodes de suivi des sédiments contaminés** qui intègrent les réponses des communautés et des écosystèmes dans un contexte de stress multiples (chimiques et physiques) afin de (iii) promouvoir des méthodes de restauration de l'intégrité des écosystèmes aquatiques durables et raisonnées. Ces derniers points nous apparaissent primordiaux. En effet, restaurer physiquement les cours d'eau en omettant la qualité des sédiments pourrait conduire à l'effet inverse de celui attendu, et de ce fait à **une forte dégradation des écosystèmes en aval** des barrages. Par ailleurs, très peu de barrages sont susceptibles d'être retirés, du fait de leur usage économique, ce qui implique la nécessité de définir et de promouvoir la réalisation du bon potentiel écologique des retenues pour **favoriser**, dans les écosystèmes en aval, **la récupération** suite aux impacts physiques associés à la présence d'un barrage.

Bien qu'il existe de nombreuses recherches sur les impacts des sédiments contaminés sur les organismes aquatiques, très peu se sont intéressées aux risques potentiels sur la **santé humaine**. Un lien indirect entre les contaminants stockés dans les sédiments et la santé humaine est reconnu du fait du rôle des sédiments comme composants de la chaîne alimentaire, mais le lien direct a reçu très peu d'attention (Owens et Xu, 2011). Bien que l'existence d'un risque sanitaire soit incertaine, les enjeux sociétaux et économiques de la gestion des sédiments peuvent être quant à eux clairement établis. En effet, **les biens et services écosystémiques** délivrés par les écosystèmes aquatiques, tels que le prélèvement en denrées alimentaires et en eau potable, la régulation du régime hydrique, l'épuration de l'eau ou les services récréatifs, peuvent être profondément **compromis par la rétention et la contamination des sédiments**. Les enjeux écologiques, réglementaires, sociétaux et économiques imposent le développement de **méthodologies robustes d'évaluation des risques** environnementaux associés aux sédiments contaminés. Il importe par ailleurs que ces méthodologies soient organisées selon **une approche graduée**, qui permette de hiérarchiser et de proportionner les efforts mis en œuvre pour l'évaluation, selon les risques potentiels sur les écosystèmes.

2. Principaux outils structurels et fonctionnels utilisés pour la bioévaluation des écosystèmes aquatiques

2.1. Compartiments biologiques

De nombreux outils ont été développés en écologie aquatique pour mesurer les composantes structurelles et fonctionnelles des écosystèmes. Ces outils ont été largement développés sur le **compartiment macrobenthique** (Rosenberg et Resh, 1993; Barbour *et al.*, 1999; Lazaridou-Dimitriadou, 2002) parce qu'ils possèdent les caractéristiques suivantes :

- ils sont nombreux et ubiquistes dans tout type d'habitats et leur diversité permet de refléter une **large gamme d'exigences écologiques**,
- ils sont relativement sédentaires, ils **intègrent** les **conditions environnementales** du milieu dans lequel ils sont prélevés,
- ils sont sensibles aux perturbations environnementales et les variations interspécifiques de cette sensibilité permet l'observation d'un **gradient de réponses des communautés** selon l'intensité et la nature du stress (Hellawell, 1986; Lewis *et al.*, 2001),
- ils sont **cruciaux pour le fonctionnement** des écosystèmes aquatiques du fait de leur rôle dans le recyclage des nutriments et dans la production primaire (Barko *et al.*, 1991; Wallace et Webster, 1996; Devine et Vanni, 2002) et parce qu'ils sont une part essentiel de la chaîne alimentaire (Lozano *et al.*, 2001)
- enfin, ils sont faciles à échantillonner et à identifier (Ricciardi et Rasmussen, 1999; Shostell et Williams, 2007).

Fig.2 : Illustration de la diversité du compartiment macrobenthique des écosystèmes aquatiques. (1) Dysticidae, (2) Hydropsychiidae, (3) Simuliidae, (4) Culicidae, (5) Lymnaeidae, (6) Perlidae, (7) Rhyacophilidae, (8) Leptophlebiidae, (9) Sericostomatidae, (10) Ephemeridae. Sources internet (cf. liste des figures)

Outre les macroinvertébrés, le **compartiment microbien**, bien que méthodologiquement plus difficile à évaluer, est également **essentiel pour le fonctionnement** des écosystèmes aquatiques. De nombreuses études ont souligné l'importance de ce compartiment dans le cycle des nutriments, la décomposition de la matière organique et dans le transfert de la production primaire aux niveaux trophiques supérieurs (Bärlocher et Murdoch, 1989; Pusch *et al.*, 1998; Feris *et al.*, 2003).

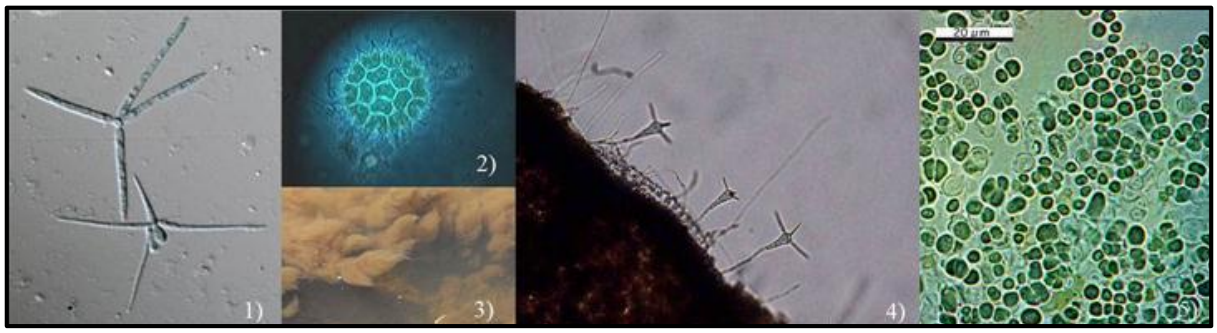

Fig.3 : Illustration de spores d'Hyphomycetes aquatiques et de bactéries. 1) spores de *Articulospora tetracladia* (?) et *Tetracladium marchalianum*, 2) *Pedastrium sp.* (bactéries Chlorophycées), 3) *Sphaerotilus natans* (bactéries filamenteuse aquatique) ;4) spores de *Clavariopsis aquatica*, 5) *Pleurocapsa sp.* (Cyanobactéries) Sources internet (cf. liste des figures)

Le processus de décomposition des litières illustre l'importance des deux compartiments dans le fonctionnement des écosystèmes aquatiques. Malgré une contribution parfois faible en termes de perte de masse foliaire (Hieber et Gessner, 2002), les communautés microbiennes sont d'une importance fondamentale pour la réalisation du processus par les invertébrés déchiqueteurs (Arsuffi et Suberkropp, 1989). En effet, ils conditionnent les litières par la production de substances à hautes valeurs énergétiques (ex. protéines et lipides) et dégradent les polysaccharides indigestes pour les invertébrés (Bärlocher et Kendrick, 1975). En retour, les déchiqueteurs, en fragmentant la matière organique en particules plus petites, augmentent la surface de colonisation pour les espèces microbiennes. Par ailleurs, la pression de pâturage exercée par les invertébrés contrôle la concurrence des champignons dominants favorisant ainsi la coexistence des espèces fongiques, leur diversité et la décomposition des feuilles associées (Mancinelli *et al.*, 2002; Costantini et Rossi, 2010). L'activité combinée de ces deux compartiments est **la garantie du bon fonctionnement** d'un écosystème aquatique et par conséquent ils devraient être considérés **conjointement** dans les méthodologies de diagnostic environnemental.

2.2. Echelles d'intégration biologique

La sélection des échelles d'observation est une étape cruciale dans la mesure où elle régit notre capacité à détecter, expliquer, comprendre et prédire les impacts des perturbations sur les écosystèmes. Le choix d'un niveau d'intégration biologique résulte d'un compromis entre précocité de la réponse et pertinence écologique, l'objectif étant de parvenir à identifier des **bioindicateurs précoces** mais également **intégrateurs des effets des perturbations** à de plus bas et hauts niveaux d'organisation biologique.

En écologie, l'étude des effets d'une perturbation se focalise essentiellement au niveau des communautés, plus rarement au niveau des écosystèmes via une **approche systémique,** tandis qu'en écotoxicologie, elle s'effectue classiquement aux niveaux cellulaire et individuel et plus rarement, au niveau des populations, via une **approche expérimentale**.

Les **communautés** sont, pour de nombreuses raisons, un niveau approprié d'organisation biologique pour examiner les effets des perturbations. En effet, elles représentent le **lien entre les populations et les écosystèmes** dans la hiérarchisation de l'organisation biologique, intégrant de ce fait la somme des effets des contaminants à une échelle d'organisation biologique inférieure tout en fournissant un critère d'évaluation des effets potentiels au niveau des écosystèmes et des biens et services écologiques qu'ils fournissent (Clements et Rohr, 2009). L'évaluation des impacts des perturbations au niveau des communautés et des écosystèmes fournit des réponses d'une grande **pertinence écologique** mais **manque** toutefois d'**explications mécanistiques** et de **précocité** et ne permet pas toujours d'identifier les mécanismes sous-jacents à la réponse (Forbes *et al.*, 2001; Vasseur et Cossu-Leguille, 2003). Qui plus est, l'évaluation des impacts des contaminants à ces niveaux d'organisation biologique peut être limitée, étant donné la **complexité des systèmes biologiques** à ces niveaux d'intégration (Artigas *et al.*, 2012).

L'évaluation des impacts des contaminants au **niveau cellulaire ou individuel** permet de mieux comprendre les **mécanismes** associés à la toxicité. Pour autant, les approches fondées sur les bas niveaux d'organisation biologique, tels que les biomarqueurs, sont plus pertinentes si elles peuvent être reliées à des effets sur les niveaux supérieurs d'organisation biologique. Cette extrapolation à des niveaux supérieurs est rendue difficile par les **effets indirects** et/ou les nombreux **mécanismes compensatoires et de régulation** (Lampert *et al.*, 1989; Ferson *et*

al., 1996; Parker *et al.*, 1999; Fleeger *et al.*, 2003). Des mécanismes de résilience et de compensation peuvent exister à chaque niveau d'organisation biologique, ce qui signifie qu'une perturbation à une échelle cellulaire ne se répercute pas nécessairement au-delà, l'organisme pouvant assurer sa survie et se maintenir dans la population, où aucun effet n'est alors détecté.

Ce constat souligne l'importance de développer des méthodologies d'évaluation des risques écotoxiques à différentes échelles d'intégration biologique, dans la mesure où à l'heure actuelle, il n'existe aucun indicateur biologique permettant de déduire des effets mesurés à un niveau d'organisation biologique les effets sur les niveaux d'organisation biologique inférieurs et supérieurs. Examiner les réponses de **plusieurs compartiments** à **différentes échelles d'intégration** peut paraître holistique mais devrait permettre d'identifier et de développer des **outils prédictifs** des effets des perturbations sur l'intégrité des écosystèmes aquatiques.

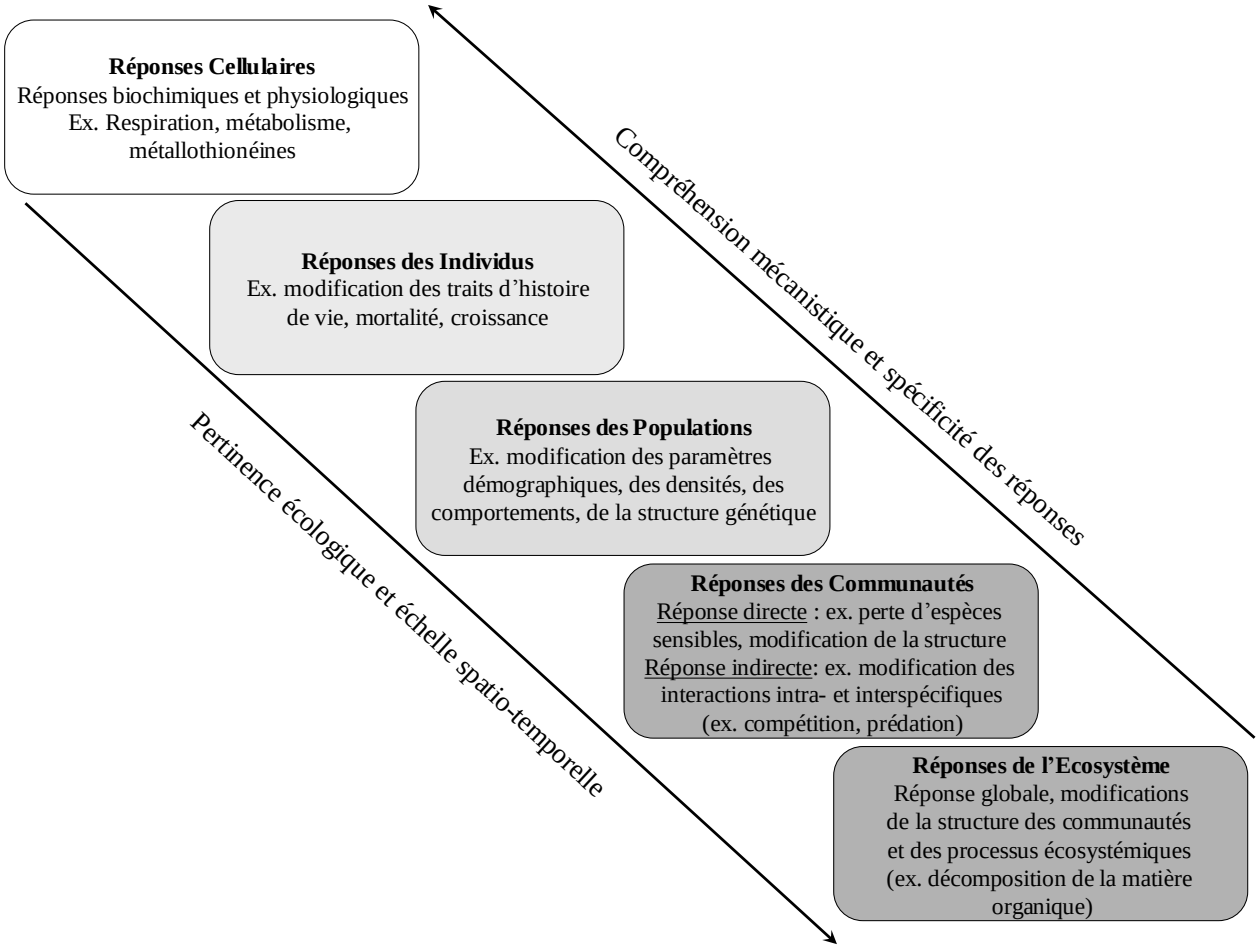

Fig.4 : Effets des contaminants à travers les différents niveaux d'organisation biologique (adaptée de la Figure 1. de Clements, 2000).

2.3. Approches structurelles et fonctionnelles

2.3.1. Approche structurelle classique

Historiquement, les méthodes de bioévaluation des écosystèmes aquatiques se sont focalisées sur le compartiment macrobenthique par l'utilisation de métriques qui décrivent la **structure des assemblages** et l'**abondance** ou la **richesse** de groupes taxonomiques indicateurs (Rosenberg et Resh, 1993; Hering *et al.*, 2006; Friberg *et al.*, 2009). En raison de leurs exigences écologiques, les **espèces indicatrices** peuvent être utilisées comme **indicateurs écologiques** d'un type de communauté, de conditions d'habitats, de changements environnementaux et des **impacts des perturbations** sur les écosystèmes (McGeoh et Chown, 1998; Carignan et Villard, 2002; Niemi et McDonald, 2004). La valeur indicatrice des macroinvertébrés est à l'origine de nombreux indices de diagnostic de la qualité des écosystèmes aquatiques à l'instar de l'Indice Biologique Global Normalisé (IBGN, A.F.N.O.R., 1992) et de l'Indice Oligochète de Bioindication des Sédiments (IOBS, A.F.N.O.R., 2002).

Quelques études ont identifié des espèces ou des assemblages d'espèces sensibles ou inversement tolérantes à la présence de sédiments contaminés ou à l'implantation de barrages. Par exemple, Beasley (2003) et Grumiaux (1998) ont identifié des taxons de macroinvertébrés sensibles à la contamination des sédiments de rivière en métaux et en HAP tel que les Gammaridae, et inversement des taxons polluotolérants comme les Chironomidae. D'autres études ont identifié des taxons sensibles à la présence d'un barrage, appartenant principalement aux ordres des Ephéméroptères, Plécoptères et Trichoptères et des taxons tolérants tels que les Chironomidae et Orthocladiinae (Bunn et Arthington, 2002; Bredenhand et Samways, 2009). Pour autant, d'autres facteurs qui ne sont pas associés aux perturbations considérées peuvent également influencer la sensibilité des espèces indicatrices, tels que le **contexte biotique** (compétition, parasitisme, prédation) et **abiotique** (disponibilité des ressources alimentaires, hétérogénéité de l'habitat) ainsi que **la présence d'autres perturbations**. Par ailleurs, une approche basée sur la sélection de taxons indicateurs requiert, pour être pertinente, une détermination au **niveau spécifique** dans la mesure où la sensibilité aux perturbations peut être considérablement différente au sein même d'une famille ou d'un genre (Resh et Unzicker, 1975).

De nombreuses études décrivent également l'évolution des indices de diversité et de richesse le long des gradients de perturbations. Cependant, la présence d'**espèces rares** peut influencer **disproportionnellement** la richesse spécifique des communautés (Gaston, 1994). L'estimation des indices de diversité donne un poids trop important à l'abondance ou à la dominance des espèces (Magurran, 2004). Les indices classiquement utilisés dans l'estimation de la diversité sont basés sur des données présence/absence ou d'abondance des espèces présentent dans un environnement. Aujourd'hui, l'utilité des mesures de diversité qui intègrent le degré de dissimilarité écologique entre les espèces est largement admise (Mason *et al.*, 2005; Baldy *et al.*, 2007; Ricotta et Szeidl, 2009; Webb *et al.*, 2010). Ces mesures peuvent être basées, par exemple, sur la taxonomie, les relations phylogénétiques entre les espèces ou les différences morphologiques et fonctionnelles. Bien que de nombreux indices ont été récemment développés, l'indice de diversité quadratique de Rao (Rao, 1982) reste un des outils les plus pertinents à utiliser dans l'estimation de la diversité biologique puisqu'intégrant le degré de dissimilarité écologique interspécifique (Botta-Dukát, 2005; Ricotta, 2005).

Un outil de diagnose structurelle pertinent pourrait être défini par sa capacité à (i) établir **un lien de causalité** entre les perturbations et la structuration des communautés et (ii) **prédire les effets** des perturbations **à un niveau supérieur** d'intégration biologique, dans le cas présent l'écosystème. Les approches structurelles classiques telles que décrites ici, bien que nécessaire pour appréhender les effets des perturbations sur la biodiversité aquatique, restent relativement descriptives et ne permettent pas d'établir un diagnostic suffisamment précis quant à l'origine et l'intensité de l'altération des écosystèmes.

2.3.2. Approche basée sur les traits : le chaînon manquant

La notion de trait peut être définie à **chaque niveau d'intégration biologique**. Au niveau individuel, un trait est défini comme une caractéristique morphologique, physiologique ou phénologique mesurable de la cellule à l'ensemble de l'organisme (Violle *et al.*, 2007). Au niveau populationnel, la notion de trait est classiquement associée aux paramètres démographiques (Caswell, 2006). Au niveau des communautés, un trait correspond à l'ensemble des informations qualitatives et quantitatives associées à la biologie et à l'écologie des espèces structurant la communauté (Bournaud *et al.*, 1992; Statzner *et al.*, 1994). Enfin,

au niveau des écosystèmes, la notion de trait se rapporte à l'efficacité d'un processus écosystémique (Violle *et al.*, 2007).

Parmi ces traits, peuvent être distingués les **traits de réponses** qui varient en réponse aux modifications des conditions environnementales et, les **traits d'effets**, dont la variation influence les conditions environnementales, les communautés et/ou les processus écosystémiques (Violle *et al.*, 2007). Suivant cette dénomination, un trait peut répondre à une perturbation (trait réponse) mais ne pas avoir d'effet sur les processus de l'écosystème (trait d'effet). Un **trait fonctionnel** correspond à l'association de ces deux propriétés, dans la mesure où il détermine la réponse à des pressions, et influence la réalisation des processus écosystémiques (de Bello *et al.*, 2010).

Le peuplement faunistique d'un écosystème aquatique est constamment soumis à la variabilité spatio-temporelle de l'environnement. Il en résulte que les espèces présentes sont celles arborant les caractéristiques biologiques et les préférendums écologiques les plus appropriés aux différents types d'habitats de la mosaïque fluviale (Townsend, 1989; Townsend et Hildrew, 1994). De ce fait, contrairement aux approches structurelles classiques où les différences et les similitudes dans l'occurrence des espèces sont analysées, une approche basée sur les traits suppose un lien entre les facteurs environnementaux et les réponses biologiques, facilitant de ce fait une **inférence causale** (Poff, 1997; Statzner et Bêche, 2010; Webb *et al.*, 2010). Outre la capacité à fournir un lien mécanistique entre réponses biologiques et conditions environnementales, les traits sont des métriques pertinentes à de larges échelles biologiques et spatiales, et présentent moins de variabilité saisonnière et interannuelle que les mesures taxonomiques. De nombreuses études ont démontré la capacité des traits biologiques et écologiques des communautés à discriminer des perturbations métalliques (Archaimbault *et al.*, 2010), hydrauliques (Snook et Milner, 2002; Griswold *et al.*, 2008) et organiques (Charvet *et al.*, 1998). Pour toutes ces raisons, l'approche trait est désormais largement utilisée en écologie où le profil des traits biologiques et/ou écologique d'une communauté associé à une variété de facteurs environnementaux est utilisé comme une métrique indiquant l'état de santé de l'écosystème (Townsend *et al.*, 1997; Heino, 2005; Statzner *et al.*, 2005; Culp *et al.*, 2010; Poff *et al.*, 2010; Mondy *et al.*, 2012).

Les traits, dans leur utilisation *in situ*, servent essentiellement à définir « l'**image fonctionnelle** » des communautés de macroinvertébrés benthiques (Bournaud *et al.*, 1992;

Statzner *et al.*, 1994), mais sont plus rarement étudiés au niveau des populations. Les modifications des profils de traits au niveau des communautés rendent essentiellement compte des effets létaux des perturbations et n'intègrent pas directement les réponses sublétales au niveau des populations. En effet, le profil biologique et écologique réel d'un taxon dans un environnement considéré peut varier au sein d'un profil théorique en réponse aux conditions environnementales. Les variations intra- et inter-populationnelle des traits sont des mécanismes importants permettant aux organismes de s'adapter aux modifications de leur environnement et par conséquent, pourraient être utiles dans le diagnostic de certains stress environnementaux (Hodkinson et Jackson, 2005).

En écotoxicologie, l'approche basée sur les traits reste marginale malgré certaines études qui illustrent son intérêt dans l'identification d'espèces susceptibles d'être sensibles aux contaminants (Ducrot *et al.*, 2005; Buchwalter *et al.*, 2008; Liess et Beketov, 2011). Pourtant, celle-ci a le potentiel de permettre d'identifier et de comprendre les mécanismes responsables de la **vulnérabilité** des populations et des communautés aux composés toxiques (Rubach *et al.*, 2011).

L'approche trait est intimement associée à la notion de niche. Cette notion recouvre à la fois les **exigences environnementales** nécessaires à une espèce pour se maintenir dans un milieu (niche « Grinnellienne »,Grinnell, 1917), et ses **relations avec les autres espèces** présentent (niche « Eltonienne », Elton, 1927). Depuis, le concept a été développé par de nombreuses définitions, de la niche en tant que « **norme de réaction** » d'une espèce à une gamme de conditions abiotiques et biotiques (Hutchinson, 1957; Whittaker *et al.*, 1973) à la niche fonctionnelle, en tant que **position ou rôle d'une espèce** au sein d'une communauté (Rosenfeld, 2002).

Par ailleurs, la niche peut être fondamentale (= théorique) ou réalisée (Fig.5). Ces deux termes sont abordés plusieurs fois dans la littérature et font l'objet de plusieurs définitions. McGill et al. (2006) définissent la **niche fondamentale** comme un sous ensemble de n dimensions environnementales parmi les conditions possibles dans lequel une espèce peut se maintenir **en l'absence de compétition**. Pearman (Pearman *et al.*, 2008) définit plus largement la niche fondamentale comme les besoins d'une espèce pour maintenir un taux de croissance de la population positif, sans tenir compte des interactions biotiques. La **niche réalisée** correspond à un sous-ensemble de n dimensions environnementales où une espèce est présente. Il est

souvent admis que la niche réalisée est **un sous-ensemble** de la niche fondamentale (McGill *et al.*, 2006). Selon Pearman (2008), elle correspond à une partie de la niche fondamentale dans laquelle une espèce à un taux de croissance positif en présence d'**interactions biotiques** comme la compétition.

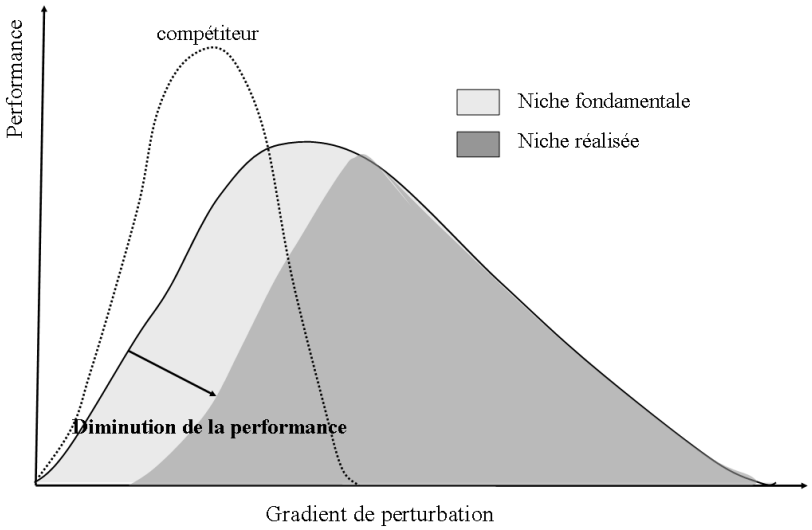

Fig.5 : Schéma conceptuel soulignant l'incidence de la compétition sur la niche réalisée des espèces le long d'un gradient de perturbation.

Cette distinction entre la niche réalisée et la niche fondamentale d'une espèce est importante, en particulier pour **fournir un lien direct** entre la performance d'un organisme, les conditions abiotiques et les interactions interspécifiques (Ellers *et al.*, 2010) et, finalement, pour **prédire** les changements de performances suite à l'interaction avec le milieu (McGill *et al.*, 2006).

2.3.3. Des traits à la diversité fonctionnelle

Intégrer le rôle fonctionnel des espèces dans l'évaluation de la biodiversité est une approche relativement récente. Rosenfeld (2002) définit la diversité fonctionnelle comme la distribution des espèces dans un espace fonctionnel où les axes représentent des caractéristiques fonctionnelles. En d'autres termes, la diversité fonctionnelle d'une communauté pourrait être définie à partir de l'ensemble des combinaisons de traits rencontrées dans la communauté (Usseglio-Polatera *et al.*, 2000).

Bien que conceptuellement simple à formuler et à comprendre, mesurer la diversité fonctionnelle est une tâche complexe. Tandis que les mesures de diversité spécifique sont basées sur le dénombrement des individus des différentes espèces constituant la communauté,

la diversité fonctionnelle doit décrire un nuage de points multidimensionnels dans un espace défini par les traits, où chaque coordonnée correspond à un trait et chaque point représente un individu ou une espèce (Schleuter *et al.*, 2010). Malgré cette complexité, de nombreux indices ont été développés à l'instar de l'indice Q de Rao (Rao quatratic entropy, 1982) défini comme la somme des distances entre paire d'espèces pondérée par l'abondance relative. Plus récemment l'indice FD (functional diversity, PetcheyetGaston, 2002) représente la somme des longueurs de branche d'une classification fonctionnelle. Le FAD/MFAD (functional attribute diversity, Walker *et al.*, 1999b, modifié par Schmera *et al.*, 2009) se définit comme la somme des distances par paires d'espèces pour des unités fonctionnelles. L'ensemble des indices disponibles mesurent différents aspects de la diversité fonctionnelle qui peut être subdivisée en trois composantes : la richesse, la divergence et la régularité fonctionnelle. Les indices précédemment cités permettent essentiellement d'évaluer la richesse fonctionnelle qui correspond au volume de l'espace fonctionnel occupé par une espèce (Mouchet *et al.*, 2010). Pour une meilleure estimation de la diversité fonctionnelle, les trois composantes doivent être évaluées conjointement.

Deux forces interviennent dans la structuration des communautés et de ce fait dans leur diversité fonctionnelle : les **filtres environnementaux** et les **interactions biotiques**. Si les conditions environnementales ont tendance à induire la coexistence d'espèces similaires (hypothèse de « niche filtering »), augmentant la **redondance fonctionnelle**, les interactions biotiques favorisent, elles, la dissimilarité fonctionnelle (hypothèse « limiting similarity »), afin de réduire la compétition via la **différenciation des niches** (Mouillot *et al.*, 2007; Mouchet *et al.*, 2010).

La différenciation des niches permet de promouvoir la coexistence des espèces et les mécanismes de **complémentarité**, mécanismes d'une grande importance dans la compréhension des relations entre biodiversité, fonctionnement de l'écosystème et contraintes environnementales (Costantini et Rossi, 2010). La diversité fonctionnelle est un paramètre primordial à intégrer dans la prédiction des trajectoires de récupération des communautés et des écosystèmes. A la suite de perturbations anthropiques celle-ci est influencée par de nombreux facteurs et notamment les **traits** d'histoire de vie des espèces dominantes (Gunderson, 2000) et l'existence de **redondances fonctionnelles** (Bellwood *et al.*, 2004). Par ailleurs, ces redondances fonctionnelles définissent l'amplitude des variations qu'un écosystème peut tolérer tout en maintenant sa fonction, c'est à dire ses capacités de

résilience. En d'autres termes, la redondance fonctionnelle fournit une **assurance** à l'écosystème dans la mesure où les espèces qui le composent exécutent des fonctions similaires mais présentent des réponses différentes aux facteurs environnementaux (Yachi et Loreau, 1999).

Contrairement à la diversité spécifique, la diversité fonctionnelle mesure la distribution et la contribution fonctionnelle des organismes dans une communauté et un écosystème, et de ce fait, intègre les mécanismes de **complémentarité** et de **redondance fonctionnelle** dans l'estimation de la biodiversité des écosystèmes (Diaz et Cabido, 2001; Petchey et Gaston, 2006).

2.3.4. Approche fonctionnelle

L'un des processus écosystémiques les plus couramment évalué pour étudier l'impact d'une contrainte environnementale sur le fonctionnement des écosystèmes est la **décomposition de la litière végétale**. Etudier ce processus a notamment l'avantage d'**intégrer** à la fois la mesure directe du **processus** et la **diversité à différents niveaux trophiques** (bactérien, fongique et macrobenthique). Gessner et Chauvet (2002) proposent par ailleurs l'étude de la décomposition des litières et de ses paramètres associés comme **outil fonctionnel** à intégrer dans l'**évaluation de l'intégrité écologique** des rivières.

Cette approche a été utilisée à de nombreuses reprises pour évaluer les impacts des toxiques présents dans l'eau sur le fonctionnement des écosystèmes et dans une moindre mesure, les impacts associés à la présence de barrages. Dans le contexte de perturbations multiples considéré dans ces travaux de recherche, la décomposition de la litière peut être perturbée par (i) l'**impact direct** des perturbations physiques et/ou toxiques sur les **invertébrés** détritivores et décomposeurs, (ii) la **disponibilité de la ressource** qui est piégée dans les réservoirs et/ou (iii) l'**altération des communautés microbiennes** et de ce fait de la **qualité des ressources,** modifiant l'activité des invertébrés responsables de la décomposition des litières.

Très peu d'études se sont intéressées aux **effets des barrages** sur la réalisation du processus de décomposition dans les écosystèmes aval. Mendoza et al (2012) ont étudié les taux de décomposition des litières et la faune associée en amont et en aval de cinq réservoirs situés en

tête de bassin. Ils mettent en évidence une **diminution des taux** de décomposition en aval résultant d'une **réduction des densités et biomasses des macroinvertébrés** associés aux litières. A l'inverse, d'autres études n'identifient pas de différences dans la réalisation du processus de décomposition, ni d'ailleurs dans la biomasse en macroinvertébrés ou dans les paramètres de qualité de l'eau entre l'amont et l'aval d'un barrage (Casas *et al.*, 2000; Muehlbauer *et al.*, 2009). Ces résultats disparates peuvent indiquer que la réponse des taux de décomposition associée à la présence de barrage est **dépendante des systèmes étudiés** et probablement **de la qualité des réservoirs** qui pour autant n'est jamais évaluée dans ce type d'étude.

Plus indirectement, d'autres études ont examiné l'**impact de modifications d'écoulement** sur les Hyphomycètes aquatiques associés aux litières. La vitesse de courant est un facteur essentiel dans la structuration des assemblages fongiques, les Hyphomycètes aquatiques colonisant préférentiellement des eaux riches en oxygène (Chauvet, 1992) et la turbulence stimulant le relargage de spores (Bärlocher, 1992). Ferreira et al (2006), en étudiant l'impact du courant sur le compartiment fongique dans des canaux artificiels, ont démontré que les taux de sporulation, la production cumulée en conidies et la richesse spécifique dans les feuilles sont plus élevés lorsque la vitesse du courant augmente.

L'impact de la contamination des sédiments sur le processus de décomposition des litières n'a jamais été examiné. Certains travaux ont toutefois étudié l'impact de l'enfouissement des feuilles dans les sédiments ou de la contamination de la colonne d'eau sur la réalisation du processus et le biota associé. De nombreuses études rapportent la **diminution des taux** de décomposition lorsque les litières sont **enfouies dans les sédiments** (ex. Reice, 1974; Herbst, 1980; Metzler et Smock, 1990; Naamane *et al.*, 1999; Benfield *et al.*, 2001; Cornut *et al.*, 2010). Ce constat peut être associé au **manque d'oxygène** qui peut affecter qualitativement et quantitativement les assemblages macrobenthiques et microbiens (Ward *et al.*, 1998). Par exemple, le manque d'oxygène sur la surface des feuilles associé au dépôt de sédiments fins, **affecte négativement** le métabolisme des **Hyphomycètes** et de ce fait leur croissance (Pascoal et Cassio, 2004; Medeiros *et al.*, 2009). Par ailleurs, la structure du sédiment peut influencer la composition, la colonisation et l'activité des assemblages biologiques associés à la décomposition des litières. Navel et al. (Navel *et al.*, 2010) mettent ainsi en évidence l'importance de la **porosité du sédiment** dans la **consommation** des feuilles par les invertébrés détritivores. Une plus faible porosité réduit la migration des macroinvertébrés

dans le sédiment et de ce fait diminue les taux de décomposition et induit un **temps de rétention plus long** de la matière organique dans le compartiment sédimentaire.
La réduction des taux de décomposition communément rapportée dans les rivières contaminées en métaux peut être associée à des effets sur le compartiment microbien et/ou macrobenthique. De nombreuses études en rivières acides montrent que la contamination métallique de la colonne d'eau associée à de faibles valeurs de pH affecte les communautés microbiennes et finalement les taux de décomposition (Maltby et Booth, 1991; Griffith et Perry, 1994; Carlisle et Clements, 2005; Baudoin *et al.*, 2008; Bundschuh *et al.*, 2011). Dans une métaanalyse (conduite sur 23 articles), Lecerf et Chauvet (2008) confirment les **effets négatifs de la pollution métallique** sur la **richesse fongique** et les **métriques de performance** associées telles que la production de spores et de biomasse et les taux de décomposition. Pour autant, les champignons incluant les Hyphomycètes aquatiques peuvent développer une **tolérance aux métaux** lourds en synthétisant des composés riches en sulfure et des peptides dérivés de glutathions (phytochélatine, (Miersch *et al.*, 1997; Sridhar *et al.*, 2001). Dans une étude réalisée en mésocosmes, Roussel et al. (2008) démontrent par exemple l'adaptation des Hyphomycètes à une pollution au cuivre et justifient la diminution des taux de décomposition par les **effets létaux** du toxique sur *Gammarus pulex*, un invertébré déchiqueteur.

La guilde trophique des déchiqueteurs est en effet particulièrement exposée aux effets toxiques des contaminants dans la mesure où **les litières** de feuilles déposées dans des eaux polluées en métaux **accumulent** une large quantité de **contaminants** tels que le fer, le manganèse et le zinc (Nelson, 2000; Batty et Younger, 2007; Watanabe *et al.*, 2008). Outre les effets létaux, des **effets sublétaux** peuvent également expliquer la diminution des taux de décomposition, particulièrement dans le cas de contaminations « modérées ». Medeiros et al. (2008) rapportent par exemple, une diminution des taux de décomposition dans des sites pollués en métaux malgré l'absence d'altération des compartiments microbien et macrobenthique. Ils supposent que la pollution n'était pas suffisante pour induire des effets létaux sur la croissance microbienne et la survie des invertébrés, mais que des effets sublétaux ont néanmoins pu affecter le fonctionnement de l'écosystème.

D'autres processus sont plus associés au **fonctionnement biogéochimique** des sédiments tels que les phénomènes de **bioturbation** et les **flux benthiques** à l'interface eau-sédiment. Ces deux processus sont intimement liés puisque les flux benthiques dépendent directement de

l'activité de la macrofaune bioturbatrice présente dans les sédiments. La mesure des flux tels que l'oxygène et les échanges de sels nutritifs à l'interface eau-sédiment a été jusqu'à très récemment déterminée à partir de carottages qui ne tenaient pas compte des processus biologiques telle que la bioturbation et sous-estimaient ainsi les flux. Les mesures *in situ* sont nécessaires et rendues possibles grâce à l'utilisation de **chambres benthiques** qui fournissent une **mesure directe des flux** (Archer et Devol, 1992).

Fig.6 : Photographie de chambres benthiques déployées en retenues en juin 2010 – Source : Wagner P.

Le principe consiste à isoler un certain volume d'eau et de sédiment et de suivre l'évolution des paramètres chimiques que l'on veut mesurer en fonction du temps. Cette approche est très peu utilisée en milieu continental. Pourtant, en milieu marin, l'incubation *in situ* des chambres benthiques a été identifié comme technique la plus sensible pour mesurer les flux benthiques (Hammond *et al.*, 1985).

Il a été démontré en milieu marin, que l'activité de la macrofaune bioturbatrice augmentait de 2 à 25 fois l'importance des flux à l'interface eau-sédiment (Pratihary *et al.*, 2009). La bioturbation est un processus qui intègre l'ensemble des modifications physiques, chimiques et biologiques des sédiments par tout type d'organismes. En d'autres termes, la bioturbation correspond à la dispersion des particules sédimentaires résultant du remaniement par la faune benthique. Elle se manifeste par le creusement de galeries ou de terriers, temporaires ou permanents, par la formation de pistes ou de sillons créés par le déplacement des organismes sur ou dans le sédiment et/ou par la production de fèces. L'activité de la faune bioturbatrice influence **la séquestration et la distribution verticale de la matière organique**, les taux et les voies de **minéralisation** en agissant sur l'oxygénation du sédiment, les mouvements des

solutés et par conséquent, **les flux de composés dissous à l'interface eau-sédiment** (Welsh, 2003; Waldbusser *et al.*, 2004), y compris les **polluants**.

De nombreuses études ont démontré l'importance de la bioturbation dans les échanges de composés métalliques à l'interface eau-sédiment et dans leur répartition verticale dans les sédiments (Soster *et al.*, 1992; Petersen *et al.*, 1998; Banta et Andersen, 2003). Par ailleurs, la bioturbation influencerait les coefficients de partition des métaux entre les phases solides et dissoutes (Vale et Sundby, 1998). L'activité de bioturbation par la macrofaune **influence** également la croissance et l'activité des **communautés microbiennes** des sédiments en favorisant l'approvisionnement en substrats, en oxygène et en nitrate (Van de Bund *et al.*, 1994). D'une manière générale, les organismes benthiques, *via* leur rôle dans le remaniement sédimentaire, sont des **acteurs incontestables** des **cycles géochimiques** globaux et du **fonctionnement** des systèmes qu'ils composent (Gilbert, 2003).

2.3.5. Les deux approches combinées pour une meilleure évaluation de l'intégrité des écosystèmes

Les **services écologiques** tels que la production de nourriture, l'autoépuration et le recyclage des nutriments, sont dépendants des fonctions des écosystèmes et de leurs **processus** sous-jacents tels que la production et la décomposition de la matière organique. Il est également largement admis que les processus écosystémiques sont étroitement liés à la **biodiversité** des espèces présentes dans les écosystèmes (Loreau, 2000; Diaz *et al.*, 2006; Luck *et al.*, 2009).

Différentes hypothèses ont été proposées pour expliquer les relations entre biodiversité et fonctionnement des écosystèmes, sur la base de la « redondance fonctionnelle », « l'idiosyncrasie », la « diversité-stabilité » ou encore « l'hypothèse du rivet ». L'augmentation de la richesse en espèces peut améliorer les processus écosystémiques en augmentant la probabilité d'y inclure des **espèces efficaces** (effet d'échantillonnage), des espèces **fonctionnellement semblables** qui augmentent l'assurance biologique contre la perte d'espèces (effet de redondance), des **traits fonctionnels** qui augmentent l'efficacité de l'utilisation des ressources (effet de complémentarité des niches) ou encore en augmentant l'apport de **nouvelles ressources** promue par la co-occurrence d'espèces (effets de

facilitation) (Huston, 1997; Naeem et Li, 1997; Duffy *et al.*, 2001; Loreau et Hector, 2001; Loreau *et al.*, 2001; Tilman *et al.*, 2001; Cardinale *et al.*, 2002; Costantini et Rossi, 2010).

Dans la mesure où des **mécanismes de compensation** existent (ex. plasticité des niches, redondance fonctionnelle), les modifications structurelles identifiées au niveau des populations et des communautés peuvent ne pas altérer la réalisation de processus fonctionnels et de ce fait le fonctionnement des écosystèmes. Bien qu'intégrant les réponses des niveaux d'intégration inférieurs, l'évaluation seule des processus écosystémiques peut donc **sous-estimer l'impact** des perturbations et de ce fait, masquer la **vulnérabilité** de l'écosystème face aux perturbations. Parce qu'un écosystème est classiquement défini par la structuration de ses communautés, par son fonctionnement, et par leurs interactions, les deux approches devraient être intégrées dans l'évaluation de l'état de santé des écosystèmes et dans l'évaluation des risques écologiques associées aux modifications environnementales.

3. Méthodologies de diagnostic de la qualité des sédiments associés à la présence de barrage : définition des besoins

3.1. Acquis méthodologiques

Afin d'évaluer le risque écotoxique des sédiments, plusieurs méthodologies ont été développées dans les domaines de l'écotoxicologie et de l'écologie ou à l'interface des deux disciplines.

L'essentiel des études en écotoxicologie se sont longtemps focalisées sur des **bioessais** qui testent en laboratoire l' écotoxicité de sédiments prélevés *in situ* sur des espèces modèles notamment des diptères à l'instar de *Chironomus riparius*, des Oligochètes (*Tubifex sp.*), des Amphipodes (*Gammarus sp.*), des mollusques (ex. *Valvata sp.*, *Potamopyrgus sp.)* et des bactéries (Posthuma et Van Straalen, 1993; Janssens de Bisthoven *et al.*, 1998; Narracci *et al.*, 2009). Ces études associent le plus souvent plusieurs biotests, dont des microbiotests (certains disponibles sous forme de kits) et des macrobiotests. Parmi ces macrobiotests, ceux sur *C. riparius* sont les plus couramment utilisés et bénéficient de protocoles standardisés et éprouvés (OECD, 2004; A.F.N.O.R., 2010). Cette espèce a fait l'objet de nombreux travaux sur l'écotoxicité de substances dans des sédiments dopés ou naturels (Péry *et al.*, 2002; Milani *et al.*, 2003; Péry *et al.*, 2003; Péry *et al.*, 2005; Bahrndorff *et al.*, 2006). L'espèce *G. fossarum* est également couramment utilisée en laboratoire pour étudier l'écotoxicité des contaminants et a notamment été utilisée dans le développement de marqueurs biochimiques (Xuereb *et al.*, 2009) et physiologiques (Felten *et al.*, 2008; Geffard *et al.*, 2010).

De ces tests de toxicité en laboratoire sur quelques espèces modèles est **extrapolé** le risque écotoxique pour l'ensemble des communautés naturelles (Heugens *et al.*, 2001), ce qui bien entendu résulte d'une **grande approximation** dans la mesure où (i) les polluants sont le plus souvent testés **individuellement** malgré leur présence en **mélange** dans les sédiments où leur effets peuvent se combiner, (ii) les tests utilisent des organismes élevés en laboratoire qui souvent ne sont pas présents dans les écosystèmes concernés et (iii) ces tests sont réalisés en conditions contrôlées et ne rendent donc pas compte des **contraintes biologiques, physico-**

chimiques et hydromorphologiques ou de la présence d'**autres facteurs de stress** auxquels les organismes sont confrontés en conditions naturelles.

Des expériences relatives à l'écotoxicité de contaminants ont été conduites sous des conditions écologiques plus réalistes *via* l'étude des effets combinés de plusieurs substances chimiques (Greco *et al.*, 1995; Vighi *et al.*, 2003), des interactions interspécifiques dans des écosystèmes modèles (Brock *et al.*, 1992) et des encagements expérimentaux (van den Brink *et al.*, 1996; Caquet *et al.*, 2000).

En écologie, les rares études sur l'impact des sédiments contaminés ont eu pour objectif d'identifier des taxons de macroinvertébrés **sensibles aux métaux** ou de décrire les **modifications de la structure** des communautés. Dans l'ensemble, l'abondance totale de la communauté d'une part, et la richesse et l'abondance des taxons sensibles (essentiellement des Ephéméroptères, Plécoptères et Trichoptères) d'autre part diminuent sensiblement avec l'augmentation des polluants métalliques dans les sédiments (Clements, 1992; Clements, 1994; Clements *et al.*, 2000; Clements *et al.*, 2002; Beasley et Kneale, 2003; Iwasaki *et al.*, 2009; Ordonez *et al.*, 2011). Une étude récente démontre la persistance des impacts de la contamination métallique (cadmium et zinc) des sédiments, dont les effets délétères sur la diversité des communautés macrobenthiques sont encore présents 70 ans après l'arrêt des activités d'exploitations minière (Lefcort *et al.*, 2010). Outre ces approches structurelles classiques, d'autres méthodes ont été testées. Par exemple, Gurrieri et al. (1998) ont examiné les relations entre des modèles de dispersion des sédiments et la sensibilité des macroinvertébrés à l'accumulation de sédiments contaminés. D'autres études consistent à évaluer l'impact du sédiment et des contaminants stockés dans des environnements contrôlés (microcosmes) sur les macroinvertébrés (Sharley *et al.*, 2008) ou *in situ* par l'utilisation de substrats artificiels (Grumiaux *et al.*, 1998). Récemment, Archaimbault et ses collègues (2010) ont testé le potentiel des traits biologiques et écologiques dans la discrimination de la contamination des sédiments de rivières par les métaux, HAP et PCB. Cette étude met en évidence l'intérêt de développer les approches basées sur les profils de traits des communautés de macroinvertébrés dans l'évaluation des risques associés aux sédiments contaminés.

A l'interface des études classiques en écotoxicologie et en écologie, l'**approche triadique** a été proposée comme méthodologie d'évaluation des risques associés aux sédiments

contaminés (Long et Chapman, 1985; Chapman, 1996). Cette approche combine l'étude de la composition chimique des sédiments, des tests d'écotoxicité en laboratoire et le suivi *in situ* des macroinvertébrés benthiques. Les analyses chimiques sont utilisées pour examiner les concentrations en contaminants et déterminer si elles excèdent des seuils prédéfinis. Les effets écotoxiques des sédiments sont évalués par les bioessais et les effets sur le long-terme par les expertises sur le terrain (Förstner et Salomons, 2010). Cette approche triadique a été largement utilisée et complétée par des évaluations de la bioaccumulation des contaminants et de divers effets écotoxiques.

A l'heure actuelle la compréhension des mécanismes responsables des effets de la contamination des sédiments sur les écosystèmes aquatiques est rendue difficile par la **complexité** des contaminations et des systèmes étudiés. En effet, des recherches ont montré que les sédiments contaminés qui excèdent les seuils de qualité n'induisent pas nécessairement d'effets toxiques sur les espèces modèles en laboratoire ou sur les communautés macrobenthiques *in situ* dans la mesure où les contaminants stockés peuvent ne pas être biodisponibles. Inversement, les sédiments peuvent être identifiés comme étant de bonne qualité car ils n'excèdent pas les seuils, et néanmoins causer des effets notables du fait de la synergie des effets toxiques ou de la présence de composés chimiques non identifiés (Brils, 2008).

Aucune étude n'a été réalisée sur l'impact des sédiments contaminés stockés dans les retenues au fil de l'eau. Si de nombreuses études ont été conduites pour associer les macroinvertébrés aux conditions d'habitats dans les lacs et les rivières, très peu se sont focalisées sur les systèmes « hybrides » tels que les réservoirs (Shostell et Williams, 2007). Blocksom et son équipe (2002) ont toutefois développé un indice sur l'intégrité des communautés de macroinvertébrés en lacs et grands réservoirs appelé LMII (Lake Macroinvertebrate Integrity Index) avec des données faunistiques collectées dans des sédiments de la zone sublittorale. Cette évaluation a conduit à la sélection de différentes métriques telles que les mesures de richesse et de diversité, de tolérance (nombre de taxons tolérants), la composition des assemblages et des groupes trophiques. Les variables les plus pertinentes sur les sédiments sélectionnés seraient le HBI (Hilsenhoff Biotic Index), le nombre de taxons appartenant à l'ordre des Diptères, le pourcentage d'Oligochètes et d'Achètes et le pourcentage de taxons tolérants (par exemple les Chironomidae).

En ce qui concerne l'étude de la contamination en système lentique, peu de travaux ont été menés. En 1996, Pinel Alloul (Pinel-Alloul *et al.*, 1996) et son équipe ont travaillé sur le suivi de la réponse de la communauté des macroinvertébrés du littoral aux variations de la qualité environnementale du lac canadien St François. Ce travail aboutit notamment à la définition de groupes d'espèces indicatrices de la qualité environnementale par le suivi de la composition en macroinvertébrés, des groupes taxonomiques dominants et des indices biotiques (ICI-SL : Invertebrates Community Index-St Lawrence) sur 16 stations variant en sédimentologie (granulométrie), chimie de l'eau et contamination. Ils ont identifiés les facteurs écologiques et écotoxicologiques les plus explicatifs de la variation observée des assemblages macrobenthiques. Ainsi, la contamination métallique de l'eau apparaît avoir plus d'importance pour le nombre de diptères et l'abondance relative des taxons polluotolérants alors que la concentration en **métaux dans les sédiments** a plus d'importance pour l'**indice biotique** et l'**abondance relative des Trichoptères**.

3.2. Manques méthodologiques et définition des besoins

D'une manière générale, les retenues sont des systèmes rarement étudiés, et par conséquent très peu d'informations sont disponibles sur la **structuration des communautés** de macroinvertébrés et le **fonctionnement** de ce type de milieu. Ce manque de considération peut être associé à la difficulté de caractériser ces systèmes complexes et d'établir un **protocole d'échantillonnage** homogène et pertinent de la macrofaune benthique. La **sélection d'une échelle spatiale** apte à discriminer les réponses structurelles et fonctionnelles à la contamination piégée dans les sédiments est de ce fait rendue particulièrement difficile, et reste à définir. L'échelle de l'habitat pourrait se révéler plus sensible à la perturbation dans la mesure où elle rend possible la considération des déplacements d'individus à l'intérieur d'un même site, tandis qu'à l'échelle **stationnelle**, les déplacements inter-habitats ne peuvent pas être pris en compte. Townsend et Hildrew (1994) prédisent d'ailleurs qu'une forte mobilité est un caractère attendu chez les organismes colonisant les habitats fréquemment perturbés. Selon cette logique, l'échelle spatiale la plus efficace pour rendre compte d'une perturbation peut éventuellement varier en fonction de l'intensité de la perturbation. En ce qui concerne l'échelle d'observation pertinente lors du suivi des effets de la contamination toxique contenue dans les sédiments, aucune étude ne semble avoir abouti.

L'évaluation de l'impact des polluants stockés dans les sédiments est également rendue difficile par la **difficulté de discriminer l'impact chimique de l'impact physique** dans (i) les retenues du fait des modifications hydromorphologiques et de l'accumulation de sédiments fins et (ii) en aval du fait des altérations physiques associées à la présence de l'obstacle. Généralement, les études évaluent indépendamment l'impact physique (colmatage du substrat, impact du barrage en comparant les stations amont/aval…) de l'impact toxique (contamination des sédiments). Communément, l'évaluation du risque écologique associé à une perturbation est réalisée sans considération de la présence d'autres perturbations, ce qui induit une incertitude relative quant à l'explication des réponses biologiques mesurées.

Pourtant, les impacts des activités humaines sur les écosystèmes résultent le plus souvent d'une myriade de perturbations, ce qui rend difficile la discrimination des pressions et de leur impact spécifique sur le biota (Ormerod *et al.*, 2010; Feld *et al.*, 2011). Cette absence de considération, de **discrimination** et de **priorisation** des perturbations dans un contexte **de stress multiples** pose un problème majeur pour la prise de décision et la planification de mesures efficaces de gestion et de restauration des écosystèmes aquatiques perturbés. Dans la mesure où la présence de sédiments contaminés est le plus souvent associée à des perturbations hydromorphologiques (ex. barrages), l'évaluation des risques écotoxiques et les stratégies de restauration (ex. retrait de barrage) devraient mieux considérer le rôle de la contamination chimique des sédiments dans un contexte de stress multiple (Burton et Johnston, 2010). En présence de retenues, les effets des deux types de perturbations (chimique et physique) peuvent se **combiner** et induire des **réponses biologiques inattendues** sur la base de l'évaluation et la prédiction des effets des perturbations considérées indépendamment. Par exemple, il est probable que lorsque la contamination des sédiments est modérée, les impacts physiques masquent les effets des contaminants sur les communautés (Rogers *et al.*, 2002) et de ce fait leur vulnérabilité. Il apparaît nécessaire d'étudier conjointement les impacts associés à la présence de barrages et de sédiments contaminés sur les communautés et le fonctionnement des retenues et des écosystèmes avals, afin d'**améliorer notre compréhension** des facteurs qui influencent les conditions biologiques et mieux **révéler les effets des contaminants**.

Cette absence de considération des effets des perturbations multiples est particulièrement problématique dans le cas de **la remise en suspension des sédiments** stockés dans les retenues lors des crues, vidanges ou retrait de barrage. Malgré le manque de connaissance sur

les effets de la remobilisation des sédiments et des polluants associés, de nombreux projets de retrait de barrages ont été prévus afin de répondre aux objectifs du Grenelle de l'environnement sur la restauration de la continuité écologique (cf. §1.3). En effet, les réponses prévues au retrait de barrages sont souvent basées sur les connaissances acquises sur des barrages de grande taille (>15 mètres), tandis que la plupart des barrages effacés sont des structures de petite taille (< 5 mètres) pour lesquelles il existe très peu d'informations sur les impacts associés (Benstead *et al.*, 1999; Hart *et al.*, 2002; Poff et Hart, 2002), dans la mesure où ce type de restauration n'a souvent fait l'objet d'aucun suivi. Pourtant, le retrait de barrage peut affecter la qualité de l'eau par le transport en aval des contaminants liés aux sédiments et la modification des cycles biogéochimiques. Par conséquent, il apparaît primordial d'étudier et de prédire les effets de la remise en suspension des sédiments contaminés sur les écosystèmes avals avant de planifier le retrait de barrages.

Enfin, d'une manière générale les méthodologies actuelles d'évaluation des risques écotoxiques associés à la présence de sédiments contaminés manquent de **pertinence écologique**. Pourtant, de nombreux auteurs ont suggéré l'importance de développer davantage les approches basées sur les **populations** et les **communautés** *via* l'étude des interactions prédateurs-proies ou de réponses comportementales telles que l'évitement ou les préférences d'habitats (Baird et Burton, 2001; Clark et Clements, 2006; Clements et Rohr, 2009). Ces mesures ont été démontrées plus sensibles à la toxicité des sédiments et à la dégradation des habitats suite aux dépôts de sédiments fins que les paramètres classiquement mesurés tels que la mortalité, la croissance ou la reproduction (Clements *et al.*, 2002; Clements, 2004; Beketov et Liess, 2008; Cover *et al.*, 2008; Brooks *et al.*, 2009).

D'une manière générale, l'évaluation du **fonctionnement des écosystèmes** n'est pas intégrée dans la définition de la qualité des masses d'eau, dans les méthodologies d'évaluation des risques écologiques associés aux sédiments contaminés et dans l'évaluation du succès des mesures de restauration. Pourtant, les polluants, en altérant la structuration des communautés et/ou l'abondance des espèces clés, peuvent induire des modifications dans la réalisation des processus écosystémiques et ainsi altérer la biointégrité des écosystèmes aquatiques. De ce fait, une caractérisation adéquate des écosystèmes requiert des informations à la fois sur **la structure et la fonction** (Gessner et Chauvet, 2002). Il apparaît donc primordial d'intégrer dans les méthodologies d'évaluation des risques associés aux sédiments contaminés des **indicateurs fonctionnels,** *via* l'étude des réponses fonctionnelles potentielles des

communautés (notamment à l'aide des traits biologiques et écologiques) ou réalisées des populations (traits mesurés) et, la mesure directe de processus écosystémiques (comme la décomposition des litières). Par ailleurs, l'intégration des mesures fonctionnelles de la biodiversité dans l'étude de processus écosystémiques tels que la décomposition des litières a été insuffisamment explorée. Pourtant, elles peuvent se révéler plus puissantes que les mesures taxonomiques en élucidant la base mécanistique des effets de la diversité sur le fonctionnement des écosystèmes (Gessner *et al.*, 2010). A l'heure actuelle, il existe un besoin croissant de mieux comprendre les relations entre contamination des sédiments et risques pour le fonctionnement des écosystèmes, afin d'être capable de prédire les effets des contaminants et de planifier des mesures efficaces de restauration des écosystèmes aquatiques.

Chapitre II

Objectifs et démarche scientifique

1. Problématique et objectifs

Le projet DIESE (Outils de Diagnostic de l'Ecotoxicité des Sédiments – ANR PRECODD) a pour vocation de proposer une méthodologie robuste d'évaluation des risques environnementaux associés à l'accumulation de sédiments contaminés dans les écosystèmes aquatiques d'eaux douces. L'objectif principal de ce projet est de développer une **approche graduée** d'évaluation des risques en associant des approches écotoxicologiques (micro- et macrobiotests) et écologiques intégratrices des réponses à différents niveaux d'organisation et pour différents compartiments biologiques.

Inscrit dans ce projet, notre travail vise à produire de nouveaux éléments de surveillance et de modélisation du potentiel écotoxique d'un sédiment, d'une part par l'étude *in situ* des populations et des communautés, via des **approches basées sur leur structure taxonomique et leur profil fonctionnel** et d'autre part par des **approches basées sur la mesure de processus fonctionnels** afin d'identifier les conséquences potentielles de cette écotoxicité sur le fonctionnement des écosystèmes.

Afin de répondre à cet objectif, l'ensemble du travail de thèse s'est articulé autour de quatre principaux questionnements (Fig.7) relatifs:

- **à la caractérisation du système « retenue au fil de l'eau »** en termes de structuration et fonctionnement des communautés macrobenthiques (**O1**)
- **aux modifications structurelles et fonctionnelles** associées aux perturbations physiques et toxiques dans les écosystèmes retenues et en aval des barrages (**O2**)
- **à la hiérarchisation des impacts** physiques et toxiques (**O3**)
- **à la sélection d'outils de diagnostic** structurel et fonctionnel de la qualité des sédiments à intégrer dans les méthodologies d'évaluation des risques écotoxiques (**O4**).

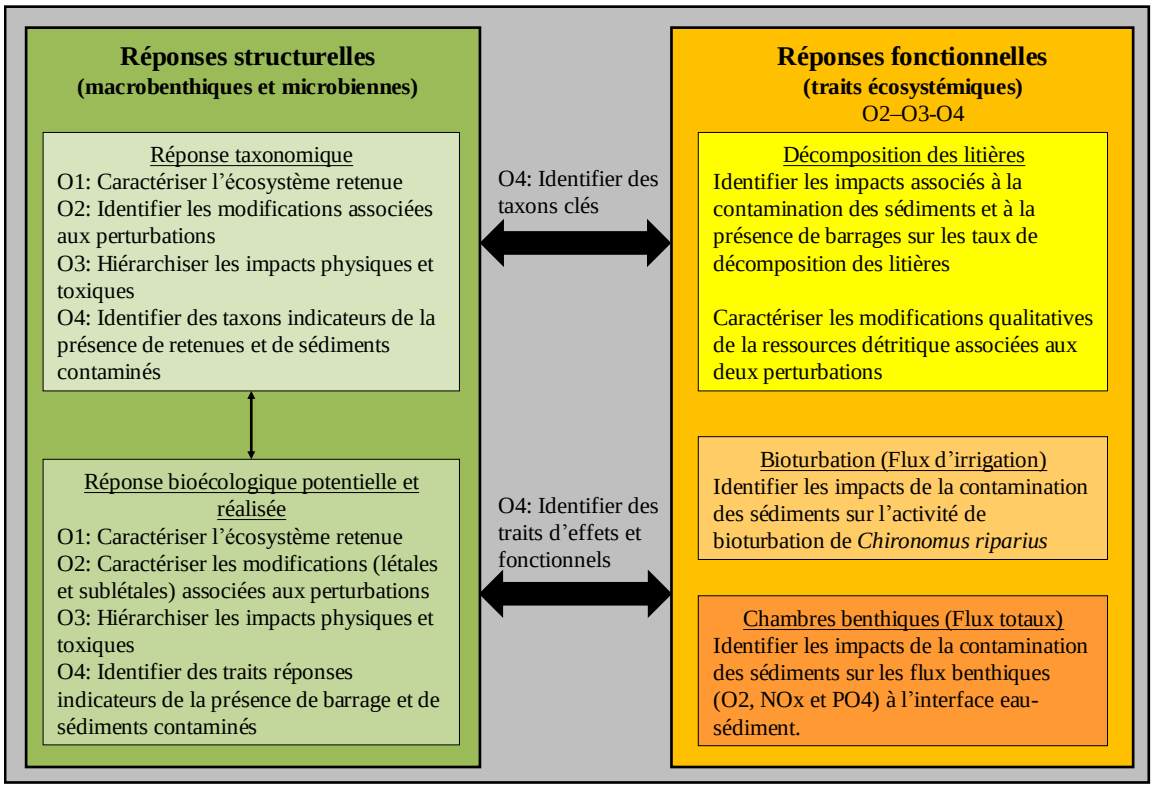

Fig.7 : Démarche scientifique et principaux objectifs développés en réponse à la problématique de la thèse.

2. Matériel et Méthode

Les méthodes expérimentales et statistiques utilisées afin de répondre aux objectifs précédemment définis seront plus précisément détaillées dans les articles présentés dans les chapitres III et IV. Dans cette partie consacrée au matériel et méthode, nous décrirons plus spécifiquement les sites d'études choisis et le protocole d'échantillonnage des macroinvertébrés benthiques développé pour les retenues au fil de l'eau. Nous préciserons aussi les outils sélectionnés pour discriminer les effets des perturbations à chaque niveau d'intégration biologique choisi et l'organisation du manuscrit de thèse.

2.1. Sites d'étude

Trois rivières ont été sélectionnées pour répondre à l'étude : le Fier (Savoie), la Bienne (Jura) et l'Ain (Jura), sur la base de connaissances acquises sur leur niveau de contamination dans le cadre du Réseau National de Bassin, de prospections terrain et de concertations avec les gestionnaires de bassins. Pour chaque cours d'eau un couple retenue référence relative/retenue perturbée a été sélectionnée.

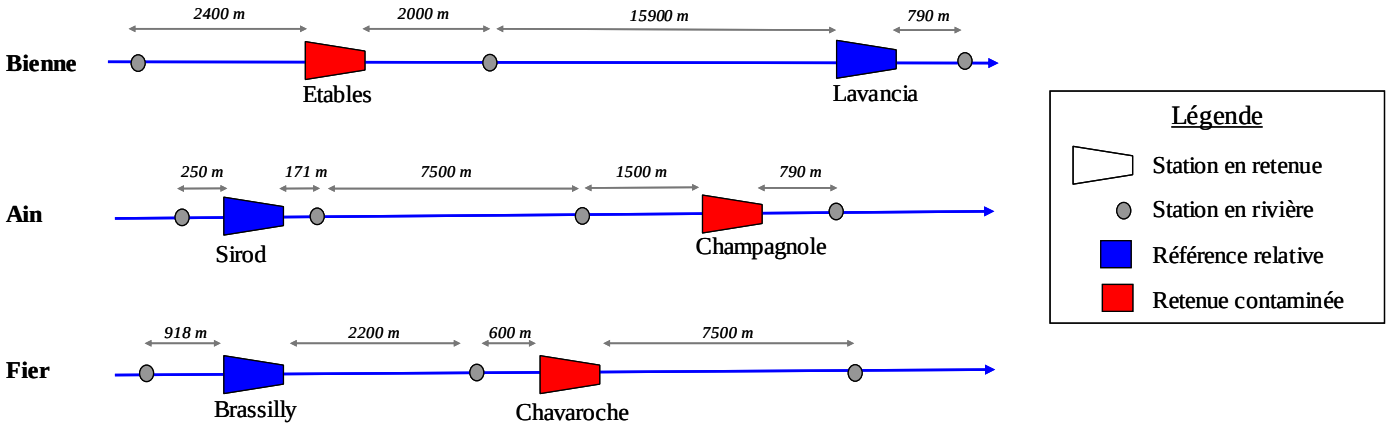

Fig.8 : Plan d'échantillonnage pour chacune des trois rivières

Les trois rivières sélectionnées appartiennent à la même hydroécorégion (Préalpes du Nord, Wasson *et al.*, 2003). Le réseau hydrographique des trois cours d'eau se développe au sein d'un système karstique. Par conséquent, la dimension des cours d'eau est difficilement comparable à celle d'autres systèmes lorsque l'on considère uniquement l'ordre de Strahler. En effet, bien que les cours d'eau sélectionnés soient d'ordre de 2 à 4 (référentiel BD Carthage), la largeur mouillée moyenne des stations varie de 19 à 35 m en rivière et de 39 à 112 m au niveau des barrages, et la profondeur moyenne échantillonnée varie de 29 à 49 cm en rivières et de 69 à 141 cm en retenues.

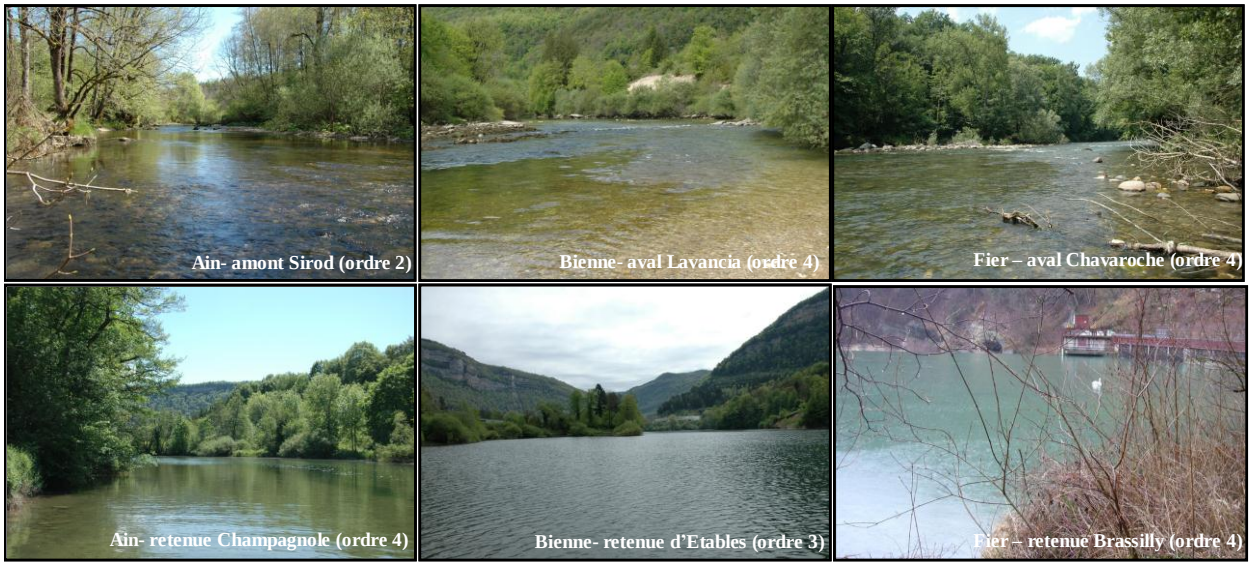

Fig.9 : Photographies des stations en rivière et en retenue sur les trois rivières sélectionnées – Source : Wagner P.

Des prélèvements de sédiments ont été réalisés à chaque campagne d'échantillonnage sur les stations en rivière et en retenues afin de caractériser les niveaux de contamination. Les six retenues sélectionnées permettent de considérer un gradient de contamination des sédiments en métaux et en HAP (Tableau 1). Le suivi du cours d'eau en amont et en aval de chaque retenue est réalisé, pour évaluer (i) l'impact physique de la retenue et (ii) définir l'échelle spatiale la plus apte à révéler les impacts de la présence de sédiments contaminés.

Cours d'eau	Retenue	Coordonnées	Altitude (m)	Surface de la retenue (ha)	Niveau de contamination		
					Métaux	HAP	Total
Fier	Brassilly	45° 54' 24.7''N 06° 05' 03.3''E	445	2	4	3	**3**
	Chavaroche	45° 54' 19.6''N 06° 03' 43.5''E	373	3.5	6	2	**5**
Bienne	Etables	42° 22' 55.4''N 05° 49' 26.0''E	431	7	5	5	**6**
	Lavancia	46° 22' 55.4''N 05° 49' 26.0''E	431	3.7	2	6	**4**
Ain	Sirod	46° 44' 19.1''N 05° 54' 42.8''E	529	2	3	1	**1**
	Champagnole	46° 20' 16.9''N 05° 41' 16.1''E	324	3	1	4	**2**

Tableau 1 : Niveau de chaque retenue en fonction de la contamination par les métaux, les HAP et l'ensemble des contaminants. Les niveaux de contamination sont exprimés en rangs représentant le degré croissant de contamination des sédiments.

2.2. Protocole d'échantillonnage des communautés de macroinvertébrés

Un total de 16 stations a été échantillonné. Les échantillonnages ont eu lieu au printemps excepté pour La Bienne qui a fait l'objet de 2 campagnes, au printemps et en automne, pour étudier l'effet d'une vidange estivale de la retenue contaminée (Etables) sur les communautés macrobenthiques et microbiennes.

En rivière, les macroinvertébrés sont échantillonnés, par filet Surber, selon le protocole RCS (Norme XP T 90-333). Le nombre d'échantillons peut cependant être supérieur à celui préconisé par ce protocole puisque nous avons décidé d'être le plus exhaustif possible et d'échantillonner tous les habitats présents. En retenue, les macroinvertébrés sont échantillonnés selon un protocole spécialement établi pour répondre aux objectifs fixés dans la thèse (Fig.9). Ce dernier scinde la retenue en trois zones longitudinales soit : la zone « queue de retenue », la zone « milieu de retenue » et la zone « barrage ». Sur chaque zone, les substrats de berges sont échantillonnés sur les deux rives (filet Surber, troubleau ou haveneau) en fonction de la diversité en habitats littoraux (minimum 3 prélèvements) et le chenal est échantillonné par dragage (3 prélèvements). En parallèle, les paramètres environnementaux tels que le pourcentage de recouvrement des habitats, l'intensité du colmatage, le degré d'enchâssement des substrats minéraux, la présence des habitats voisins, la distance à la rive la plus proche sont relevés.

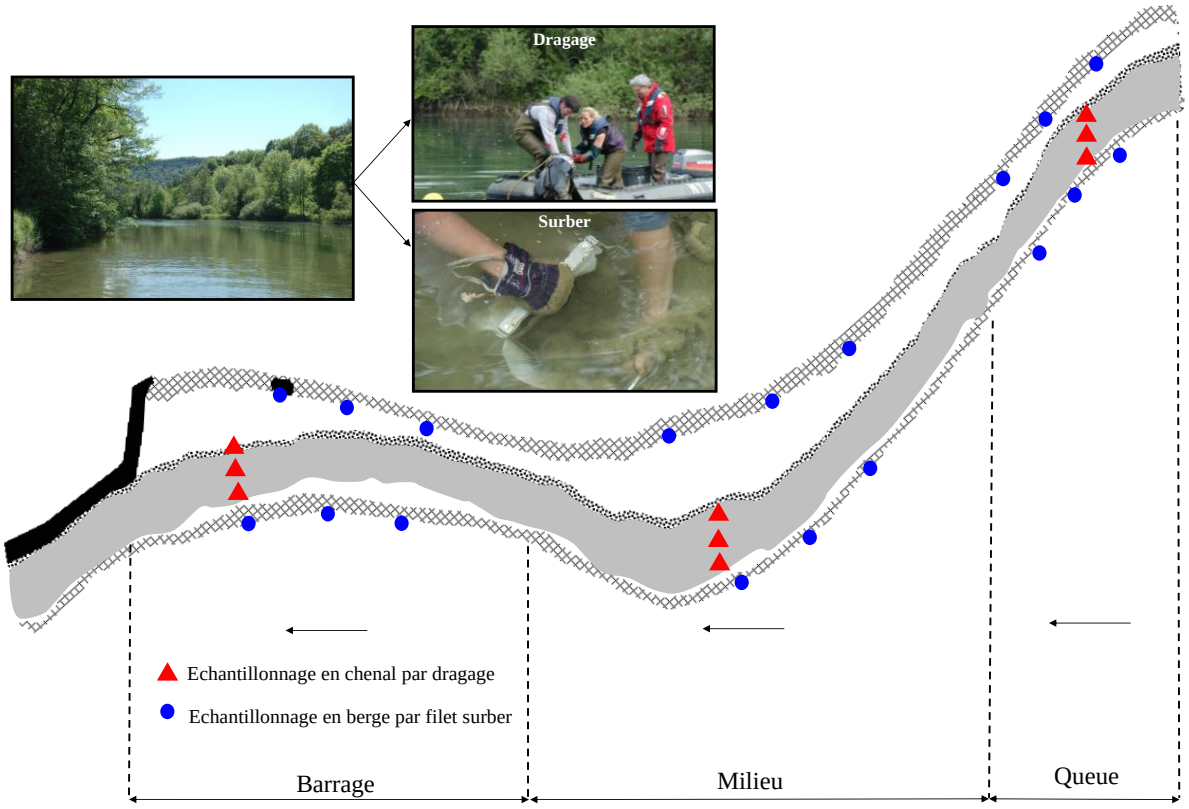

Fig.10 : Protocole d'échantillonnage des communautés macrobenthiques des stations de retenues au fil de l'eau. Source des photographies : Wagner P.

2.3. Outils sélectionnés et inventaire du travail réalisé

De nombreux outils à l'interface entre écotoxicologie et écologie ont été utilisés à différentes échelles d'organisation biologique de la population à l'écosystème (Tableau 2) afin de

répondre aux objectifs fixés par la thèse (Fig. 7). La description détaillée des méthodes et outils spécifiques à chaque questionnement est réalisée dans les articles correspondants (Chapitres III et IV).

Cours d'eau		Fier		Ain		Bienne	
Stations		Retenue	Rivière	Retenue	Rivière	Retenue	Rivière
Echelle populationnelle	Niche spatiale (stratégie d'occupation de l'habitat) Plusieurs espèces	×	×	×	×	×	×
	Niche trophique (Régime alimentaire) *Gammarus pulex*			×	×		
	Distribution des tailles Plusieurs espèces			×	×	×	×
Echelle des communautés (microbiennes et macrobenthiques)	Structure taxonomique (indices et assemblages)	×	×	×	×	×	×
	Structure fonctionnelle : - Biolog (microbien)			×		×	×
	- Traits bioécologiques (macroinvertébrés)	×	×	×	×	×	×
Echelle écosystémique	Décomposition des litières (taux et consommation)			×	×	×	×
	Bioturbation			×		×	
	Flux benthiques			×		×	

Tableau 2 : Inventaire des outils utilisés pour chaque niveau d'organisation biologique considéré et du travail réalisé sur l'ensemble des stations d'étude.

3. Organisation de la thèse

L'ensemble des travaux de thèse sera restitué en accord avec notre démarche scientifique générale (§II.1, Fig.7) sous la forme d'articles acceptés, soumis ou en préparation. Les articles seront de ce fait regroupés en deux chapitres, d'une part les réponses structurelles et d'autre part, les réponses fonctionnelles.

Les réponses structurelles aux perturbations toxiques et physiques concernent les échelles de la population et de la communauté. Elles font l'objet de quatre articles concernant :

- la structuration spatiale des réponses des communautés des deux retenues du Fier aux perturbations toxiques:
  Article 1: « *Scale-dependency of macroinvertebrate communities: responses to contaminated sediments within run-of-river dams* »..Science of the Total Environment. 2011. 409 (7). 1336-1343.
- la description des modifications structurelles et fonctionnelles des communautés de macroinvertébrés des retenues à la présence de sédiments contaminés et la sélection d'indicateurs benthiques de la perturbation :
  Article 2: « *Benthic indicators of sediment quality associated with run-of-river reservoirs"*. Soumis à Hydrobiologia.
- les réponses fonctionnelles et structurelles des communautés macrobenthiques et microbiennes à la remise en suspension de sédiments contaminés :
  Article 3: *« Multicompartment responses to contaminated sediment resuspension: first prospect for dam removal strategy implementation".* Soumis à Environmental Toxicology and Chemistry.
- les réponses des populations à la présence de sédiments contaminés et de barrage:
  Article 4: *« Populations niche shift and niche narrowing under chemical and physical pressures: a new frontier for ecotoxicological risk assessment »*. En préparation

Les réponses fonctionnelles sont relatives à la mesure de processus à l'échelle de l'écosystème et concernent :

- la mesure des flux benthiques à l'interface eau-sédiments dans les retenues :
  Article 5: *« Benthic fluxes from small run-of-river reservoirs across a gradient of sediment contamination »*. En préparation

- la mesure des taux de décomposition des litières (*Alnus glutinosa*) dans les retenues et les stations rivières associées (amont/aval) :
  Article 6: *« Synergistic impacts of sediment contamination and dam presence on river' functioning »*. Soumis à Freshwater Biology.
- l'impact des perturbations toxiques et physiques sur la qualité de la ressource détritique et ses conséquences sur la réalisation du processus de décomposition des litières :
  Article 7: *« Importance of river continuity for detrital resource quality: implications for assessing ecosystem integrity »*. Soumis à Journal of Applied Ecology.

L'expérience réalisée sur la réponse de l'activité de bioturbation des sédiments issus des retenues par *Chironomus riparius* ne sera pas restituée dans cette thèse. En effet, la mesure de l'activité de bioturbation a été réalisée en deux temps, à l'issue de 14 jours et de 28 jours. Seule la deuxième date a été analysée et les résultats obtenus ne sont pas concluants. Nous supposons que les densités de chironomes bien qu'en correspondance avec les densités identifiées dans les sites d'études, n'étaient pas suffisantes pour mesurer des activités de bioturbation et/ou que les outils analytiques déployés n'étaient pas adaptés pour ce type d'expérience. Toutefois, le reste des colonnes sera analysé ultérieurement.

Chacun des chapitres (III et IV) sera introduit par une synthèse de l'ensemble des travaux présentés sous forme d'article. Les principales conclusions issues des résultats obtenus seront rappelées à la fin de chaque chapitre sous la forme d'un tableau. Enfin, l'ensemble des résultats de la thèse sera synthétisé et discuté dans le Chapitre V.

Chapitre III

Réponses structurelles aux perturbations toxiques et physiques

Préambule

L'objectif principal de ce chapitre est d'examiner la structuration des communautés macrobenthiques dans les retenues afin de sélectionner l'échelle spatiale la plus apte à discriminer les effets de l'accumulation de sédiments contaminés et de caractériser les modifications structurelles et fonctionnelles associées.

Les deux premiers articles présentés dans ce chapitre répondent spécifiquement à ces deux objectifs. Un premier travail (article 1), exploratoire, a été réalisé sur les deux retenues du Fier afin d'identifier la structuration spatiale des réponses structurelles et fonctionnelles des communautés macrobenthiques à la présence de sédiments contaminés. Afin de valider ces premiers résultats et sélectionner des indicateurs de contamination des sédiments, un second travail (article 2) a été accompli sur l'ensemble des données faunistiques récoltées sur les six retenues étudiées. La confrontation des assemblages faunistiques identifiés sur les stations en rivière situées en amont des barrages avec ceux des retenues nous a permis de déterminer l'échelle spatiale la plus appropriée à discriminer (i) le gradient de contamination et (ii) un cortège de taxons indicateurs de la présence de retenue. Grâce à l'identification d'un assemblage faunistique caractéristique de ce type de système, nous avons pu sélectionner des indicateurs benthiques de la contamination des sédiments : d'une part, des taxons dont l'abondance a diminué significativement le long du gradient de contamination, et d'autre part, des traits réponses à la perturbation.

Les effets de la contamination des sédiments peuvent s'exporter en aval, via la remise en suspension des sédiments et/ou le relargage des polluants dans la colonne d'eau. La vidange de la retenue d'Etables (Bienne), réalisée pour des travaux d'entretien, a été l'occasion d'étudier les effets de la remise en suspension des sédiments contaminés sur les paramètres physico-chimiques et les communautés microbiennes et macrobenthiques (réponses structurelles et fonctionnelles) des cinq stations identifiées sur le linéaire (article 3). Cette étude nous a conduits à une réflexion sur les risques écologiques des retraits de barrages pour

les écosystèmes avals, dans le cas de l'accumulation de sédiments contaminés dans les retenues

Fig.11 : Photographies du barrage d'Etables (Bienne) avant la vidange et après, avant la remise en eau de la retenue. Source : Colas F.

Enfin, parce que la présence de sédiments contaminés et de barrages peut avoir induit des réponses sublétales qui ne sont pas identifiées par l'étude des assemblages faunistiques et des profils bioécologiques, un dernier travail (article 4) a examiné les modifications dans l'expression de traits biologiques et écologiques au sein des populations de plusieurs taxons de macroinvertébrés le long du gradient de perturbations. La confrontation des niches réalisées et théoriques des populations de macroinvertébrés a été opérée afin d'explorer le bénéfice d'une telle approche dans l'évaluation des risques écologiques associés à la contamination des sédiments.

Article 1: **Scale dependency of macroinvertebrates communities responses to contaminated sediments within run-of-river dams**

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Abstract

Due to their nutrient recycling function and their importance in food-webs, macroinvertebrates are essential for the functioning of aquatic ecosystems. These organisms also constitute an important component of biodiversity. Sediment evaluation and monitoring is an essential aspect of ecosystem monitoring since sediments represent an important component of aquatic habitats and are also a potential source of contamination. In this study, we focused on macroinvertebrate communities within run-of-river dams that are prime areas for sediment and pollutant accumulation. Little is known about littoral macroinvertebrate communities within run-of-river dam or their response to sediment levels and pollution. We therefore aimed to evaluate the following aspects: the functional and structural composition of macroinvertebrate communities in run-of-river dams; the impact of pollutant accumulation on such communities, and the most efficient scales and tools needed for the biomonitoring of contaminated sediments in such environments. Two run-of-river dams located in the French alpine area were selected and three spatial scales were examined: transversal (banks and channel), transversal×longitudinal (banks/channel×tail/middle/dam) and patch scale (erosion, sedimentation and vegetation habitats). At the patch scale, we noted that the heterogeneity of littoral habitats provided many available niches that allow for the development of diversified macroinvertebrate communities. This implies highly variable responses to contamination. Once combined on a global 'banks' spatial scale, littoral habitats can highlight the effects of toxic disturbances.

Keywords: Contaminated sediments – Scale-dependency – Invertebrates – Run-of-river dams – Functional traits

1. Introduction

1.1. Research context

Considering that only 0.014% of Earth's water occurs in the biosphere, water should be regarded as a limiting resource (Gleick, 1993). An increasing need for water resources for human populations, agriculture and energy production has induced an excessive development of dams or weirs, resulting in many hydromorphological or chemical disturbances of river systems (Zwick, 1992; Ward and Stanford, 1995; Bredenhand and Samways, 2009). The presence of a dam disrupts river continuity (Stanford et al., 1996; Poff et al., 1997; Born et al., 1998) and results in the accumulation of sediment within impoundments, thus limiting sediment transport further downstream. This accumulated sediment becomes a sink and a source of historic contamination. Sediments have a strong adsorption capacity for pollutants (Cairns et al., 1984; Chapman, 1990; Estebe et al., 1997), with contamination levels often being greater within sediments than in the whole water column (Chapman, 1992). Moreover, when disturbed and resuspended, sediments can release adsorbed contaminants into the water-column, resulting in further dispersal within the run-of-river dam and in downstream ecosystems. Historical contamination is thus a real threat to the ecological integrity of many aquatic ecosystems (Sheppard, 2005; Norris et al., 2007; Johnston and Roberts, 2009).

1.2. Biomonitoring of contaminated sediment

Contaminants stored within sediments exert a persistent pressure, which implies chronic and sublethal responses that impact on macroinvertebrate communities (Field and Pitt, 1990; Beyer et al., 2000; Viganò et al., 2002). The effects of these contaminants may, however, extend beyond sediment habitats as they can be transferred to other components of aquatic habitats — for example, into the water column (Larsson, 1985; Asare et al., 2000; Coulthard and Macklin, 2003). For all these reasons, various biomonitoring tools have been developed for the study of contaminated sediments. Sediment toxicity is normally assessed by means of biotests carried out in laboratories. Such tests do not, however, adequately account for responses at the community level (Lafont et al., 2007). Because contamination can induce modifications in ecosystem's processes, thus affecting ecosystem integrity (Kiffney and

Clements, 1994), it is necessary to focus on community- and ecosystem-contamination levels. Triadic studies that combine chemical, ecotoxicological and ecological approaches to evaluate sediment toxicity appear to be more appropriate tools than 'traditional' laboratory evaluations, but such studies still neglect ecosystem functioning (Long and Chapman, 1985; Borgmann et al., 2001; Sorensen et al., 2007). Despite these challenges associated with sediment biomonitoring, sediment storage – the principal concern of the present paper – is rarely studied, partly because storage is not considered within legal texts. This is surprising, considering that 60,000 dams are referenced in France. There is a paucity of knowledge of the impacts of contaminated sediments on macroinvertebrate communities (Ramsey et al., 2005); thus, attempting to understand such impacts on the community structure and functioning of run-of-river dams is an important challenge.

In this context, we aimed to assess structural and bio-ecological responses to contamination across several spatial scales, by means of various ecological indicators. We hypothesized that: (i) invertebrate communities should respond functionally and structurally to sediment contamination, but we forecast multiple responses according to various spatial scales; and (ii) when contamination is low, community response to pollutants should be overshadowed by habitat heterogeneity.

2. Material and methods

2.1. Sampling design

2.1.1. Study area and contamination status

Two run-of-river dams on a French alpine river – the name of which has not been given because of confidentiality agreements with the hydroelectric company exploiting the dams – were selected to examine macroinvertebrate composition associated with various levels of sediment contamination. The catchment area is predominantly industrial and urbanized, inducing an accumulation of metallic pollutants in the sediment of two successive hydroelectric dams. The physico-chemical characteristics of the sediments and the water column were assessed in samples realized during the field campaign and sent to a specialized

laboratory. PCBs and most of PAHs in the dams were below detection limits, and organic contamination was low. Monitoring of physicochemical parameters, such as dissolved oxygen concentration, temperature and conductivity, was also undertaken (Table 1). The data indicated differences in metallic contamination between the two systems.

2.1.2. Macroinvertebrates sampling

Macroinvertebrates were sampled in May 2008 using a newly designed sampling protocol. To distinguish influences of various hydraulic and hydro-morphological conditions, sediment accumulation areas associated with run-of-river dams were subdivided into three zones, termed ‘tail’, ‘middle’ and ‘dam’. The ‘tail’ is closest to river conditions, the ‘dam’ is typical of a lentic system and the ‘middle’ exhibits intermediate characteristics. Similarly, communities of the banks and of the channel were sampled separately. Habitats on each bank were described prior to sampling macroinvertebrate communities using a Surber net (mesh size 500 µm, sampled area 0.05 m2). Macroinvertebrates in the channel were sampled by means of dredging from a boat perpendicular to a transect in each of the three areas defined above. For each transect, the left side, the middle and the right side of the channel were sampled. Samples were preserved in 4% formalin in the field and then transferred to the laboratory where they were sieved and sorted, and identified to genus level — using Tachet et al. (2000). Diptera were, however, identified to family and tribe level and Oligochaeta and Nematoda to higher taxonomic levels. Individuals within each taxon were then counted.

Contaminant concentrations in sediments

	Metals (mg kgDW^{-1})										PAH (µg kgDW-1)				
	Al	Cr	Co	Cu	Fe	Mn	Ni	Pb	Zn	As	BaP	BaA	BgP	Fluo	Ind
Reference site	9.2x10^3	38	4	14	6.5x10^3	169	7.7	22.5	90	1.9	18	24	27	101	24
Contaminated site	19.7x10^3	83.5	9	31	15x10^3	423	54.7	17.8	108	1	18	24	27	98	25

Water chemistry

	Cond	pH	Temp.	O_2	COD	DBO	Ca	Mg	K	NH4	Cl	NO_3	NO_2	SO_4	PO_4
	µS cm^{-1}		°C	mg l^{-1}											
Reference site	411	8.2	18.7	8.6	1.9	1.5	70	5	2	0.3	15	16	0.28	15	0.218
Contaminated site	390	8.15	17.6	9.2	1.8	0.9	68	5	1.7	0.1	13	9.9	0.11	14	0.251

Table 1: Principal physico-chemical parameters characterizing contamination of sediments and the water column.

2.2. Data analysis

Three spatial scales were investigated: a) transversal scale: samples pooled according to their bank or channel origin; b) transversal×longitudinal scale: samples pooled according to the two factors considered together, for instance banks×tail; and c) patch scale: samples pooled according to habitat type (categorized as ‘erosion’, ‘sedimentation’ or ‘vegetation’). For each scale, data were explored using three types of indicators: structure indices, taxonomic assemblages, and bio-ecological traits structure. Richness, abundance, proportion of main groups (EPT, Diptera, Mollusca, and Crustacea), Shannon and Weaver diversity indices, Simpson Evenness Index, and Rao Functional Diversity Index (Lavorel et al., 2008; de Bello et al., 2009) were calculated. The functional diversity represents the overall differences among species in a community according to their traits. We applied this index to the distribution of categories within 22 traits (Table 2) describing biological and ecological traits of macroinvertebrates (Usseglio- Polatera et al., 2000). At the transversal scale, Principal Component Analysis (PCA) was used to investigate differences between run-of-river dams. At the patches scale, the interaction between the two tested parameters (habitat type and contamination status) was also assessed using ANOVA (normal distribution and homoscedasticity respected when the two factors are considered). Student's t-test and Mann–Whitney test were used to identify the intra-factor differences (when factors are considered independently, parametric conditions were not always respected). The vegetation habitat type was not investigated because the number of sampled substrates was too low in the reference run-of-river dam.

3. Results

3.1. Selection of relevant spatial scales

To select the most relevant spatial scales, permutation tests were realized on the multivariate analysis performed at the three spatial scales. They test the null model, i.e. whether the structure of data links to a particular factor (in this case, the contamination level) or is only the result of stochastic processes. Results are synthesized in Table 3. Statistical analysis indicates that the transversal scale provides evidence of significant faunistic and functional differences between the two stations, while the patch scale discriminates the two stations only

on the basis of indices. Lastly, the transversal×longitudinal scale does not highlight inter-site differences. For these reasons, only results obtained for transversal and patch scales are detailed below.

Biological Traits	Categories	Ecological Traits	Categories
Maximal size (cm)	≤ 0.25	Transversal distribution	river channel
	> 0.25 to 0.5		banks, connected side-arms
	> 0.5 to 1		ponds, pools, disconnected side-arms
	> 1 to 2		marshes, peat bogs
	> 2 to 4		temporary waters
	> 4 to 8		lakes
	> 8		
		Longitudinal distribution	groundwaters
Life span (year)	≤ 1		crenon
	> 1		epirithron
			metarithron
	< 1		hyporithron
Number of reproductive cycles per year	1		epipotamon
	> 1		metapotamon
			estuary
Aquatic stages	egg		outside river system
	larva		
	nymph	Altitude	lowlands
	adult		piedmont level
			alpine level
Reproduction	Ovoviviparity		
	Isolated eggs, free	Biogeographic area	Pyrenees
	isolated eggs, cemented		Alps
	clutches, cemented or fixed		Vosges, Jura, Massif Central
	clutches, free		lowlands (oceanic)
	clutches, in vegetation		lowlands (mediterranean)
	clutches, terrestrial		flags/boulders/cobbles/pebbles
	asexual reproduction		
		Substrate preferences	gravel
Dispersal	Aquatic passive		sand
	Aquatic active		silt
	Aerial passive		macrophytes
	Aerial active		microphytes
			twigs/roots
Resistance forms	Eggs, statoblasts		organic detritus/litter
	Cocoons		mud
	Housings against desiccation		
	Diapause or dormancy	Current velocity	null
	None		slow (< 25 cm/s)
			medium (25-50 cm</s)
Respiration	Tegument		fast (> 50 cm/s)
	Gill		
	Plastron	Trophic status	oligotrophic
	Spiracle		mesotrophic
	Hydrostatic vesicle		eutrophic
Locomotion	Flier	Salinity (preferences)	freshwater
	Surface swimmer		brackish water
	Full water swimmer		
	Crawler	Temperature	Psychrophilic (< 15°C)
	Burrower		Thermophilic (> 15°C)
	Interstitial		Eurythermic
	Temporarily attached		
	Permanently attached	Saprobity	Xenosaprobic
			Oligosaprobic
Food	Microorganisms		β-Mesosaprobic
	Detritus (< 1mm)		α-Mesosaprobic
	Dead plant (>= 1mm)		Polysaprobic
	Living microphytes		
	Living macrophytes	Low pH sensitivity	≤ 4
	Dead animal (>= 1mm)		> 4 to 4.5
	Living microinvertebrates		> 4.5 to 5
	Living macroinvertebrates		> 5 to 5.5
			> 5.5 to 6
Feeding habits	Vertebrates		> 6
	Absorber		
	Deposit feeder		
	Shredder		
	Scraper		
	Filter-feeder		
	Piercer		
	Predator		
	Parasite		

Table 2: The 22 biological and ecological traits used in the analysis, and their categorization.

Scales	Indices	Faunistic assembages	Bioecological traits
Transversal	p-value = 0.001	p-value =0.001	p-value= 0.004
Longitudinal x transversal	NS	NS	NS
Patches	p-value = 0.001	NS	NS

Table 3: p-value results for permutations (Monte Carlo tests) carried out on multivariate analyzes, corresponding to spatial scales and indices, taxonomic or functional indicators.

3.2. Response of indices to the two selected space scales

3.2.1. Transversal scale

The first axis of the PCA (Fig. 1a), based on various indices (Table 4a), separates the reference banks from channels and disturbed banks. Correlation circle results (Fig. 1b) indicate that this axis is strongly correlated with richness and diversity indices. This suggests that, even if the banks offer more habitats than the channel, the contaminated banks exhibit less than half the species occurring in the reference banks and, on average, as many species as found in the channel. Similar observations can be made with respect to taxonomic and functional diversities. The EPT (Ephemeroptera, Plecoptera and Trichoptera) and Mollusca have been more severely impacted by the disturbance. The second axis of the PCA defines an abundance gradient positively correlated with the reference channel.

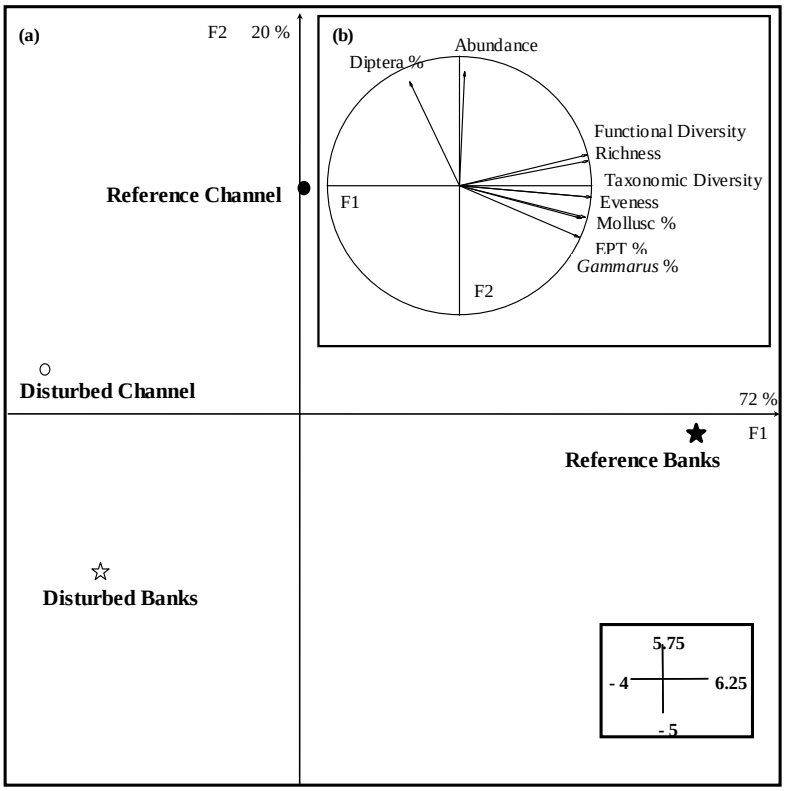

Fig.1: PCA performed at the transversal scale on the indices table: (a) factorial plane of two run-of-river dams, and (b) correlation circle for the nine indices. The circles and stars represent channel and bank samples, respectively; black and white symbols indicate the reference system and the disturbed system, respectively.

Thus, the reference run-of-river dam is characterized by rich and diverse littoral communities and high abundances in the channel. In contrast, the analysis indicated impoverished communities within disturbed banks. In spite of a marked reduction of abundance, the 'disturbed channel' seems less disturbed than the contaminated banks, the indices of the former being similar to those of the reference channel. To some extent, at this level of investigation, channels show structural similarities whereas the banks index distinguishes both of the run-of-river dams.

		Banks		Channel	
		Reference	Contaminated	Reference	Contaminated
a)	Richness	20 ± 8	10 ± 2	16 ± 6	10 ± 6
	Abundance	746 ± 578	619 ± 604	4347 ± 4665	595 ± 733
	EPT %	25 ± 24	5 ± 6	5 ± 8	12 ± 19
	Diptera %	27 ± 18	22 ± 12	61 ± 26	52 ± 34
	Mollusc %	3 ± 4	0,59 ± 0,84	1 ± 2	0,48 ± 0,78
	Gammarus %	20 ± 21	17 ± 18	6 ± 8	6 ± 12
	Functional diversity	0,72 ± 0,16	0,56 ± 0,29	0,56 ± 0,27	0,51 ± 0,28
	Taxonomic diversity	2,57 ± 0,73	1,83 ± 0,96	1,83 ± 1	1,71 ± 1
	Equitability	0,42 ± 0,12	0,30 ± 0,16	0,30 ± 0,17	0,28 ± 0,18
		Erosion		Sedimentation	
		Reference	Contaminated	Reference	Contaminated
b)	Richness	19 ± 6	15 ± 4	15 ± 4	7 ± 2
	Abundance	1553 ± 3461	220 ± 81	3965 ± 3873	812 ± 733
	Functional diversity	0,71 ± 0,26	0,81 ± 0,03	0,57 ± 0,06	0,33 ± 0,2
	Faunistic diversity	2,61 ± 1	2,89 ± 0,28	1,70 ± 0,33	1 ± 0,65

Table 4: Mean ± standard deviation values of (a) the nine indices calculated at the transversal scale and (b) the four indices calculated at the patch scale.

3.2.2. Patches scale

Depending on contamination status and habitat type, the responses of richness, abundance, taxonomic and functional diversities, were tested using ANOVA. The absence of a significant interaction between the factors (Table 5) permits us to test them independently. All variables responded significantly to habitat type (Table 5). Conversely, at the patches scale, only richness discriminated toxic contamination status. Results, summarized in Table 4b, indicate that the sedimentation habitats at the 'disturbed' station are impoverished, which can be related to the accumulation of metals in the sediments.

Variables	Interaction	Status factor	Habitat factor
Abundance	p = 0.44	p = 0.458	p = 0.035
Richness	p = 0.57	**p = 0.011**	**p < 0.001**
Taxonomic Diversity	p = 0.17	p = 0.167	p<0.001
Functional Diversity	p = 0.06	p = 0.186	p<0.001

Table 5: Habitat and contamination effects at the patch scale on four structural and compositional indices. Interaction was assessed by ANOVA. Status and habitat effect were investigated using the Mann and Whitney test, except for values in bold, for which a Student's t test was performed.

3.3. Taxonomic structure versus bio-ecological structure

3.3.1. Transversal scale

The first axis of the correspondent analysis (Fig. 2) shows differences, in terms of taxa assemblages, between reference dams and disturbed run-of-river dams. The second axis reveals similarities between banks and channels in the reference system, while differences are evidenced in the 'disturbed' sample. According to the fuzzy coding analysis (Fig. 3), the relative importance of the two factors (transversal localization and contamination status) is inverted when compared to the taxonomic analysis. The first axis indicates that assemblages are functionally similar in banks and channels in the reference system and different in the contaminated system, while the second axis separates the contamination level. Moreover, the percentage of explained variance is higher (77% versus 44%) when using the fuzzy coding analysis.

3.3.2. Patches scale

The main factor controlling functional analysis is the habitat type instead of the contamination (Fig. 4). The factorial plane F1F2 provides evidence that differences between samples were governed by the habitat type, with discrimination along the F1 axis. Conversely, within a habitat type, no differences are observed according to the contamination status. Similarly, analysis of the faunistic assemblage does not reveal significant responses. As was found in the analysis of various indices, at this scale, differences between habitats rather than between contamination status are indicated.

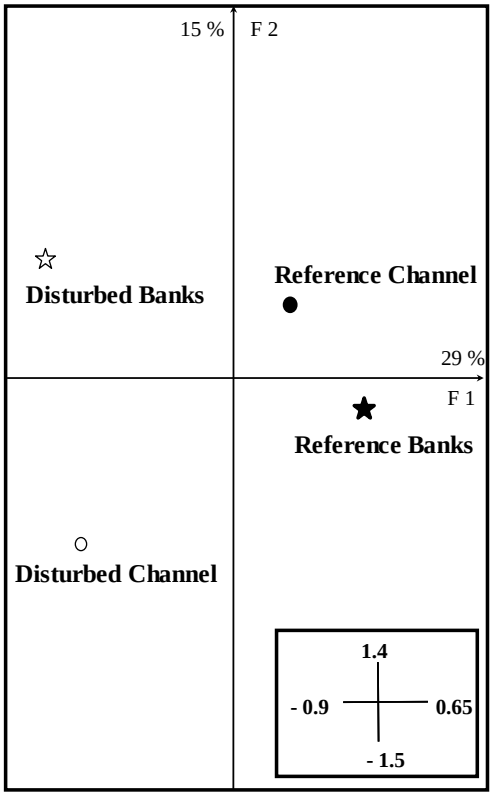

Fig. 2:. Factorial plane of Correspondence Analysis performed at the transversal scale on the faunal list with log-transformed abundances. The circles and stars represent channel and bank samples, respectively; black and white symbols indicate the reference system and the disturbed system, respectively.

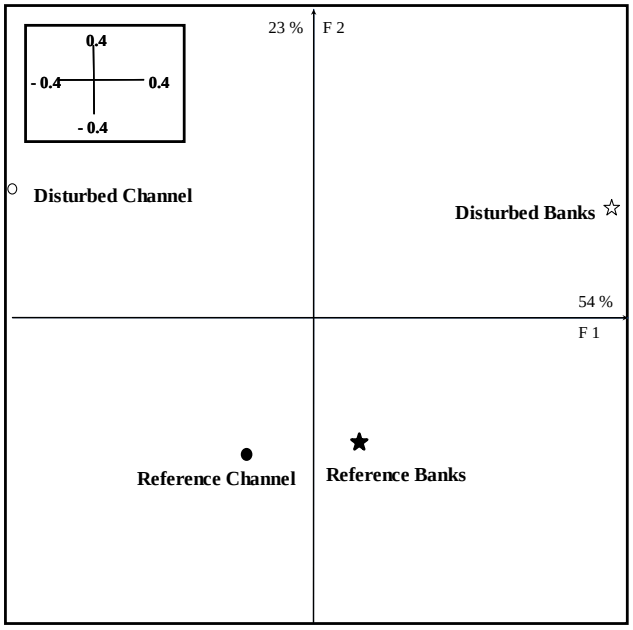

Fig.3: Factorial plane of the Fuzzy Coding Analysis performed at the transversal scale on the bioecological traits. The circles and stars represent channel and bank samples, respectively; black and white symbols indicate the reference system and the disturbed system, respectively.

4. Discussion

4.1. Spatial scale

Because observation scale governs our ability to detect and explain the impacts of contamination on macroinvertebrate communities, it is important to determine which spatial scale, and which indicators (indices, taxonomic, and bio-ecological traits) are the most useful and efficient for detecting the consequences of sediment contamination. This is important for the development of suitable tools for the biomonitoring of sediment contamination.

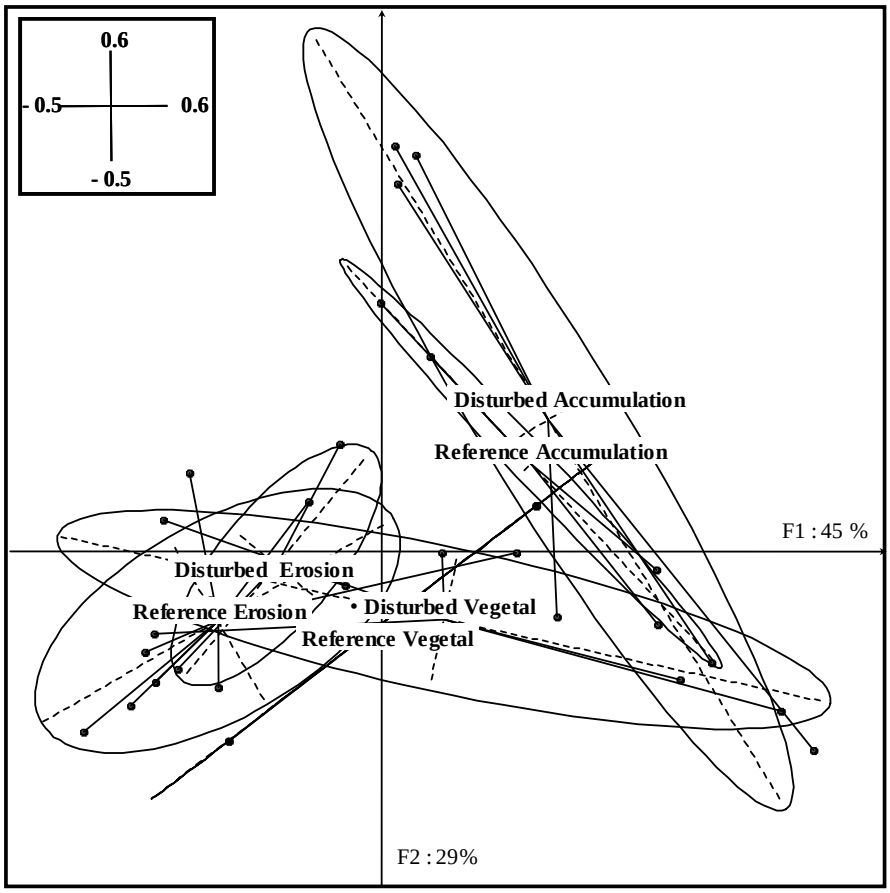

Fig.4: Factorial plane of the Fuzzy Coding Analysis performed at the patch scale on bioecological traits.

4.1.1. Transversal scale

Results demonstrated that macroinvertebrate communities associated with banks are suitable for indicating the effects of contamination, in contrast to those of channel habitats. At this spatial scale, between-station differences associated with contamination levels over-ride within-station substrate heterogeneity effects. Moreover, the habitat constraint is weaker in banks, that have higher levels of diversity in terms of niches and macroinvertebrate communities (Heino, 2000; Harrison and Hildrew, 2001). This explains why banks, in comparison with channels, are more prone to differences between sites with various contamination levels. Being located at the land/ water interface, banks play a key role in the ecosystems' processes. This emphasizes the importance of knowledge of the structure and functioning of the littoral environment. For example, the bank area in lakes has been identified as an important hydro-morphological component supporting ecological quality (Naiman and Décamps, 1997; Rowan et al., 2006; Elosegi et al., 2010). Free et al. (2009) demonstrated the close association of ecotone integrity to fulfilling the habitat requirements of

mayfly adults. James et al. (1998) insist on the importance of this habitat for overall production and in terms of allochthonous carbon contribution to the system.

4.1.2. Patches scale

In contrast with the results of studies of river systems (Pardo and Armitage, 1997), our analysis at the patches scale was not relevant for discriminating contamination effects. This could be explained by the extreme variability and complexity of patch communities, which reduces the sensitivity of impact detection (Donohue et al., 2009). Our study reveals that taxonomic and bioecological structures of macroinvertebrate communities were mostly governed by habitat type, while contamination only influenced richness. Since few studies have focused on run-of-river dams, we can only compare our results to those obtained from lakes or ponds. Nevertheless, even in those systems, few studies have focused on the use of littoral habitats for ecological assessment. Even though White and Irvine (2003) recommend that sampling strategies should be based on pebble or boulder habitats, our results indicated no significant interactions between habitat type and contamination. This could, however, be explained by the analytical strategy, all erosion habitats being pooled. Smaller scales should also enhance such information. As Levin (1992) noted, “The key for understanding how information is transferred across scales is to determine what information is preserved and what information is lost from one scale to the other”. We observed that our ability to find evidence for a response of communities to contaminated sediment depends on the level at which the observations are made. Our results suggest that focusing sampling effort on banks is relevant and practical for the biomonitoring of contaminated sediment.

4.2. Indicator scales

Previously, only taxonomic responses to environmental variables and to contamination have been evaluated, with the consensus that the loss of species is associated with disturbances of the ecosystem. Changes in the distribution and abundance of one species can, however, result in disproportionate and unexpected responses of other species due to attempts to compensate functional changes within the community (Naeem, 1998). This suggests that studying spatial scales will not be enough, and that it is also necessary to consider relevant indicators in order to identify and evaluate perturbations. Indeed, when we use taxonomic or functional

indicators, we do not necessarily observe the same response: the loss of species does not systematically imply a response of the functional structure. Different species may appear to perform the same function (i.e. be redundant) under a restricted set of conditions, yet their functional roles may vary in naturally-heterogeneous environments (Walker, 1992; Wellnitz and Poff, 2001). Traits are one of the tools developed to investigate functional characteristics of a community. By definition, a trait is a surrogate of an organism's performance and/or its individual fitness (Violle et al., 2007). Numerous studies have demonstrated the ability of biological and ecological traits to discriminate metallic (Archaimbault et al., 2010), hydraulic (Snook and Milner, 2002; Griswold et al., 2008) or organic (Charvet et al., 1998) perturbations. In the same way, even if we had observed responses, in terms of species composition, to contamination, our results would still indicate the relevance of bioecological structure, which is a better indicator of the impact of contamination in run-of-river dams.

Nevertheless, this trait-based approach assumes that these biological and ecological parameters (autoecology of species) are relevant indicators of species' functions within the community. The concept of ‘trait’ is particularly important when referring to functional traits (Chapin et al., 2000). Potentially, the traits defined by Usseglio-Polatera et al. (2000) could be considered to be functional traits within ecosystem communities, because the changes that they describe could directly affect ecosystem processes through changes in biotic controls (i.e. predation) and indirectly through changes in abiotic controls (i.e. availability of limiting resources). For example, in the case of species traits that relate to food resources and habits, habitat use and dispersal capacities could be regarded as responses to contamination, while driving changes in ecosystem processes. In the same way, life history traits related to demographic parameters (life cycle, fecundity, maximum size, and number of generations) could be affected by metallic contamination and could thus indirectly alter ecosystem functioning by cascade effects (Zavaleta et al., 2009). Traits described in this article are potential traits based on the literature, and are regarded as ‘response traits’, i.e. a measure of how the trait assemblages react to environmental parameters at the community level. This response may or may not be correlated with the effects on functional processes. It is thus necessary to discern, and be cautious of, the notions of functional response traits and functional effect traits (Lavorel and Garnier, 2002; Violle et al., 2007). Future research should also assess ecosystem's processes, to compare ecosystem functional responses to variations in community traits, in order to identify whether functional traits in response to, and/or as an effect of, contaminated sediment can be defined.

4.3. Ranking impacts

Our results led us to wonder about the hierarchy of impacts, i.e. whether physical constraints could mask the effects of a moderate toxic contamination. Water flow governs the fundamental nature of streams and rivers (Poff et al., 1997; Hart and Finelli, 1999), so modifications of flow, caused by dams, alter the structure and function of river ecosystems (Malmqvist and Englund, 1996; Hart et al., 2002). However, very few studies have concentrated on the adverse effects of dams on the physical, chemical and biological characteristics of rivers (Poff and Hart, 2002). The presence of dams implies two perturbation types: a physical disturbance due to sediment accumulation and the modification of river flow; and a toxic disturbance, due to potential pollutant accumulation within sediments. These perturbations cannot be dissociated in the present study of communities in run-of-river dams. The results obtained for the two studied systems revealed that habitat characteristics of the channel are more significant than differences related to contamination levels between the dams. No clear pattern was, however, indicated, highlighting the need to consider the dams-and-rivers continuum as a means of discriminating these two sources of community modification.

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Article 2: **Benthic indicators of sediment quality associated with run-of-river reservoirs**

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Abstract

Freshwater ecosystems have been fragmented by the construction of large numbers of dams. In addition to disruption of ecological continuity and physical disturbance downstream, the large accumulation of sediments within run-of-river reservoirs constitutes a latent ecotoxic risk for aquatic communities. To date, run-of-river reservoirs are little studied as well as ecotoxic risks associated with contaminated sediment on biodiversity and functioning of such systems. Therefore, the main objective of this study was to describe macroinvertebrates assemblages and functioning of these systems, and to propose indicators of sediment contamination to integrate in in situ risk assessment methodologies. To identify specific assemblages of run-of-river reservoirs, we first compared macroinvertebrates assemblages and their biotrait profiles (i.e. coming from database of biological and ecological traits) of reservoirs (n=6) and associated river sites (upstream and downstream of dam). Then, we compared responses of assemblages and biotrait profiles to sediment contamination in banks and channel of reservoirs to select the most useful spatial scale to identify sediment contamination. Nineteen indicator taxa were observed to have a specific association to channel habitats of reservoirs. Among them, the abundance of three taxa revealed the impact of metal sediment contamination [Tanypodinae (Diptera), Ephemerella (Ephemeroptera) and Atherix (Diptera)]. “Between-reservoirs” differences in their biotrait profile were found along the contamination gradient, with a shift of communities’ composition and functionalities, and an increase in functional similarity. Many traits (response trait) were specifically linked to the metallic contamination of sediments such as “maximal size”, “transversal distribution”,

"substrate preferences", "saprobity", "temperature", "resistance forms" and "locomotion". This study indicates how sediment contamination can change the structural and functional composition of run-of-river reservoirs assemblages. Indicator taxa and response traits identified in this study could improve the current risks assessment methodologies and potentially predict risks of contaminated sediments stored in reservoirs on downstream ecosystems.

Keywords: run-of-river dams; macroinvertebrates; sediment contamination, indicator species, response traits

1. Introduction

Despite their number and their suspected impact on ecosystem integrity, run-of-river reservoirs remains rarely studied. In France, more than 60,000 small run-of-river reservoirs exist (i.e. dam height inferior to 15 meters) and many are impounded by dams or weirs that are aging and in disrepair (70% are without economic use). Although they represent artificial habitats (conversion of lotic to lentic systems), they nevertheless represent important parts of aquatic ecosystems that should be managed and monitored to ensure proper health and functioning of river systems. The role of reservoirs in the transport and storage of toxins within river systems is especially important, as they provide sinks for sediment and associated toxins that would otherwise not be stored in many river systems (Cairns et al. 1984; Chapman 1990; Estebe et al. 1997). Then, these contaminated sediments can potentially act as source of contamination insofar bioaccumulated pollutants could be released into the water column over the long term in response to ambient chemistry variations, sediment resuspension or climatic changes (Lafont et al. 2007). Consequently sediment stored in reservoirs constitutes a latent ecotoxic risk for reservoir biota as well as for downstream living resources.

Risk assessment associated with contaminants stored in sediments is currently performed on the basis of laboratory toxicity tests. Nonetheless, extrapolation from these tests to natural population and communities remains a key challenge, and still rely on large uncertainties (Forbes et al. 2001; Calow and Forbes 2003; Leung et al. 2005; Rubach et al. 2011) because (i) multi-stressor condition (chemicals mixtures and others disturbances) are rarely considered, (ii) standard ecotoxicity tests use laboratory-culturable species which are not

always ecologically relevant and (iii) these tests are usually conducted under one set of fixed conditions and consequently do not consider the effects of environmental parameters undergone on the field. Because contamination can induce modifications in aquatic communities and associated ecosystem's processes, thus affecting ecosystem integrity, it is necessary to focus on community-contamination levels.

The sediments are not only traps for contaminants; they also shelter an important diversity of species, including many macroinvertebrates species. Benthic macroinvertebrates are a main food source for higher trophic levels that strongly influence nutrient cycling and primary productivity (Wallace and Webster 1996). Traditionally, stream bioassessment methods have focused on benthic macroinvertebrate communities (Rosenberg and Resh 1993) as they reflect the overall ecological integrity and provide a holistic measure of the impact of pollutants (Cain et al. 1992; Gurrieri 1998). Due to their close relationship with habitat quality, macroinvertebrates may be relevant indicator of sediment contamination. Nonetheless, there is a paucity of knowledge of the impacts of contaminated sediments on macroinvertebrates communities, specifically in run-of-river reservoirs while these systems are the privileged sites of sediments accumulation and with them of contaminants.(Beasley and Kneale 2003; Ramsey et al. 2005).

To realistically evaluate communities' vulnerability to contaminated sediments, we must take into account their exposure and their sensitivity to disturbance as well as their abilities to sustain in the contaminated environment. In addition to ambient conditions such as organic matter, pH and temperature, the biological and ecological characteristics of species govern their exposure pathway, their pollutant absorption and elimination (Ducrot et al. 2005) but also their abilities to cope with disturbances. Thus, species traits determine the ability of species to deal with environmental problems and opportunities and can be used to explain their occurrence under particular environmental conditions (Keddy 1992; McGill et al. 2006). Moreover, contrary to taxonomic approaches, trait-based approaches provide knowledge about the toxicity mechanisms and the potential ecosystems impacts, and thus have the potential to be more powerful and sensitive biomonitoring tools (Culp et al. 2010). Numerous studies have demonstrated the ability of biological and ecological traits to discriminate metallic (Archaimbault et al. 2010), hydraulic (Snook and Milner 2002; Griswold et al. 2008) and organic (Charvet et al. 1998) perturbations.

Ecosystem assessment and monitoring requires the development and applications of suitable indicators with a measurable and quantifiable relationship to biodiversity (Balmford et al. 2005). This relationship should be direct and should account for different aspects of biodiversity such as taxonomic richness, composition and structure or functional diversity (Noss 1990). In order to select relevant ecological indicators of sediment contamination associated with the presence of dams, we examined macroinvertebrates assemblages and biotraits profiles of six small run-of-river reservoirs. The main objectives of this study were 1) to determine whether metal toxicity in reservoir sediments induces detectable changes in benthic invertebrate community assemblages and biotrait profiles, 2) to identify taxa and biotraits that may be sensitive bioindicators of sediment contamination in reservoirs, and 3) to highlight the need to better monitor ecological heath of reservoirs as an important component of European waterways.

2. Materials and Methods

2.1. Study area

Six run-of-river reservoirs on three French rivers (‘Ain”, “Bienne” and “Fier”) belonging to the same ecoregion (Northern Prealps, Strahler number 2 to 4) were selected to study the macroinvertebrate assemblages associated to various levels of sediment contamination. River sites located upstream and downstream of each dam were selected to enable comparisons with reservoir assemblages and to identify specific assemblages of run-of-river reservoirs. In spring, the average flow of stations on Ain, Bienne and Fier rivers were 7.8 m3s-1(± 3.44), 5.27 m3s-1 (± 3.8) and 11.23 m3s-1 (± 3.40) respectively. The mean of wetted width of the sampled stations ranged from 19 to 35 meters in rivers and from 39 to 112 meters in reservoirs. The sampled average depth of stations ranged from 29 to 49 centimetres in rivers and from 69 to 141 centimetres in reservoirs. Although watersheds of three rivers are mainly forested (Ain: 57.31%, Bienne: 72.6% and Fier: 61.4%) and agricultural (Ain: 36%,Bienne: 22% and Fier: 28.4%; dairy exploitations), the historical industrial activities, have led to the construction of dams and to the discharge of many industrial effluents. Table 1 summarizes main environmental characteristics of selected reservoirs sites.

	Fier		Bienne		Ain	
	Brassilly	Chavaroche	Etables	Lavancia	Sirod	Champagnol
Catchment attributes						
Catchment area (km2)	222	222	216	650	197	432
Latitude N	45° 54' 24.7''	45° 54' 19.6''	46° 22' 55.4''	46° 20' 16.9''	46° 44' 19.1''	46° 20' 16.9''
Longitude E	06° 05' 03.3''	06° 03' 43.5''	05° 49' 26.0''	05° 41' 16.1''	05° 54' 42.8''	05° 41' 16.1''
Altitude (m)	445	373	431	324	615	529
Area (ha)	2	3.5	7	3.7	2	3
Water characteristics (mean value)						
Temperature (°C)	18.7	17.6	8	13	10.5	13.1
pH	8.2	8.15	8.25	8.5	8.1	8.15
O_2 (mg L^{-1})	8.6	9.2	11.4	12.5	12.4	11.9
Conductivity (µS cm^{-1})	411	389	305	329	416	364
NO_3 (mg L^{-1})	16	9.9	2.3	2.2	4.1	3
NO_2 (mg L^{-1})	0.28	0.11	0.02	0.02	0.02	0.03
NH_4 (mg L^{-1})	0.32	0.13	0.05	0.05	0.05	0.05
SO_4 (mg L-1)	15	14	2.5	3.7	4.4	3.6
PO_4 (mg L-1)	0.218	0.251	0.005	0.009	0.005	0.005

Table 1: Principal environmental characteristics and physico-chemical parameters of water that characterize the six run-of-rivers reservoirs sites on three selected rivers.

2.2. Sediments contamination

The physico-chemical characteristics of sediments in reservoirs and rivers sites (Ekman grab, sampling depth of 20-30 centimetres) were measured by a specialized laboratory (LDA26, Valence, France) on samples collected during the spring field campaign according to standards for metals [ISO 11885 (Fe, Al, Mn, Zn) ; NF EN ISO 17294-2 (Cd, Cr, Co, Cu, Ni, Pb, As) and NF EN 1483 (Hg)] and for PAH and PCB (method XP X33012) quantification. Concentrations of eleven metals, eight PCBs and ten polycyclic aromatic hydrocarbons (PAH) were investigated in sediments. PCBs were always below their quantification limit (5µg/kg DM). Table 2 shows (a) concentrations in metals and PAH quantified in reservoirs sites and (b) gradient of contamination identified in rivers sites. Levels of sediment contamination in reservoirs were defined according to the mean ranks for each pollutant concentration measured in each sites. A higher rank represents the highest level of contamination. The selected reservoirs described a significant gradient of sediment contamination in metals and PAH (Friedman' test – $p < 0.001$), from a reference reservoir (Re1) to a highly contaminated reservoir (Re6).

	Fier		Bienne		Ain	
	Brassilly	Chavaroche	Etables	Lavancia	Sirod	Champagnole
Grain size distribution (%)						
Clay (< 2 µm)	0.4	0.9	2.2	1.9	1.7	0.3
Silt (2 to 50 µm)	8.5	19.2	39.5	24.4	27.4	5.3
Sand (> 50 µm)	91	79.9	58.1	73.7	71	94.5
Metals concentration (mg kg DW^{-1})						
Aluminium (Al) (g kg DW^{-1})	9.2	19.7	4.4	2.1	3.7	2.5
Cadmium (Cd)	0.02	0.02	0.3	0.2	0.02	0.02
Chromium (Cr)	38	83.5	32.8	14.9	21.3	12.8
Cobalt (Co)	4	9	3.4	2.3	3.4	2.5
Copper (Cu)	14	31	32.2	24	4.1	45.3
Iron (Fe) (g kg DW^{-1})	6.5	15	7	3.9	9.9	4.9
Manganese (Mn)	169	423	180.8	133.3	284.1	150.2
Nickel (Ni)	7.7	54.7	16.9	10.8	9.4	6.5
Lead (Pb)	22.5	17.8	23.9	32	9.1	11.5
Zinc (Zn)	90	108	78.2	52.4	26.9	85.7
Arsenic (As)	1.9	1	5.9	4.9	10.6	4.6
Contamination level	4	6	5	2	3	1
PAH concentration (µg kg DW^{-1})						
Benzo(a)pyrene (BaP)	20	28	286	535	23	62
Benzo(a)anthracene (BaA)	15	18	233	649	20	46
Benzo(k)fluoranthene (BkF)	12	11	121	206	12	28
Benzo(ghi)perylene (BgP)	37	30	133	43	<10	47
Fluoranthene (Fluo)	54	89	545	1919	46	127
Indeno(1,2,3-cd) pyrene (Ind)	27	15	118	395	21	29
Contamination level	3	2	5	6	1	4

2a)

		Metal contamination in sediments (mg $kgDW^{-1}$)									
		Al	Cd	Cr	Co	Cu	Fe	Ni	Pb	Zn	As
Upstream (n=6)	Minimum	0.5	0.1	4.9	1.4	2.1	2.2	4.3	4.9	17.5	0.1
	Mean	4.5	0.3	23.2	3.0	13.3	5.8	15.2	15.6	42.4	4.4
	Maximum	15.2	0.3	65.0	6.0	23.9	11.0	35.6	41.2	65.2	8.7
Downstream (n=6)	Minimum	0.7	0.1	4.9	1.4	1.7	1.7	3.1	4.7	13.9	0.1
	Mean	3.3	0.1	17.0	2.6	9.0	5.5	11.6	23.2	32.5	3.8
	Maximum	8.6	0.3	40.6	4.9	21.6	8.9	30.0	82.9	55.5	11.4

		PAH Contamination in sediments (µg $kgDW^{-1}$)					
		BaP	BaA	BkF	BgP	Fluo	Ind
Upstream (n=6)	Minimum	5	5	5	5	20	5
	Mean	109	104	55	73	246	58
	Maximum	393	379	201	220	846	187
Downstream (n=6)	Minimum	5	5	5	5	20	12
	Mean	64	38	33	52	147	41
	Maximum	197	68	90	153	443	108

2b)

Table 2: a) Grain size distribution and concentrations in metals and in PAH in sediments of run-of-river reservoirs; metal (Mercury) and PAHs (Anthracene, Chrysene, Naphthalene, Phenanthrene) which concentrations were inferior to detection thresholds were not included in the table. Contamination levels correspond to the mean of ranks for each site according each concentration in metals or in PAHs. A higher rank corresponds to the higher level of contamination. b) Gradient of concentrations in metals and in PAHs in sediments at upstream and downstream sites of dams; Minimum: minimum concentration, Maximum= maximal concentration and Mean= mean value of concentrations.

2.3. Macroinvertebrates sampling

Macroinvertebrates in run-of-river reservoirs were sampled using a newly designed sampling protocol (Colas et al. 2011). To reflect the effects of various hydraulic and hydro-morphological conditions, sediment accumulation areas associated with run-of-river dams were subdivided into three zones (tail, middle and dam). The tail is closest to river conditions, the dam is typical of a lentic system and the middle exhibits intermediate characteristics. Banks and channel communities were sampled separately. Three samples were collected on both banks for each zones defined above thanks to a Surber net (mesh size 500 µm, sampled area 0.05 m2). Macroinvertebrates in the channel were sampled by dredging (triangular dredge, mesh size 500 µm, sampled area 0.15 m2) from a boat perpendicular to a transect in each of the three areas defined above. For each transect, left, middle and right sides of the channel were sampled. To evaluate the contribution of stations upstream and discriminate species assemblages strictly related to run-of-river dam systems, macroinvertebrate communities of upstream stations were sampled according to a normalized protocol (Multi-Habitat Sampling, norm XP T 90-333 in, A.F.N.O.R. 2009) designed to fulfill the European Water Framework Directive (WFD) requirements. All samples were preserved in 4% formalin in the field and transferred to the laboratory where they were sieved and sorted. Organisms were mainly identified at genus level (using (Tachet et al. 2000), except for some groups, which were identified at higher taxonomic level [i.e. Diptera (family or tribe level), Oligochaeta (Class), Nematoda (Order)]. Individuals within each taxon were then counted. The rare taxa (which abundance on each station was inferior to 3 individuals) were not included in the analysis of faunistic data. Abundances of taxa in each sample were weighted considering the sampled area to allow the comparison between channel of reservoirs and banks or river sites.

2.4. Selection of relevant spatial scale to survey sediment contamination

Like reveals it the first axis of principal component analysis (PCoA) (Fig.1) performed on bray-Curtis distance matrices obtained from abundance data from rivers and run-of-river reservoirs sites, reservoirs exhibit specific macroinvertebrates assemblages. Spearman's correlations between coordinates of the PCoA analysis, the indices of functional diversity and levels of contamination in metals and PAHs (Table 3) enable selection of the most relevant spatial scale to survey the impact of sediment contamination. A first study examined relevance of three spatial scales [transversal (banks and channel), transversal x longitudinal

(banks/channel x tail/middle/cue) and patch scale (erosion, sedimentation and vegetation habitats)] to elucidate impacts of contaminated sediments on macroinvertebrates communities in two run-of-river reservoirs (Colas et al. 2011). This study revealed that focusing on communities at transversal scales allows elucidating effects of sediment contamination, contrary to the longitudinal and patch scales. Consequently this present study focuses on assemblages at transversal scales where samples are pooled according to their bank or channel origin. The Spearman's correlations indicate a strong influence of the level of metal contamination on run-of-river dam communities, especially in the channels. In comparison, no significant response of assemblages and indices was observed for rivers communities in upstream of dams, probably due to low concentrations in metals and PAH in rivers sediments. These results evidenced that the channel is the most useful spatial scale to identify sediment contamination by metals in reservoirs and allows us to justify its consideration of channel assemblages in order to identify species common to all reservoirs sites and indicators of the effects of sediment contamination.

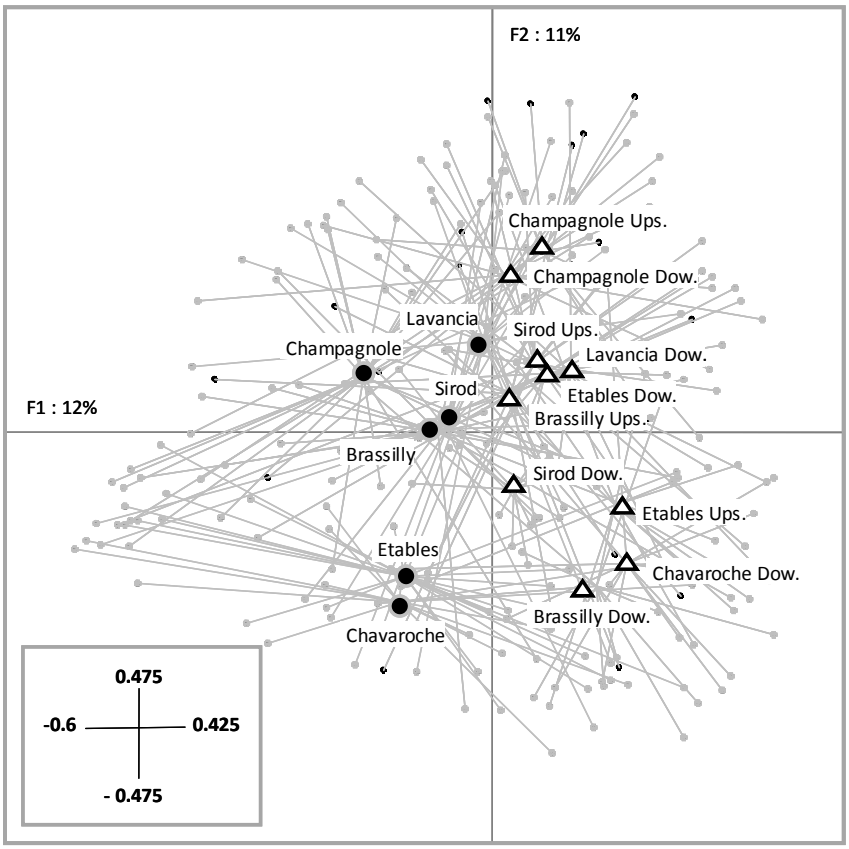

Fig.1: Factorial plane of the principal coordinate analysis of the macroinvertebrate channel abundance at six run-of-river dam stations and ten river stations. The triangles represent the river sites and the circles represent run-of-river reservoir sites.

	Reservoirs sites				River sites	
	Channels		Banks		Upstream of dams	
	Metals	PAHs	Metals	PAHs	Metals	PAHs
PCoA	-0.96***	NS	NS	NS	NS	NS
S	NS	NS	NS	NS	NS	NS
H	NS	NS	NS	NS	NS	NS
MFAD	-0.93***	NS	-0.85*	NS	NS	NS
FD	-0.95***	NS	-0.87*	NS	NS	NS

Table 3: Spearman's correlations between coordinates of sites coming from the PcoA analysis performed on faunistic distributions (PCoA), indices of taxonomic structure (S: richness, H: diversity index of Shannon and Weaver), indices of functional structure (MFAD: modified version of functional attribute diversity, FD: functional diversity index based on dendrograms) and levels of contamination in metals and in PAHs for channels, banks and rivers spatial scales. NS: no significant, * p-value < 0.01, *** p-value < 0.0001.

2.5. Data analysis

Indicator species of run-of-river reservoir were selected on the basis of abundance data of the selected assemblages (i.e. channel of reservoirs) using the IndVal index (Dufrêne and Legendre 1997). We considered two groups of sites i.e. in upstream of dams in rivers or in reservoirs. For each species i in each site group "reservoir", we computed the mean abundance of species i in the sites of group "reservoir" compared to group "river" (Ai reservoir) by the relative frequency of occurrence of species i in the sites of group "reservoir" (B i reservoir)), as follows:

$A_{i\ reservoir} = Nindividuals_{i\ reservoir} / Nindividuals_{i}$

$B_{i\ reservoir} = Nsites_{i\ reservoir} / Nsites_{reservoirs}$

$IndVal_{i\ reservoir} = A_{i\ reservoir} \times B_{i\ reservoir} \times 100$

Where IndVal is the indicator value of species *i* in reservoirs expressed in percentage.

The maximum value of this index for one species is 100% when the individuals of a species are observed in all sites of only one group. In addition to IndVal, the richness and Shannon and Weaver diversity index were determined for each site. Biotrait responses were investigated using the distribution of categories within 22 traits describing biological and ecological characteristics of macroinvertebrates (Usseglio-Polatera et al. 2000). The biological and ecological categories of traits were weighted by the log-transformed abundance of each taxon. Therefore, for each trait category, the sum of weighted scores was expressed as the relative abundance distribution within a trait (Thioulouse et al. 1997). We choose to study two facets of functional diversity: the functional richness and the functional divergence.

Functional richness indices measure how much of the niche space is occupied by the species present and functional divergence indices, how this space is filled. We used a functional diversity index based on dendrograms (Petchey and Gaston 2002; Petchey and Gaston 2006) to examine functional richness. This functional diversity index (FD) is the total branch length of the functional dendrogram that can be constructed from information about species functional traits. Regarding, functional divergence, we used the modified version of functional attribute diversity (Walker et al. 1999; Walker and Langridge 2002) proposed by Schmera et al (2009) called MFAD.

"Between-reservoirs" comparisons of trait' category utilization were performed with Student' t-tests after arcsin (√p) transformations (normality and homoscedasticity being respected). Significant differences were evaluated after Bonferroni correction of p-values. Percentages of similarity (Jaccard distance) used for complete-linkage clustering analysis were calculated on the basis of trait categories exhibiting a significant "between- reservoirs" difference. Finally, Spearman's correlations were used to explore the relationship between indices and sediment contamination. We used ADE4 (Chessel et al. 2004) and Indicspecies libraries (De Cãceres and Legendre 2009) of R software (Team 2008). The FDiversity software (Casanoves et al. 2010) was used to analyze the functional diversity.

3. Results

3.1. Selection of indicator species

The comparison between the rivers and run-of-river dams communities, performed with the IndVal method, allowed us to identify 19 typical species for channel stations, regardless of the level of sediment contamination (Table 4). The three taxa that were the most common in the channel, with IndVal indexes higher than 60%, were Oligochaeta, Chironomus and Tanypodinae. Among them, only the abundance of Tanypodinae was significantly correlated to the levels of metallic contamination (rspearman= 0.98, $p<0.001$) with a decreasing abundance when the metal contamination increased. Similarly, the abundance of Ephemerella and Atherix exhibit the same trend (rspearman=0.94, p=0.006 for Ephemerella, rspearman=0.89, p=0.016 for Atherix).

Order	Taxon	Indval index
Oligochetea	Oligochetea	79.1
Diptera	*Chironomus*	75.9
Diptera	Tanypodinae*[p]	75.5
Ephemeroptera	*Ephemerella**[p]	58.3
Plecoptera	*Leuctra**	55.3
Diptera	Tanytarsini	53.4
Diptera	*Atherix**[p]	46.9
Trichoptera	*Psychomyia pussilla**	46.8
Pulmonata	Lymnaeidae	43.3
Diptera	Ceratopogoninae	37.0
Nematoda	Nematoda	35.6
Ephemeroptera	*Ecdyonurus**	35.3
Trichoptera	*Allogamus*	32.2
Coleoptera	Dysticidae	29.9
Trichoptera	*Polycentropus**	29.4
Ephemeroptera	*Torleya*	27.4
Rhynchobdellida	*Glossiphonia*	16.0
Heteroptera	*Micronecta*	15.6
Diptera	*Tipula*	12.7

Table 4: Nineteen indicator taxa identified with Indval index (percentage) classified by decreasing order.

3.2. Toward the selection of response traits to contaminated sediment

The biotrait profiles based on the abundances of 19 indicator taxa were used to characterize the functioning of run-of-river reservoirs and to identify response traits to the sediment contamination. The cluster analysis (Fig.2) discriminates two groups: a first one represented by the stations in which the sediments are contaminated (called disturbed stations) and a second one composed of least or not contaminated stations (reference stations).

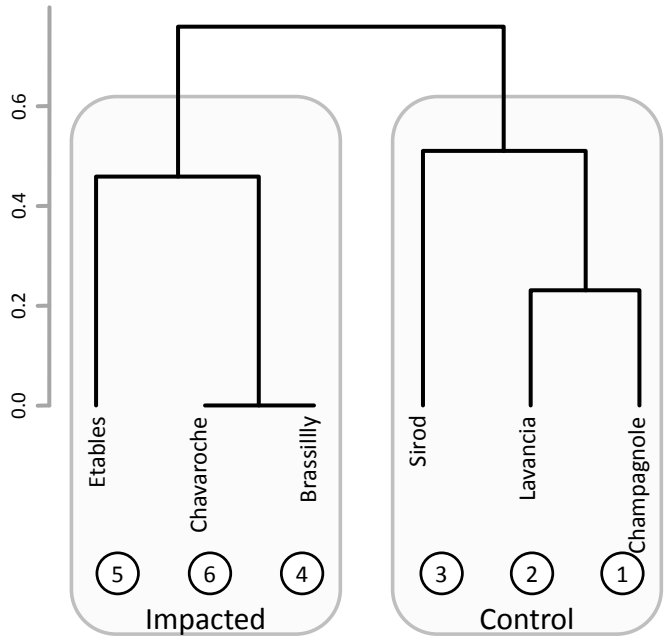

Fig.2: Hierarchical clustering dendrogram of the Jaccard distances between the biotraits profiles based on the abundances of the nineteen indicator taxa of channel of each run-of-river reservoirs sites. Numbers represent levels of metal contamination.

Student's t-tests revealed distinct patterns of bioecological modalities between these two groups of stations (Table 5). The reference stations displayed a higher proportion of organisms that were more characteristic of river channels with rapid flow conditions and

coarse grain-size distribution. Corresponding organisms are shredders of intermediate size, eurythermic, with low reproduction (one cycle per year). Dispersion mechanisms are active, either aerial or aquatic. Organisms in these stations are not resistant to organic pollution (xenosaprobic to oligosaprobic), but can resist disturbance owing to the production of eggs and statoblasts. In contrast, the contaminated stations shelter organisms common to the metapotamon, which corresponds to the sedimentary zones of large rivers in lowlands. As a result, they require essentially lentic, eutrophic and organic habitats, consisting of areas such as mud substrates in ponds, marshes and lakes. Corresponding organisms are polluo-resistant (α-mesosaprobic) and primarily feed on fine detritus. Those communities are characterized by an important proportion of macroinvertebrates parasites such as Nematoda.

Overall, levels of contamination decrease significantly the functional diversity indices of channel communities (see Table 3). Investigation of the correspondence between functional shifts and sediment quality indicate that the functional divergence index of seven traits is significantly correlated with the levels of metal contamination (see Table 6).

Traits	Functional divergence
Maximal size (cm)	r= -0.82*
Transversal distribution	r= -0.94**
Substrate preferences	r=-0.84*
Saprobity	r=-0.84*
Temperature	r=-0.87*
Resistance forms	r=-0.98***
Locomotion	r=-0.82*

Table 6: Spearman's correlations between functional diversity (MFAD) of seven traits selected according to results of Student' t-tests and levels of contamination. * p-value < 0.01, ** p-value < 0.001, p-value < 0.0001.

Traits	Controls	Impacted	Control *vs* Impacted
Dispersal forms			
Aerial active	0.25(0.03)	0.08(0.05)	↘
Aquatic active	0.27(0.04)	0.12(0.01)	↘
Feeding habits			
Parasite	0.01(0.01)	0.08(0.04)	↗
Scraper	0.22(0.06)	0.09(0.005)	↘
Food			
Dead plant (≤ 1mm)	0.16(0.02)	0.01(0.004)	↘
Detritus (< 1mm)	0.27(0.08)	0.47(0.04)	↗
Longitudinal distribution			
Metapotamon	0.07(0.02)	0.17(0.03)	↗
Locomotion			
Crawler	0.56(0.04)	0.20(0.08)	↘
Burrower	0.12(0.03)	0.23(0.01)	↗
Maximal size (cm)			
> 0.5 to 1	0.62(0.08)	0.14(0.04)	↘
Number of reproductive cycle per year			
1	0.73(0.002)	0.31(0.04)	↘
> 1	0.22(0.06)	0.68(0.05)	↗
Reproduction			
Isolated egg, cemented	0.45(0.07)	0.03(0.02)	↘
Terrestrial clutches	0.01(0.003)	0.0004(0.0006)	↘
Resistance forms			
Eggs, statoblaste	0.22(0.04)	0.01(0.004)	↘
Saprobity			
Oligosaprobic	0.32(0.04)	0.18(0.04)	↘
α-mesosaprobic	0.18(0.05)	0.44(0.09)	↗
Substrate preferences			
Mud	0.08(0.02)	0.16(0.01)	↗
Temperature			
Eurythermic	0.66(0.04)	0.53(0.01)	↘
Transversal distribution			
Channel	0.31(0.08)	0.09(0.03)	↘
Lakes	0.15(0.03)	0.21(0.02)	↗
Marshes	0.02(0.004)	0.08(0.02)	↗
Ponds	0.05(0.01)	0.16(0.02)	↗
Trophic status			
Eutrophic	0.12(0.04)	0.42(0.12)	↗

Table 5: Frequencies of biotraits modalities (with standard deviation) identified as significantly different by Student't-test and Tukey's HSD post-hoc test performed on reservoir biotrait profiles. Each trait modality utilization in "impacted reservoirs" was compared to that in the 'control reservoir'. The difference was illustrated by an arrow, when the p-value (after Bonferroni correction) was significant: upward = "decreasing in control" or downward = "increasing in control".

3.3. Transversal and longitudinal contributions: a confounding factor

The relationships of the three components of biodiversity investigated in this study (functional diversity, richness and taxonomic diversity) are presented in Table 7. Our results evidenced that these parameters did not vary independently from each other. The richness and diversity (either taxonomic or functional) of channels were positively correlated with that of the upstream stations, while only functional diversities were correlated between banks and channels.

		Channel		
		Functional diversity	Richness	Taxonomic diversity
Banks	Functional diversity	r=0.99***		
	Richness		r=0.77	
	Taxonomic diversity			r=0.36
Upstream	Functional diversity	r=0.82*		
	Richness		r=0.94**	
	Taxonomic diversity			r=0.84*

Table 7: Spearman's correlations between functional diversity, richness and taxonomic diversity of channel and banks or upstream. * p-value<0.01; *** p-value <0.0001.

4. Discussion

Run-of-river reservoirs constitute an ecosystem that is distinct from the associated rivers, with specific macroinvertebrates assemblages. Identifying their specificity and the underlying mechanisms that drive biodiversity within these systems is essential to understand biodiversity patterns in response to sediment contamination at both the local (i.e. reservoir) and the whole river course scales.

In this study, even if the bank communities of reservoirs discriminated levels of sediment contamination, the channel communities are more efficient to discriminate response patterns to the metallic sediment contamination. Mousavi et al. (2003) shown similar patterns with study of communities structure of chironomid larvae at profundal zones in lakes to elucidate impacts of heavy metal contamination. Due to the strong physical constraints (e.g. habitat poverty, strong sedimentation, silting), heterogeneity of macroinvertebrate assemblages should be weaker in channel than in reservoir banks and rivers, and consequently habitat effect on macroinvertebrates responses may masked effect of sediment contamination at banks scales. In addition, the accumulation of sediment is more important in the channel,

while banks provide a greater diversity of refuge habitats. As a result, the communities inhabiting the channel are more in contact with the sediments and the accumulated pollutants. These physical and chemical constraints specific to channel of run-of-river reservoirs lead to the identification of characteristic species assemblages and biotrait profiles.

Indicator species can be used as ecological indicators of community types, habitat conditions, or environmental changes due to their niche preferences (McGeoh and Chown 1998; Carignan and Villard 2002; Niemi and McDonald 2004). Nineteen indicator taxa were identified for the channel of run-of-river reservoirs. This abundance of indicator taxa underlines the specificity and diversity of the channel assemblages. Indeed, if the dominant indicator taxa are generalists, such as Oligochaeta, *Chironomus* and Tanypodinae, the channel also shelters specialists indicator taxa that are more sensitive to disturbances such as *Ephemerella*, *Ecdyonurus*, *Allogamus* or *Leuctra*. (McGeoh and Chown 1998) suggested that indicator species could be used in three distinct ways: (1) to reflect the biotic or abiotic state of the environment; (2) to reveal the impact of environmental changes; and (3) to indicate the diversity of other species, taxa, or communities within an area. Species selected in our study reflect the biotic and abiotic conditions of run-of-river reservoirs, and among them, the abundance of three taxa revealed the impact of the metallic contamination of sediments.

The three taxa indicator of metal contamination in sediments (i.e. Tanypodinae, *Ephemerella* and *Atherix*) are intimately associated with the sediment (Nebeker et al. 1984; Larsen et al. 2009) and consequently with bound contaminants; however, different exposure pathways are related to the biological and ecological characteristics of these species. Specifically, the feeding habits, substrate preferences, resistance forms, number and duration of aquatic stages and respiration can determine the specific responses to pollutants (Koivisto et al. 1992; Escher and Hermens 2002; Spromberg and Birge 2005). Increased metal concentrations in aquatic systems have been reported to result in decreased abundances of benthic invertebrates, including Chironomidae (Winner et al. 1980; Richardson and Kiffney 2000) especially in the subfamilies of Tanypodinae in lakes (Mousavi et al. 2003), and *Ephemerella* (Beasley and Kneale 2003; Armitage et al. 2007; Clements 1994; Pond 2010). Beasley and Kneale (2003) reported the sensitivity of *Ephemerella* to metals (Zn, Pb, Cu, Cd, Cr and Fe) in water but, a tolerance to PAHs such as Benzo(b)fluoranthene, Fluoranthene, Naphthalene and Dibenzo(a,h)anthracene. That is consistent with the results of the present study. There is little information available regarding the sensitivity of *Atherix* to metals. Only Marquès et al.

(2003) identified this Diptera family as sensitive to disturbances such as an increase of heavy metals and conductivity in the water column, but not to the metal content in sediments. The lack of correlations between the abundance of the other indicator taxa and the gradient of sediments contamination is not inevitably related to the absence of toxic effects. Tolerant species could have compensated toxic effects owing to decreased interspecific competition or local adaptation through niche plasticity. These adaptations of tolerant or resistant species can be useful to identify responses traits to sediment contamination.

Trait-based approaches are now widely used in studies from the organism level to the ecosystem level (Violle et al. 2007). The traits of taxa present at a site can be used to indicate environmental conditions and further infer mechanisms by which the community composition is shaped. The linkage of response traits to stressor gradients promises to expand biomonitoring approaches beyond traditional taxonomic-based assessments that identify ecological effects, thereby enabling a causal diagnosis (Culp et al. 2010). A previous study highlighted the power of a multimetric approach based on biological and ecological traits of benthic macroinvertebrates to elucidate the sediment contamination effects in streams (Archaimbault et al. 2010). In accordance with this study, our results underline the relevance of using traits-based approaches in order to discriminate effects of sediment contamination. Indeed, unlike the faunistic structure, functional diversity profiles enables to discriminate the effects of sediment contamination on assemblages in banks and channel of reservoirs. Differences in the biotrait profile were found between reference and contaminated run-of-river reservoirs. While functional characteristics were close to those of lotic habitats for reference run-of-river reservoirs, a shift from these characteristics occurred in contaminated ones. The corresponding communities are typical of lentic and eutrophic habitats of potamic areas. The attributes of species found in frequently disturbed systems (e.g. multivotinism, polysabrobic, metapotamon) were associated with contaminated run-of-river reservoirs, whereas traits common in more stable and favorable environments such as semi-voltinism, isolated eggs and active dispersal were found in reference run-of-river reservoirs. In addition to traits identify by Archaimbault et al. (2010) like more specifically linked to the ecotoxic impact of stream sediments i.e. “saprobity” and “trophic level”, we identified other traits specifically linked to the impacts of metallic sediment contamination such as “locomotion”, “transversal distribution”, “substrate preferences”, saprobity, “temperature”, “resistance forms” and “maximal size”. These traits are closely related to the resilience of the communities to disturbances and govern level of exposure, its duration (Koivisto et al. 1992)

and bioaccumulation of pollutants into organisms in contact with the sediment. For example, body size and related surface-area-to-volume relationships can be determinant for pollutants bioconcentration in organisms (Dolédec and Statzner 2008; Preuss et al. 2008). Indeed, some studies suggest that species with large, massive body shape presented the lowest ratio of toxicants intake, while small individuals presented higher values (Ippolito et al. 2012). This hypothesis could explain the selection of larger species in contaminated run-of-river reservoirs. These responses traits should be integrated into *in situ* risk assessment methodologies associated with sediment contamination but also to improve laboratory biotests to select (i) model species which share the same biological and ecological attributes than indicator species of the ecotoxic impact and, (ii) traits that reveal the response of *in situ* communities to sediment contamination. More research could also examine the variations intra- and inter-populations in the expression of these traits in response to the sediment contamination. These variations of traits could be useful in the diagnosis of sediment contamination and in improve current laboratory methodologies.

Finally, the biotrait profiles changes in contaminated run-of-river reservoirs could indicate (1) a stronger accumulation of fine sediments, (2) weaker resilience or resistant potentials to disturbances such as decreased numbers of small species, less resistance forms and reproduction types, and increased sensitivity to temperature changes, (3) a lower input in the abundance and/or quality of allotochnous organic matter, (4) lower primary production and (5) a higher abundance of parasites such as nematodes. Overall, sediment contamination results in increasing similarity of macroinvertebrate community traits. Decreased functional diversity in contaminated stations associated with the increase in functional redundancy may induce: (1) a decrease of the complementarity between species (lower interactions) and thus, (2) a potential diminution of the effectiveness of ecosystemic processes such as leaf litter breakdown. Future research should combined the evaluation of communities biotrait profiles with ecosystemic processes study in order to examine if these structural and functional changes in communities could be indicator of functional impairment at ecosystem level ; consequently identify if these response traits to the contamination are also effect traits on ecosystem processes.

Although the biological and ecological changes reported in this study were significantly associated with sediment contamination, other parameters can also explain the responses of macroinvertebrate communities. For instance, even if sediment grain size were quite similar

between run-of-river sites, the accumulation of fine sediments could potentially impacted macroinvertebrate communities. In an experimental study, Larsen et al.(2011) examined the response of stream invertebrates to fine sediment addition (i.e. inert sand). They reported a decrease in richness and overall trait diversity and a selection of few traits in the community associated to sediment addition such as "polyvoltinism", "tegumental respiration" and 'burrowing behavior". It remains difficult in situ to separate the impact of sedimentation (i.e. accumulation of fine sediment) from the ecotoxic impact of sediment contamination. We assume that functional changes in this study are associated to sediment contamination because sediment grain size and accumulation were quite similar. Nonetheless, studies in mesocosms could allow dissociating the relative importance of the both disturbances on the structural and functional responses of macroinvertebrates communities, probably dependent on the extent of contamination.

Because the quality of channel reservoirs is also closely dependent with the quality of upstream areas (rivers) and of banks, we must also consider in the bioassessment scheme of run-of-river reservoirs, the quality of the longitudinal (upstream) and transversal (banks) contributions. These items are considered to be confounding factors because the biodiversity of upstream dams and banks can induce a bias in the evaluation of sediment contamination impacts, either increasing (via low diversity and recolonization) or compensating (via high diversity and recolonization) the effects on community. Our results illustrate that reference reservoirs are associated to diversified upstream sites, and that contaminated reservoirs are associated to impoverished and poorly diversified sites. Upstream stations represent a regional species pool and should consequently influence the trajectories of recovery of run-of-river reservoirs communities by sustaining their richness and taxonomic diversity. In this study, no significant impact of sediment contamination was observed on assemblages in upstream river sites, probably due to a moderate contamination. Nonetheless, other disturbances (e.g. physical) in studied sites or in more upstream areas may also reduce regional pool of species likely to colonize run-of-river reservoirs and consequently participate in the explanation of the observed responses. If run-of-rivers reservoirs should be integrate to evaluate ecological status of rivers due to their potential impact on downstream reaches, the quality of river upstream should be also integrate to evaluate vulnerability and recovery trajectories of run-of-river reservoirs to presence of contaminated sediment. This research and integration of the nature and intensity of these confounding factors are essential in the development of

methodologies to evaluate the risks associated with contamination of the run-of-river reservoir sediments.

5. Conclusions

Knowledge regarding run-of-river reservoirs and the mechanisms that govern their biodiversity and functioning is still very scarce, even though these systems are numerous and pose a potential risk to downstream areas. The biodiversity and good functioning of run-of-river reservoirs may be crucial to the recovery trajectories of the communities downstream from dams by providing a regional pool of species and supporting recolonization. The European Water Framework Directive should include the biomonitoring of run-of-river reservoirs, and the development of risk assessment methodologies associated with the accumulated sediment contamination in these systems. Biological and ecological traits could provide new methods for risk assessment associated to contaminated sediment. However, we need to increase the number of sites to improve the tools' precision and to study in situ communities' response to contamination conjointly with current laboratory methodologies. More research should be developed to improve our knowledge of run-of-river reservoirs and the effects of contaminated sediment on communities in reservoirs but also downstream. Such studies should not only consider these systems as altered environments, but rather as ecosystems with specific biodiversity, goods and services that must be assessed.

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Article 3: **Multicompartment responses to contaminated sediment resuspension: first prospect for dam removal strategy implementation**

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Abstract

We examined the effects of contaminated sediment resuspension associated with a reservoir draw-off on microbial and benthic macroinvertebrates communities, at taxonomic and functional levels, as an opportunity for learning about the mechanisms driving communities' responses to future dam removal projects. We compared contamination levels in sediments, physical parameters, responses of microbial and macroinvertebrates communities before and after the draw-off on five stations: upstream dam, the reservoir and three downstream stations. Our results evidenced a significant export of sediment and pollutants downstream and inversely a decreasing in the sites under the draw-off influence. The microbial functional response was closely correlated to the levels of chronic contamination before the draw-off. Historic contamination may have led to a selection of tolerant species and to a reduction of the metabolic activities. The macroinvertebrates communities' responses brought out the impacts of physical and toxic disturbances associated with sediment resuspension. The communities were structurally and functionally disturbed, up to 18 kilometres downstream dam. Finally, we debate on resistance and resilience abilities to an additional potential disturbance (e.g. dam removal) of these communities. This study provides new insights concerning the short term effects of dam removal in the case of contaminated sediments and supports the need to develop long-term studies on recovery capacity of the communities and specific functionalities of lotic environments.

Keywords: Communities Ecotoxicology - Ecological continuity restoration - Multiple stressors – Contaminated sediment – Multicompartment risk assessment

1. Introduction

Water is a limited resource providing lots of goods and ecological services which all living species depends on. The increasing need of freshwater for human populations, agriculture and energy led to manipulate stream corridor through an excessive construction of dams during the 20th century [1]. Thus, 45000 large dams (superior to 15 metres, World Commission on Dams, 2000) were built in the world. In France, in addition with 700 large dams, more than 60000 weirs and small run-of-river dams have been referenced (Fig.1) including 70% which are without economic use [2]. Globally, human activities capture 50% of the available freshwater flow [3]. It led to in-depth modifications of the resource quality, and this permanent pressure undoubtedly will not cease with the predicted increase of the human population. Dams disturb dramatically rivers and aquatic biota by altering the biological and physical characteristics of river channels and floodplains and fragmenting the continuity of rivers [4, 5]. This ecological continuity is fundamental for the migration of not only amphialin but also holobiotic organisms [6], for nutrient exchanges and for sediment transport. Indeed, sediments that are trapped in run-of-river dams induce a change of the river's structural habitat [7]. Organic materials associated to sediments, which provides vital nutrients for downstream food webs, are also lost for downstream ecosystems. Finally their strong adsorption capacity for pollutants lead accumulated sediments to become a sink and a source of historic contamination [8].

However, with an important species diversity, the sediments constitute an essential compartment in the functioning of aquatic ecosystems [9]. Because they affect processes that take place at the water/sediment interface and are likely to be mobilized during the sediments resuspension, the contaminants stored in the sediments threaten the integrity of the river on its broader scale. The national and international policies aim to find answers to the dependant issues. In Europe Union, the European Water Framework Directive (WFD) sets the main objective to reach the ecological good state of at least two thirds of the rivers by 2015 for all Member States. To achieve this herculean objective, the development of methods to partially or fully restore degraded aquatic resources became a research priority [10]. Dam removal has been proposed as an effective method of river restoration [11]. However, dam removal can potentially affect downstream systems physically and chemically through the transport of the contaminants bound to the sediment. Studies on the impact of the dam removal were primarily focused on large ones (> 15 meters), while most of the dams removed and identified

are smaller structures [12]. We thus have little information on the ecological impact of these small dams and more generally on the impact of the contaminated sediment resuspension. Consequently, before planning restoration of the ecological continuity by dams' removal, it is important to predict the effects of the sediment and pollutants resuspension on downstream ecosystems.

To date sediment toxicity is classically assessed by biotests carried out in laboratories. However, such tests don't consider responses at the community or ecosystem levels [13], while contamination can induce modifications in ecosystem's processes and affect ecosystem integrity [14]. The microbial and macrobenthic compartments are directly associated with the benthos, consequently they are likely to be deeply influenced by the presence of a dam and its removal [15]. These two compartments play an essential role in the structure and the functioning of aquatic ecosystems. Numerous studies have demonstrated the importance of microbial communities for processes such as nutrient cycling, decomposition of organic matter and primary production transfer towards upper trophic levels [16]. Similarly, secondary producers such as macroinvertebrates are a direct food source for most fish and strongly influence nutrient cycling and primary productivity [17]. The combined activity of both compartments is the guarantee of good functioning of aquatic ecosystems.

In this context, the main objective of the present study was to assess the effects of contaminated sediment resuspension associated with reservoir draw-off on taxonomic and functional components of benthic communities below dam. We hypothesize that downstream communities will be affected by both physical and chemical impacts. The taxonomic and functional responses would depend on resistance abilities of downstream communities already stressed. Finally we support that assessment of resuspension sediment effects associated with a reservoir draw-off could constitute an opportunity to predict the effects of future dam removal project.

2. Materials and methods

2.1. Study area

Bienne is a French mountain river which takes its source at 1200 meters of altitude. The industrial activity, very developed in the upstream sector, has led to the construction of dams and to the discharge of many metallic effluents. Since 1995, the local policies have

imposed the reduction in industrial effluents discharge and the monitoring of river contamination levels. Despite decreasing discharges, contamination has been entrapped in the sediments accumulated within several successive dams. One of these dams, called "Etables" is the first large obstacle along the watercourse. The associated reservoir has an area of about twenty hectare (550,000 m^3 at the normal level of exploitation) and a maximal depth of 16 meters. The dam has induced an important sediment accumulation, which contamination levels were followed for many years. A first draw-off of reservoir was carried out in 2005 for maintenance work, resulting in the exportation of 12 000 m^3 of sediments downstream. It deeply altered the natural hydromorphology of the river. The river bed fouling was measured up to 2 400 metres downstream, inducing a habitat loss. Following the draining, an important mortality of grayling (*Thymallus thymallus*) and trout (*Salmo trutta*) was recorded downstream. The analyses realized on dead fishes have evidenced a toxicological origin, while the habitat fouling and the decrease in oxygen concentration could also explain this fish mortality. Investigations were thus realized on toxic risks of dam sediments, and evidenced their strong metallic contamination, particularly in Lead and in Arsenic in deepest layers, in relation with the historic industrial discharges (Table 1).

		Depth of sample (cm)	
		0 to 60	60 to 200
Contaminants	Cd	0,2	0,6
	Cr	10,5	9,7
	Co	1,6	1,3
	Cu	44,1	32,4
	Ni	9,7	8,7
	Zn	100,8	83,9
	Pb	**42,8**	**277**
	As	**3,7**	**16,8**
	PAH	5341	5187

Table 1: Metals and PAH concentrations measured in sediment of Etables dam in 2008 inside two layers: one superficial (0 to 60 cm) and the other more historic (60 to 200 cm). Concentrations are expressed in mg/kg Dry Weight.

In spite of the toxic risk associated with contaminated sediments resuspension, a second draw-off was carried out in June 2009. Nonetheless, to reduce sediment exportation downstream, a cofferdam was placed in front of the valves, maintaining a minimum of 1.70 metre of water behind them. The turbidity and suspended matter fluxes have been examined during the three days of the reservoir draw-off. The maximum value of suspended matter released in the river was 182 mg/l up to three kilometres downstream. The water filling of reservoir was performed five months after the draw-off in November 2009. In order to evaluate the short-

term effects of this draw-off and particularly the ecotoxic effects on aquatic biota, five sites were identified along the watercourse (Fig.1): a site two kilometres upstream Etables reservoir (Ups_ED), the Etables reservoir (ED), a site two kilometres downstream Etables reservoir (Dow_ED) and two last sites at sixteen and eighteen kilometres downstream, Lavancia (LD), a small reservoir and its site downstream (Dow_LD), respectively. Two field campaigns were performed before the draw-off of Etables reservoir in May 2009 and after, four months later and before the reservoir filling in October 2009. During these field campaigns, sediments and biota sampling, as well as habitat quality assessment, were carried out.

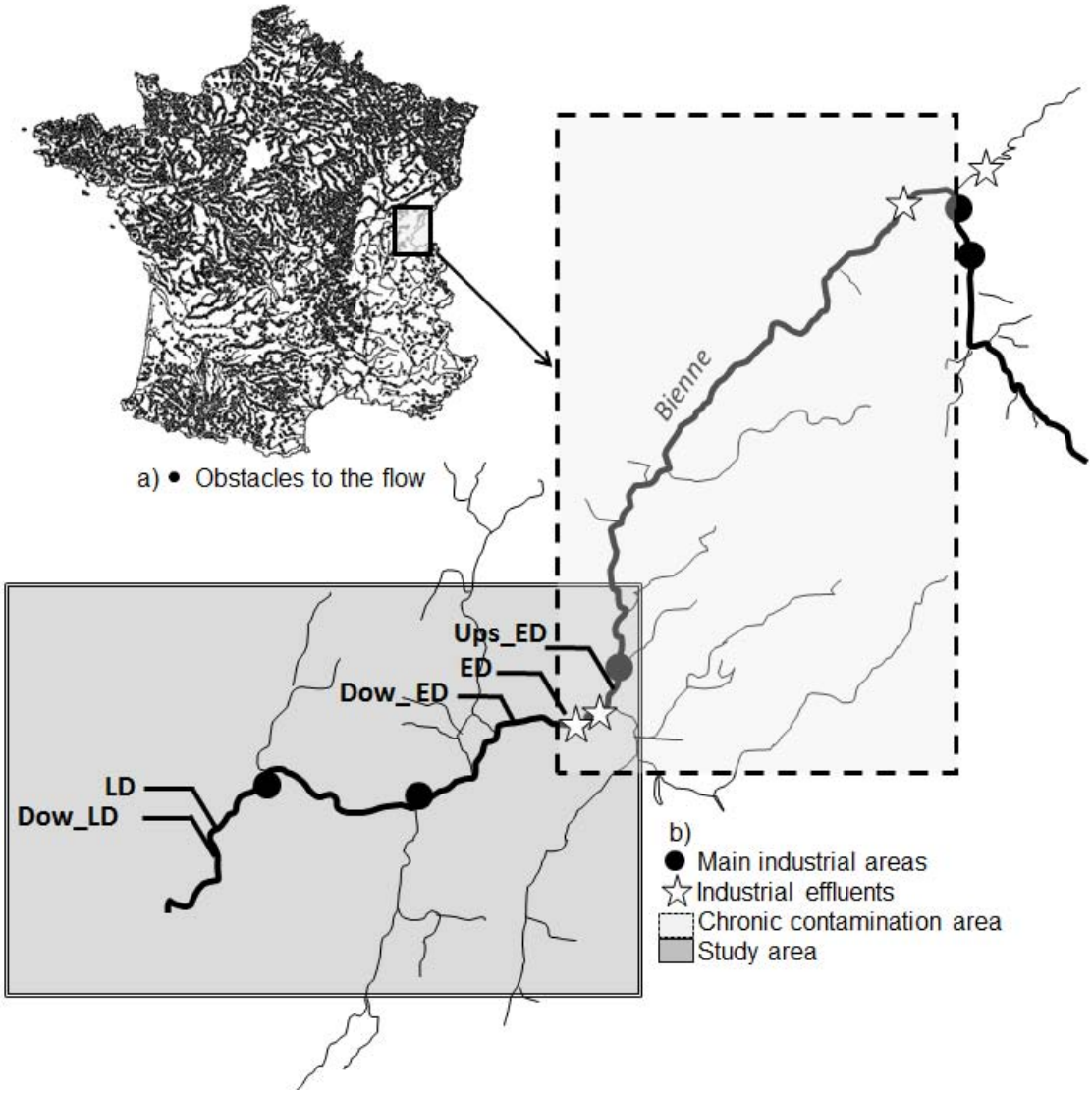


Fig. 1: Mapping the study area: a) Mapping of 60 000 referenced obstacles in France (source ROE - ONEMA). b) Watershed of Bienne and the situation of five stations.

2.2. Environmental assessment of study sites

The physicochemical characteristics of the sediments were assessed in samples realized during the both campaigns (sampling depth of 20 to 30 centimetres) and sent to a specialized laboratory. Environmental parameters such as sediment grain size, total organic carbon and nitrogen concentrations were measured. Concerning the expertise of contamination levels, 11 metals and 10 polycyclic aromatic hydrocarbons were quantified in the sediments. PCBs were below quantification limits (5µg/kg DM). Habitat characteristics (e.g. water depth, channel substrate, channel width, mean monthly flow) and water column quality (e.g. temperature, dissolved oxygen concentration, pH, conductivity) were unchanging between both field. The second field campaign took place before the filing in water of Etables reservoir, thus were not sampled on the Etables reservoir in October.

2.3. Sediment microbial communities

Sediments were sampled after the draw-off on the five sites. For each station, three sediment samples homogenized by sieving (2-mm mesh size) were collected on about 20 centimetres deep with a shovel for sediment on littoral areas. A part of samples was stored at -80°C for DNA extraction and PCR-DGGE analysis and the other part was analysed using the BIOLOG GN2 MicroPlateTM. For each sample, three replicates were analyzed. Sediment DNA extractions were performed using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA) according to the manufacturer’s instructions. Primers 341F-GC and 907R [18] were used for partial PCR amplification of bacterial 16S rRNA genes as described by Muyzer and Smalla (Muyzer and Smalla, 1998). Fungal partial 18S rRNA gene fragments were amplified using a two-step PCR protocol. The first amplification used primers NS1 and EF3. Diluted amplicons (1:500) from first step were used as template for the second amplification with primers NS1 and FR1-GC as described by Oros-Sichler [19]. The amplification products were controlled on 1% (w/v) agarose gel and separated with the DCODE Mutation Detection System (Bio-Rad, Hercules, CA). The vertical electrophoresis was performed with a denaturing gradient from 40 to 60% for bacterial communities and with from 25 to 40% for fungal communities (100% denaturant corresponds to 40% (v/v) formamide and 7 M urea).

DGGE were run for 16 h at 100 V and 60°C (bacteria) and at 180 V and 58°C (fungi). The gels were stained with SYBR Green I and were imaged with a STARION FLA-9000 scanner (Fujifilm Life Sciences FSVT, Courbevoie, France). Secondly, community-level physiological profiles were assessed using the BIOLOG GN2 MicroplateTM (Biolog Inc., Hayward, CA). 5 g of each fresh replicates were homogenized in 45 ml of sterile physiological water and shaken 30 minutes at 150 rpm. After decantation, 150 µl of supernatant for each replicate were inoculated into wells of three plates. Each Microplate™ contains 95 wells of different sole-carbon-sources. Plates were incubated at 25°C in the dark and OD600nm were recorded every 12 h during 60 h using an Expert Microplate Reader (ASYS, Eugendorf, Austria). Data were normalized by the average well colour development (AWCD) [20]. Kinetic of microbial activity was assessed through the Area Under the absorbance versus time Curves (AUC) [21].

2.4. Macroinvertebrates communities

Macroinvertebrates were sampled before (May) and after (October) the draw-off on each site except in October on the Etables reservoir. Two protocols of sampling were carried out. For the run-of-river dams, macroinvertebrates were sampled according to an original protocol [22]. This protocol defines three zones which exhibit various hydraulic and hydro-morphological conditions. For each zone, banks and channel were sampled separately. Habitats on each bank were described prior to sampling macroinvertebrates communities using a Surber net (mesh size 500 µm, sampled area 0.05 m^2). Macroinvertebrates in the channel were sampled by dredging from a boat perpendicular to a transect in each of the three zones defined above. For each transect, the left side, the middle and the right sides of the channel were sampled. Concerning the stations in river, macroinvertebrates were sampled according to RCS protocol (circular WFD 2007/22) conceived to fulfil the requirements of the European Water Framework Directive (WFD). This protocol consists in the sampling on each station of 12 habitats realized in proportion to their relative surfaces on the station. All samples were preserved in 4% formalin in the field and transferred to the laboratory where they were sieved and sorted. Organisms were mainly identified at genus level (using Tachet [23], except for some groups, which were identified at higher taxonomic level (i.e. Diptera (family or tribe level) and Oligochaeta or Nematoda). A trait-based approach was used to

assess functional diversity of macroinvertebrates communities in accordance with statistical protocol described in the following section.

2.5. Statistical analysis

Principal Component analyses (PCA) were carried out to identify the sites distribution according to contamination levels and microbial functional diversity. We used a trait-based approach to identify potential "between-sites" differences in biological and ecological attributes of macroinvertebrates assemblages. Twenty two fuzzy-coded traits [24], each described by a set of categories (=modalities), were examined. Mean weighted (by log-transformed abundances) trait profiles of site assemblages were calculated and expressed as relative abundance distributions of trait categories within the assemblages [25]. "Between-sites" comparisons of each functional category (i.e. Biolog substrate for microbial communities and bioecological traits categories for macroinvertebrates) were performed with one-way ANOVAs after arcsin (√p) transformations for bioecological traits categories (normality and homoscedasticity being respected). Responses of both assemblages were studied using Principal Coordinates analyses (PCoA), performed on Bray-Curtis distances matrices. Usual indices such as faunal richness, abundance or Ephemeroptera-Plecoptera-Trichoptera (EPT) percentage were calculated for macroinvertebrates communities. Comparisons between taxonomic and functional responses of both compartments have been performed using diversity indices (i.e. Rao Functional Diversity index [26], Shannon and Weaver diversity index). Faunal similarities between sites were evaluated thanks to Jaccard's index on macroinvertebrates and microbial communities. The functional similarity performed on the microbial and macroinvertebrates functional profiles were calculated on the basis of significantly different categories. Finally, Mantel tests were performed to compare biological responses (taxonomic and functional for both compartments) with the contamination levels recorded before and after the reservoir draw-off. We used R software (R development Core Team, 2008) and the ADE4 library [27] for all statistical analysis.

3. Results

3.1. Evolution of the sediments contamination

In May, the sites distribution (Fig 2) has elucidated: i) the strong metallic contamination entrapped within the Etables reservoir sediments, (ii) a buffer effect of sediments accumulation within reservoirs, that have stored the contamination, sparing dams downstream, and iii) the upstream origin of contamination. In October, the PCA has showed a homogenization of the disturbance with a reduction of contamination levels for upstream sites and reservoirs (a decrease of about 60% for Etables Dam) and inversely an increase for sites downstream. Table 2 summarized contamination variation associated with the draw-off effect. The decrease of contamination levels (except for Lead, which is more present in profundal sediment layer) recorded within Etables reservoir (ED) sediments was associated with a flush effect that leached fine sediments (clay and silt) and organic compounds. The same variations were recorded for upstream site (Ups_ED) and for Lavancia reservoir (LD), i.e. a general decrease of metallic concentration in sediments. In contrast, the concentrations in Chromium, Nickel, Iron, Lead and PAH in sediments downstream Etables reservoir (Dow_ED) have increased along with the fine sediment deposit and the increase in total organic carbon content. Similarly, contamination levels in Chromium, Copper, Nickel, Iron, Zinc and PAH has increased downstream Lavancia reservoir (Dow_LD). This increase was also associated with fine sediment and organic carbon deposits.

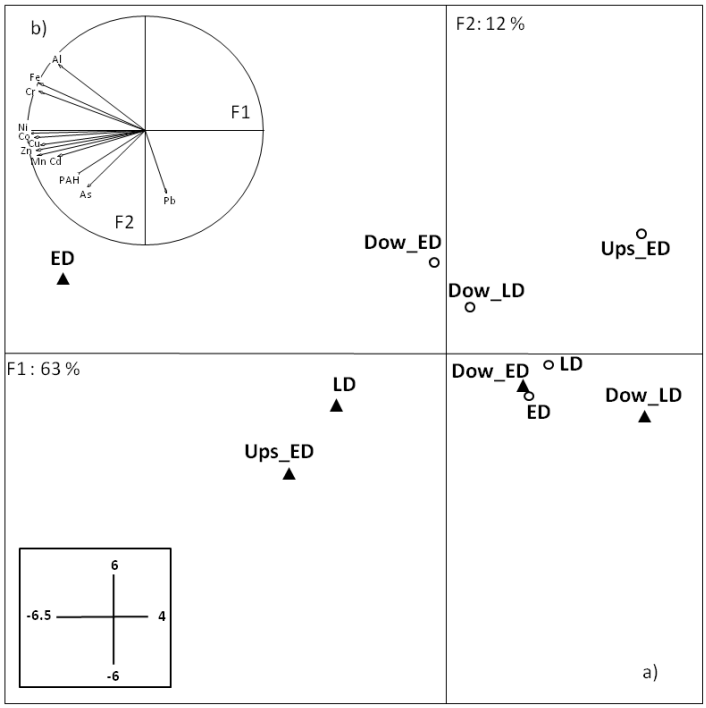


Fig. 2: Results of PCA analyses performed on physic-chemicals analysis of sediments: a) factorial plane of five stations for both seasons and b) correlation circle of detected contaminants. The triangles represent the position of five stations before the draining (May) and the circles represents the position of stations after the draining (October).

		Upstream Etables			Etable Run-of-River Dam			Downstream Etable			Lavancia Run-of-River Dam			Downstream Lavancia		
		MAY	OCTOBER		MAY	OCTOBER		MAY	OCTOBER		MAY	OCTOBER		MAY	OCTOBER	
Sediment characteristics	Cr	13	7.7	↘	32.8	7.7	↘	4.9	14.3	↗	14.9	7.9	↘	6.3	15.4	↗
	Co	2.1	0.9	↘	3.4	1.1	↘	1.4	1.5	≈	2.3	1.1	↘	1.4	1.2	≈
	Cu	23.9	3.7	↘	32.2	20.1	↘	21.6	21.8	≈	24	15.5	↘	5.5	17.4	↗
	Ni	11.3	3.7	↘	16.9	7	↘	4.3	8.1	↗	10.8	5.1	↘	4.9	6.5	↗
	Fe	4.28	3.3	↘	7	2.6	↘	2.2	4.6	↗	3.87	2.8	↘	1.73	3.8	↗
	Mn	149.7	80.5	↘	180.8	88.2	↘	105.1	92.7	↘	133.3	86.1	↘	102.4	91.8	↘
	Zn	65.2	18	↘	78.2	44.7	↘	55.5	47.3	↘	52.4	33.8	↘	22.3	44.4	↗
	Pb	41.2	3.6	↘	23.9	77.1	↗	18.8	23.3	↗	32	16.4	↘	82.9	39.1	↘
	Hap	2952.0	192	↘	1813.0	880.0	↘	427	846	↗	4265	1525	↘	474	2075	↗
	Clay	0.3	0.2	≈	2.2	0.4	↘	0.1	1.6	↗	1.9	0.7	↘	0.4	0.6	≈
	Fine silt	4.4	1.6	↘	19.7	4.4	↘	1.5	16.9	↗	13.9	6.4	↘	5.5	7.5	↗
	Coarse silt	5.2	0.8	↘	19.8	3.2	↘	1.4	10.3	↗	10.5	4.1	↘	7.0	8.2	↗
	Fine sand	24.6	8.4	↘	35.9	12.4	↘	10.0	19.8	↗	33.3	19.7	↘	13.3	18.9	↗
	Coarse sand	65.7	89.0	↗	22.2	79.5	↗	86.8	51.5	↘	40.4	69.0	↗	74.0	64.8	↘
	Texture	Sand	Sand		Sandy loam	Sand		Sand	Loamy sand		Loamy sand	Sand		Sand	Sand	
	TOC	10.1	2.9	↘	26.9	4.9	↘	0.5	12.2	↗	8.6	9.1	≈	6.4	15.9	↗

Table 2: Principal physicochemical parameters that characterize contamination of sediments before and after the reservoir draw-off. Metals and PAHs concentrations are expressed in mg/kg Dry Weight. TOC are expressed in g(C)/kg Dry Weight and grain-size distribution in percentage. Evolution of sediments characteristic is illustrated by arrows upward or downward.

3.2. Microbial community analysis

The first axis of the PCoA separates reservoir sites and “Dow_LD” site from “Ups_ED” and “Dow_ED” sites due to a greater bacterial richness (Fig.3a) and inversely a lower fungal richness on the first sites (Fig.3b). A greater faunal similarity was found between two reservoir sites in particular concerning bacterial assemblages (0.71 of similarity for bacterial communities versus 0.40 for fungal communities). Indeed, reservoir bacterial communities were significantly different of river microbial communities (Monte-Carlo test on PCoA results, $p < 0.001$). However, no significant correlation was found between microbial assemblages and sediments characteristics. The functional diversity discriminated the two downstream sites from the others (Fig.4), with a higher efficiency in substrates degradation. The second axis separates Etables reservoir (ED) of the other sites by a high degradation of the alcohols guild substrates. Great similarities in substrates degradation activities were found: i) for "ED" with its upstream (0.94 of similarity) and Lavancia reservoir (0.91) and ii) between the two downstream sites (0.93). No significant correlation was found between microbial functional diversity and sediments characteristics in October. In contrast, microbial functional diversity was significantly correlated with chronic levels of contamination measured in May (Mantel test, $p < 0.01$).

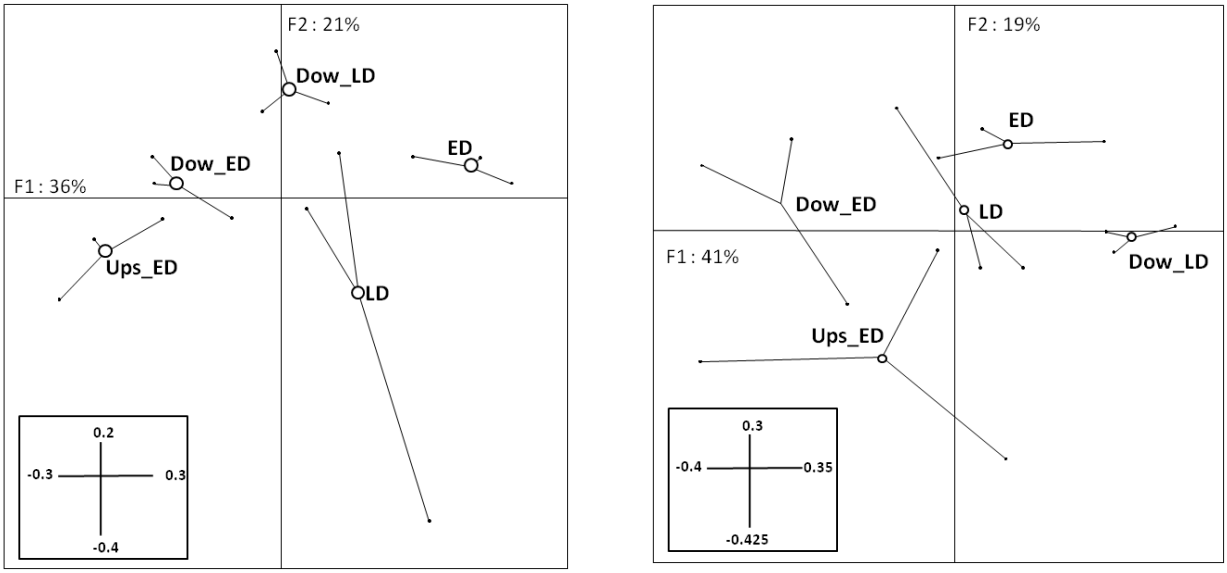


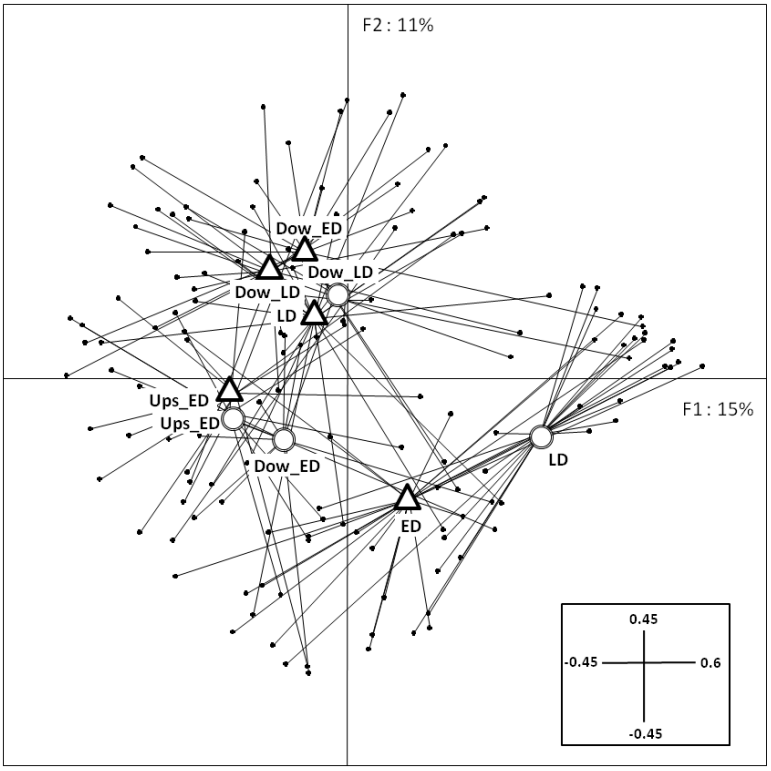
Fig.3: Factorial plane of the Principal Coordinates analysis performed on faunistic results from DGGE method for the microbial compartment of five stations in October, 3a) factorial plane for bacterial communities and 3b) factorial plane for fungal communities.

3.3. Macroinvertebrates communities

Focusing on May samples, the PCoA analysis (Fig.5) discriminates the communities of downstream sites and Lavancia reservoir from communities of Etables reservoir, the upstream site occupying an intermediate position. Macroinvertebrates assemblages of Etables upstream and Lavancia downstream site were relatively unchanged between the two campaigns, while drastic changes were observed for the two sites more impacted by the draw-off, i.e. downstream Etables and Lavancia. These changes results in an increasing similarity with Etables macrobenthic assemblages of May, due to a decreasing in abundances, in EPT percentages and a proliferation of more resistant taxa (Table 3).

	Upstream Etables			Etable Run-of-River Dar		Downstream Etable			Lavancia Run-of-River Dam			Downstream Lavancia		
	MAY	OCTOBER		MAY	OCTOBER	MAY	OCTOBER		MAY	OCTOBER		MAY	OCTOBER	
Abundance	1455	1278	↘	1979		2699	1126	↘	3743	4325	↗	3143	2119	↘
Richness	45	50	↗	41		47	48	≈	58	54	↘	48	46	≈
EPT richness	17	22	↗	12		19	19	≈	24	21	↘	20	18	↘
EPT percent	33.99	19.97	↘	4.78	No data	31.06	21.37	↘	47.12	9.11	↘	26.35	12.55	↘
Diptera percent	37.91	33.35	↘	11.5	Draw-off	31.67	34.49	↗	24.19	38.62	↗	36.3	19.41	↘
GOLD percent	57.15	48.68	↘	70.05		56.37	70.43	↗	43.06	81.13	↗	50.19	34.39	↘
Shanon diversity	3.65	4.37	↗	1.85		3.51	3.74	↗	3.25	3.06	↘	3.58	3.32	↘
Pielou equitability	0.60	0.72	↗	0.30		0.57	0.61	↗	0.53	0.50	≈	0.59	0.54	≈

Table 3: Main indices performed on faunistic data of macroinvertebrates compartment for the five stations before and after the reservoir draw-off. EPT means Ephemeroptera Plecoptera Trichoptera and GOLD Gastropoda Oligochaeta Diptera. Evolution of indices is illustrated by arrows upward or downward.



Fg.5: Factorial plane of the Principal Coordinates analysis performed on faunistic results for the macroinvertebrates compartment of five stations for both seasons. The triangles represent the position of five stations before the draining (May) and the circles represents the position of stations after the draining (October).

The draw-off effect on the functional diversity was investigated through (i) changes in intra-sites bioecological profiles and (ii) similarities with Etables profile (Table 4). Excepted for Lavancia, bioecological profiles remains relatively similar between the two campaigns. This stability fits with the assemblages' response for Ups ED and Dow LD, but not for Dow ED. The bioecological profiles of Lavancia reservoir was more disturbed, with 50 significantly different bioecological categories between the two campaigns. The principal modifications were related to the reproduction, the organic pollution tolerance (saprobic value), the habitat (relation with the substrate, distribution, velocity) and the maximal size. Globally, an increase of functional similarity with Etables was observed for all the sites under the influence of the draw-off, associated with the traits "maximal size" and "reproduction". Specifically, for Etables downstream site (Dow_ED), the functional similarity with Etables profile was also associated with the traits: "resistance forms", "trophic status" and "tolerance to organic pollution". For Lavancia site (LD), the functional similarities have also concerned the "food", "substrate preferences" and "tolerance to organic pollution". Lastly, on Lavancia downstream site (Dow_LD), the profiles of traits "life cycles" and "food" were closer to those of Etables site.

	Evolution before and after Draining					Comparison with Etables profile							
	Number	Ups_ED	Dow_ED	LD	Dow_LD	Ups_ED		Dow_ED		LD		Dow_LD	
Traits						May	October	May	October	May	October	May	October
Maximal Size	7	0	1	3	1	3	4	5	2	5	2	6	2
Life cycle	2	0	0	0	0	0	2	0	0	2	0	2	0
Number of generation per year	3	0	0	2	0	0	0	0	0	2	1	0	0
Aquatic step	4	0	0	2	0	2	3	2	0	2	3	2	0
Reproduction meaning	8	1	2	4	4	4	2	4	1	3	0	5	1
Dispersal forms	4	0	0	2	0	2	3	3	2	3	1	3	2
Resistance forms	5	0	0	1	1	3	2	3	1	3	2	3	3
Respiration	4	0	0	2	0	3	4	3	3	4	4	4	4
Relation with substrates	8	0	1	5	1	1	3	2	3	4	1	2	3
Food	9	0	0	2	0	5	5	5	3	6	3	7	5
Food habits	8	0	0	1	0	2	4	3	4	3	5	4	4
Transversal Distribution	7	0	0	3	0	3	4	3	2	3	2	3	2
Longitudinal Distribution	8	0	0	5	0	3	4	3	3	3	5	3	4
Altitude	3	0	0	2	0	1	2	1	1	0	2	2	1
Biogeographic area	5	0	0	2	0	3	4	4	4	4	4	3	4
Substrat preferendum	9	0	0	3	1	4	5	4	3	5	2	4	3
Velocity	4	0	0	3	0	2	2	2	1	3	2	3	2
Trophic statut	3	0	0	2	0	1	2	2	0	2	3	2	2
Salinity	2	0	0	2	0	0	2	0	2	0	2	0	0
Temperature	3	0	1	0	0	1	2	2	2	3	2	2	3
Saprobic value	5	0	0	4	0	4	4	4	1	4	0	4	4
pH	6	0	0	0	2	0	0	1	0	0	0	0	3
Total of Modalities	117	1	5	50	10	47	63	56	38	64	46	64	52
Jaccard similarity percentage		**99.1**	**97.7**	**56.9**	**91.4**	**59.5**	**45.7**	**51.7**	**67.2**	**44.8**	**60.3**	**44.8**	**55.2**

Table 4: Results of ANOVA performed for the five stations and both seasons in order to compare stations before and after the draw-off and with the Etables dam profiles. The total of modalities represents the number of modalities significantly different between two stations considered.

4. Discussion

4.1. Evidence of contaminated sediment resuspension

The resuspension of contaminated sediment induces multiple disturbances; a physical one through sediment resuspension in water-column and depositions (e.g. clogging, deoxygenating and habitat loss) and a toxic one through remobilization and deposition of contaminated sediment. It is important to define and dissociate the quantitative and qualitative effects of sediments export and resuspension, including the fate of contaminants accumulated within sediments. In our study, the reservoir draw-off has induced a significant export of sediment and of pollutants downstream, despite the presence of cofferdams. The sediment export is evidenced by an increasing sediment particle size in reservoirs and inversely more fine-grained sediment on the downstream sites, leading to clogging, a pattern already evidenced after obstacle removal [28, 29]. The concentrations of pollutants in sediments have evolved concomitantly with the sediment export, by decreasing in the sites under reservoir draw-off influence or increasing on the deposit sites downstream. Associated with these

deposits of contaminated sediments, the increase in total organic carbon and resulting substrate clogging reduces the amount of dissolved oxygen and contributes to anoxic conditions that can promote the release and bioavailability of metals stored in the sediments. The effects of these multiple stressors induced by the reservoir draw-off on aquatic biota (i.e. microbial and macrobenthic compartment) may be additive or be combined to be either larger or smaller than the effects of single-stressor due to synergistic or antagonistic interaction of stressors, respectively [30].

4.2. Multiple stressors effects on aquatic biota

Our results evidenced a weaker richness of fungal communities in reservoirs. Low water velocities and dissolved O2 levels in these systems could reduce the number of Hyphomycetes species [31]. A drastic decline in diversity and sporulation of aquatic Hyphomycetes, accompanied by changes in species dominance (e.g. top conidia producers) has also been reported in habitats polluted by heavy metals [32]. In contrast, the reservoirs have a bacterial richness greater than river stations; we suppose that their environmental conditions promote their diversity. That could be related to a greatest quantity and stability of sediments, leading to a greater availability in ecological niches [33]. Other factors such as the increase in temperature and luminosity, or the modification of oxygen profile can support the bacterial communities of reservoirs [34]. There are little data on those reservoir communities, and particularly for small size reservoirs. Because they are intermediate systems between lakes and rivers, it is possible that these systems present original characteristics and particularly specific associations strongly influenced by the river channel. Because the richness of bacterial communities is more important in reservoirs sediments, we expected a stronger diversity of metabolic activity on these sites. Nonetheless, a lower functional diversity - and a greater functional similarity - were recorded on these sites. This absence of diversity-function relationship could be related to the metallic contamination. Indeed, metabolic activity is correlated with chronic levels of contamination rather than with levels recorded after the reservoir draw-off. Many studies showed an increase in the levels of metals tolerance and a reduction in the metabolic potential associated to the presence of metals [35]. The historic and persistent contamination by metals probably induced a strong selective pressure on the microbial communities whose structure and composition are modified.

However, considering bacterial richness, this selection pressure is compensated by a greater availability in ecological niches for reservoirs [36] while in the meantime it induces a loss of potential functional diversity.

Structural and functional modifications of macroinvertebrates associated with reservoir draw-off were recorded up to nineteen kilometres downstream. For the structural issue, impact of reservoir contamination was significant on reservoir downstream and on the second reservoir and characterized by a decrease of abundances, a loss of sensitive species and a proliferation of tolerant taxa such as Chironomidae and Oligochaeta. Discriminating the relative importance of both types of perturbations in the observed structural changes is difficult; these impairments could elucidate both an impact of the metal contamination exported by the draw-off [37, 38] and/or a habitats deterioration [39]. The bioecological shifts could be helpful in identifying the nature and intensity of both stressors inherent to the reservoir draw-off. Southwood [40] hypothesized that tolerance to harsh conditions is possible through physiological adaptations, efficiency in food harvesting, effort in reproduction, in habitat use and in effective defence against other animals. Our results totally support this hypothesis: the disturbance has selected species on the basis of criterion related to reproduction, tolerance to the organic matter, habitat use and size. The bioecological profiles downstream reservoirs respond to combined effects, but we suspect that physical effects are greater downstream Etables (two kilometres below dams) while toxic effects are greater in the more downstream sectors (up to nineteen kilometres), notably on the second reservoir and its downstream due to dilution of the physical effects along the watercourse. The kinetic model of [41] predicted that dissolved concentrations of metals will be highest at some distance (2.5 – 7km) downstream from a point of dredging. We presume that the effects of contaminants resuspension may also persist longer in the community than physical impacts.

4.3. Relevance of biological tools

The apparent contradiction between microbial taxonomic and functional diversity could be solved through two hypotheses: (i) an increase in functional redundancy and/or (ii) species that exhibit original metabolic abilities within the community are the most sensitive ones, thus are less competitive and less abundant in this contaminated context. Nonetheless, the link between community structure and metabolic potential is made difficult by the used tools.

Indeed, independently of the techniques employed, only a small fraction of the micro-organisms can be studied [42] thus the interpretation and the extrapolation of the results remain limited for the microbial compartment. For instance, Biolog MicroplateTM approach concerns a small proportion of bacteria detached from the sediment matrix and able to degrade the substrates and thus could lack of relevance to explain the overall community functional responses [43]. Similarly, DGGE method reveals a genetic diversity rather than a taxonomic diversity and concern essentially the dominant and potentially tolerant species. These methods, although they are integrative, illustrate only a potential response of the communities. Conversely, tools associated to macroinvertebrates are more representative of community responses *in situ*. Indeed, this study highlights the relevance of the macroinvertebrates' responses to consider sediment resuspension impacts on freshwater ecosystems. This compartment, through the chosen scales (spatial, temporal and taxonomic) and tools used, reflects the intensity of disturbance. Due to the strong sensibility and relevance of traits-based approach we assume that bioecological responses traits should be integrated into ecological risks assessment related to contaminated sediment presence. In addition, these bioecological modifications investigations could be useful to predict ecosystem functioning impairment insofar as response traits could be related to ecosystem functions.

The physical parameters that we measured have failed in explaining the biological responses, contrary to sediment contamination. Nonetheless, we cannot assert the absence of physical effects associated with hydromorphological changes following the reservoir draw-off. During sediment resuspension events, toxicity may result both from aqueous contaminant exposure (contaminants released from particulates) and from contaminants associated with suspended sediments that are ingested by organisms [44]. Assessing the pollutants bioavailability stored in resuspended sediments may be crucial to understand contaminants fate during a reservoir draw-off and potential risks of toxicity for aquatic biota downstream, but it is difficult given their complex and often dynamic interactions with organic and inorganic compounds.

4.4. Implications

Evaluate the resilience abilities of communities as well as identify the ecotoxic risks associated with the resuspension of contaminated sediment are essential before planning restoration programs such as the dam removal. The impact of a dam removal could be higher than the resistance capacity of the communities to new disturbance and/or the expected recovery reduced due to low resilience abilities. For instance, the absence of microbial communities response to modification of contamination profile may be explained by i) high resistance abilities to a new disturbance ("stability" of communities), but also ii) low resilience abilities. A selection of tolerant species to contamination could eliminate or prevent the re-colonization of the sensitive species after removal of the disturbance [45]. A loss of this tolerance would be a relevant indicator of recovery after dam and contaminants removal. Negative impacts of dam removal are supposed to occur at short term, associated with increase in suspended sediments [15], while the beneficial changes should act in the longer term, thanks to the recovery of a hydromorphological natural status of the stream. Nonetheless the recovery of the biota is more uncertain. With ecotoxic risks, it is probable that such restoration led to physically restore the stream but, chemically impair it, owing to contaminated sediment export, thus the physical restoration cannot substitute for chemical restoration. This sediment contamination would potentially limit the communities' resilience due to seasonal and episodic variations in metal concentrations which can prevent the re-colonization by the sensitive species [46]. This contamination could also induce different recovery trajectories for each levels of observation chosen. For instance, at the patches scale, communities of the water column could recover more quickly than communities closely related to the sediment. In contrast, at the river scale, recovery trajectories could be related to the proximity of dam and to the hydromorphological characteristics: the lentic area should be more disturbed and thus recover more slowly. We should be aware that dam removal is a disturbance whose magnitude will depend on the amount of accumulated sediment and stored contaminants but also of the quality of upstream (for the re-colonization) and downstream (for the resistance) ecosystems. Finally, we assume that it is critical in future studies for learning about the mechanisms driving communities' responses and guiding future dam removal projects in the case of sediment contamination retention in reservoirs.

5. Conclusion

Connectivity is an important component of rivers functioning, including flow maintenance, water quality, temperature and sediment transport. Because dam' presence interrupts ecological continuity and compromises the well-being of freshwater ecosystems, dam removal could contribute to restore aquatic ecosystems. However, dam removal can potentially affect river ecosystems through sediments resuspension and co-occurring events (contaminants remobilisations, habitat clogging, deoxygenating...). To predict effective river restoration, it's important to diagnose the primary constraint to ecological recovery, and then to identify a hierarchy of stressors in order to target management activities most effectively. The success of this restoration will depend on the resistance and resilience capacities of communities. For instance, in this study, this resilience has been reduced by the multiple and long-term perturbations, thus communities may no longer respond to changes of environmental conditions or to the disturbances removal. So, to determine the relative strengths of different factors affecting recovery after restoration, we should elaborate long-term and multicompartment pre and post-removal risks assessment that should include the responses of communities to the multiple stressors and identify the potential of species for re-colonization.

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Article 4: **Populations niche shift and niche narrowing under chemical and physical pressures: a new frontier for the ecotoxicological risk assessment**

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Abstract

This study aims: (1) to evaluate whether differences in realized niches of macroinvertebrates species along a gradient of disturbances is the result of abiotic (sediment contamination and dam presence) or/and biotic constraints (competition) and (2) to examine the relevance of the measurement of niche discrepancy (fundamental *vs.* realized niche) as an indicator of population vulnerability for *in-situ* risk assessment. First, the measure of taxa abundance evolution along the disturbance gradient has elucidated three groups of taxa: sensitive (i.e. abundance decreases significantly along the disturbance gradient), indifferent (i.e. steady abundance) and beneficiary taxa (i.e. abundance increases significantly along the disturbance gradient). The second step aimed to elucidate the observed taxa distribution by the interaction with their environment (abiotic and biotic). For sensitive taxa, competition, metal contamination and spatial niche breadth were the best predictors of taxa distribution. Metal contamination in sediments led not only to species spatial niche breadth decrease but also to an increasing competition insofar as communities were aggregated in the same habitats. Thirdly, realized niche shifts of sensitive species were described using habitat occupancy, trophic niche and body-size distribution. Sensitive species tends to avoid sediment habitats and to be aggregated in erosion habitat. Increase in PAH contamination led to *Gammarus pulex* trophic niche breadth decrease and to leaf detritus diet specialization. In addition, sediment contamination (PAHs and Metals) conduced to small body-size organisms'

selection. Lastly, disturbance gradient was clearly identified by comparison between fundamental and realized spatial niche. Indeed, discrepancy between both niches of sensitive species increased significantly along disturbance gradient. Joint study of species' realized niche and abiotic and biotic context assessment enables not only to identify population vulnerability but also to predict communities and ecosystem vulnerability due to biotic interaction changes and potential cascading impacts on ecosystem processes. Thus, field ecotoxicological risk assessment in multiple stressors context should be reinforced by exploring and integrating indicator species' niche response, a new promising approach.

Keyword: risk assessment; realized niche; fundamental niche; sediment contamination; dam presence.

1. Introduction

Risk assessment associated with pollutants accumulation in aquatic ecosystems is currently performed on the basis of laboratory toxicity tests. Nonetheless, extrapolation from these tests to natural population and communities remains a key challenge, and still rely on large uncertainties (Forbes et al., 2001; Calow and Forbes, 2003; Leung et al., 2005; Rubach et al., 2011) because (i) multi-stressor condition (chemicals mixtures and others disturbances) are rarely considered, (ii) standard ecotoxicity tests use laboratory-culturable species which are not always ecologically relevant and (iii) these tests are usually conducted under one set of fixed conditions and consequently do not consider the effects of environmental parameters undergone on the field.

To realistically evaluate population vulnerability, we must take into account their exposure and their sensitivity to disturbance as well as their abilities to sustain in the considered environments. These components of population vulnerability are directly related to the species' reproductive strategy, feeding behavior or relation to substrata (Van Straalen, 1994; Stark et al., 2004; Hommen et al., 2010). In this preliminary study, we chose to explore the realization of three traits (body size, habitat's occupancy and food diet). Body size is the most important trait of a species (Brown et al., 1993; McGill et al., 2006) due to a strong influence on competitive dominance, on predator-prey interactions (Yodzis and Innes, 1992) and on

physiological rates (Calder, 1984). In addition body size and related surface-area-to-volume relationships can be determinant for pollutants bioconcentration in organisms (Dolédec and Statzner, 2008; Preuss et al., 2008). In the other way, food and habitat preference are the two key factors determining exposure, either through food or the ambient matrix (Kearney et al., 2010; Rubach et al., 2011) but also to evaluate potential accumulation in the food chain.

Trait-based approaches are widely used in ecology to link trait composition and environmental drivers: trait composition becomes a metric of community health in a biomonitoring context allowing predicting disturbances of ecosystem functioning (Heino, 2005; Townsend et al., 2008; Culp et al., 2010; Poff et al., 2010). In contrast to taxon-based analyses, where differences and similarities in species occurrence are analyzed, a trait-based approach presumes some direct or mechanistic linkage between environmental drivers and biological responses that facilitates causal inference (Poff, 1997; Statzner and Bêche, 2010; Webb et al., 2010). The trait-based approach is intimately associated with "the niche concept". The term “niche” covers two distinct components: (i) the environmental requirements needed for a species to subsist without immigration (Grinnell, 1917), and (ii) its relationships to other species (Elton, 1927). A species can be defined by its fundamental niche (i.e. the subset of n-dimensional environmental space of all possible conditions in which a species can maintain itself in the absence of competition) and its realized niche, the portion of the fundamental niche in which a species is present, given biotic constraints that displace species niche optimum (Ellers et al., 2010). The distinction between realized and fundamental niches is important for studying niche dynamics (Pearman et al., 2008), particularly to provide a direct link between organism performance, abiotic environmental conditions and interspecific interactions (Ellers et al., 2010). However, to date, this mechanistic approach is scarcely included in ecotoxicological risk assessment.

Efficiency of this trait-based approach at a population level will be tested in a multi-stress context of sediment contamination within run-of-river dams. Indeed, due to their high pollutants adsorption capacity, sediments represent a serious threat for ecological integrity of many aquatic ecosystems, exerting a persistent pressure implying chronic and sublethal responses of macroinvertebrates communities. These chemical pollutions are often associated to non-chemical stressors (Chapman, 2007) such as presence of dams, which reduce downstream sediment transport and then led to their accumulation in reservoirs. To date, sediments contamination and dams’ presence have never been considered together despite their potential cumulative impacts on aquatic biota. The difficulties to distinguish individual

effects of each disturbance in a multi-stressor context can explain this lack of consideration, insofar effects can be independent (additive) but also more (synergistic) or less (antagonistic) important than the theoretically expected effect by simple addition of independent effects (Folt et al., 1999; Vinebrooke et al., 2004; Teplitsky et al., 2005). A detailed study of species traits might be helpful to understand and predict the potential adverse effects of chemicals on a wide range of species (Rubach et al., 2011) and to better understand mechanisms and effects of multiple stressors on organisms.

Indeed, we hypothesized that, differences can be observed between the realized niches of macroinvertebrates species, traducing the gradient of physical or chemical disturbances. Thus, we evaluate whether differences in realized niches of each species results of natural heterogeneity or of abiotic (sediment contamination and dam presence) and/or biotic constraints (competition) and we examine the discrepancy between fundamental and realized niche as an indicator of population vulnerability to integrate in *in-situ* risk assessment associated with the presence of contaminated sediment.

2. Materials and Methods

2.1. Step one: lethal effects - Species abundances along the disturbance gradients

The main objective of this first step was to measure the response of taxa abundance along an *in situ* disturbance gradient, defined by sediments contamination and physical disturbances (i.e. dam presence). Fourteen sites were selected with similar habitat characteristics for reservoirs and rivers sites.

Sediments (banks) and macroinvertebrates samples (banks & channel) were collected during one spring campaign, in four reservoirs and ten rivers stations. Concentrations of eleven metals, eight PCBs and ten polycyclic aromatic hydrocarbons (PAH) were investigated in sediments (sampling depth: 20-30 cm) by a specialized laboratory (LDA26, Valence, France, see Table 1). PCBs concentrations were always below their quantification limit (5µg/kg DM). The 14 sampled sites were classified along the sediments contamination gradient on the basis

of the mean rank of a site among all sites for (i) all metals and (ii) all PAHs. This synthetic variable is thereafter called contamination level.

		Reservoir (n=4)			River (n=10)		
		Minimum	Mean	Maximum	Minimum	Mean	Maximum
Water Chemistry (mg.L^{-1})	T°	8.00	11.15	13.10	8.40	10.00	12.30
	pH	8.10	8.23	8.50	8.10	8.25	8.50
	Dissolved oxygen	8.60	11.00	12.50	8.30	9.66	11.30
	Conductivity (µS.cm-1)	305.00	369.00	416.00	317.00	381.30	485.00
	Calcium	64.00	71.00	82.00	65.00	72.00	82.00
	Magnesium	2.90	4.70	7.20	3.30	4.92	7.52
	Dissolved Organic Carbon	1.40	1.73	1.90	1.40	1.75	2.00
	Biological Oxygen Demand	0.50	1.00	1.50	0.50	0.81	1.50
Metal contamination in sediments (mg kgDW^{-1})	Aluminium (Al) (g kg DW^{-1})	2.08	6.93	19.70	0.71	3.87	15.20
	Cadmium (Cd)	0.10	0.15	0.30	0.10	0.14	0.30
	Chromium (Cr)	12.80	33.88	83.50	4.90	19.55	65.00
	Cobalt (Co)	2.30	4.10	9.00	1.40	33.09	307.00
	Copper (Cu)	4.10	25.10	45.30	1.70	9.91	23.90
	Iron (Fe) (g kg DW^{-1})	3.9x10^3	7.9x10^3	15.0x10^3	1.7x10^3	5.6x10^3	8.9x10^3
	Nickel (Ni)	6.50	17.67	54.70	3.10	12.67	35.60
	Lead (Pb)	9.10	19.46	32.00	4.70	20.48	82.90
	Zinc (Zn)	26.90	73.53	108.00	13.90	35.24	65.20
	Arsenic (As)	1.00	4.82	10.60	0.10	5.64	11.40
PAH Contamination in sediments (µg kgDW^{-1})	Anthracene (Anth)	10.00	13.50	31.00	10.00	19.70	80.00
	Benzo(a)pyrene (BaP)	20.00	159.00	535.00	5.00	97.10	393.00
	Benzo(a)anthracene (BaA)	15.00	163.50	649.00	5.00	74.60	379.00
	Benzo(k)fluoranthene (BkF)	11.00	65.00	206.00	5.00	48.50	201.00
	Benzo(ghi)perylene (BgP)	5.00	49.17	133.00	5.00	67.10	220.00
	Chrysene (Chry)	25.00	124.84	483.00	25.00	78.40	328.00
	Fluoranthene (Fluo)	46.00	463.33	1919.00	20.00	220.70	846.00
	Indeno(1,2,3-cd) pyrene (Ind)	15.00	100.83	395.00	5.00	52.40	187.00
	Phenanthrene	25.00	50.83	180.00	25.00	85.40	318.00

Table 1: Principal physicochemical parameters characterizing sediments contamination gradient in metals and PAHs for reservoirs and river stations.

Macroinvertebrates were sampled following two protocols. In reservoirs, macroinvertebrates were sampled using an original protocol (Colas et al., 2011). Banks of reservoirs were sampled according three zones, termed “tail”, “middle” and “dam” reflecting their various hydraulic and hydro-morphological conditions. In river sites, macroinvertebrates were sampled according to a normalized protocol (Multi-Habitat Sampling, norm XP T 90-333 in AFNOR, 2009). A total of 12 samples were realized in rivers and 18 in reservoirs stations, and pooled according to four categories of habitat type: litter, vegetation (Bryophytes, macrophytes, algae and roots), erosion (i.e. superior to 2000 µm e.g. boulders, cobbles) and sedimentation habitats (i.e. inferior to 2000 µm e.g. mud, silt, sand). All samples were

preserved in 4% formalin in the field and transferred to the laboratory where they were sieved and sorted. Organisms were mainly identified at specific or genus level (using Nagel, 1989 and Tachet et al., 2000), except for some groups, which were identified at higher taxonomic level (i.e. Diptera: family or tribe level, Oligochaeta: Class, Nematoda: Order).

The 22 taxa present on at least 12 stations were selected. Spearman rank correlation of abundance with contamination levels were used to depict the various effects of pollutants on each taxon. Wilcoxon-Mann-Whithney tests were used to detect effects of dams' presence on abundance of each taxon. Next, groups of taxa were identified according to the relationship between their abundances and the contamination levels (Table 2).

	Taxon	Metals	PAHs	Stream / Reservoir	
Sensitive taxa	*Psychomia*	-0,61*	ns	ns	Lethal effect
	Leuctra	-0,59*	ns	ns	
	Clinocerinae	-0,57*	ns	ns	
	Esolus	-0,57*	ns	ns	
	Elmis	-0,56*	ns	ns	
	Limnius	-0,55*	ns	ns	
	Sericostoma	-0,54*	ns	ns	
	Ephemerella	-0,53*	ns	ns	
	Orthocladiinae	-0,5*	ns	847 / 311*	
	Tanytarsinii	-0,46*	ns	ns	
	Gammarus	ns	-0,65*	ns	
Steady taxa	*Antomyidae*	no effect on abundances			Potential sublethal effect
	Atherix				
	Hemerodrominae				
	Baetis				
	Limoniidae				
	Ephemera				
	Ancylus				
Beneficiary	*Chironomini*	0,7*	ns	204 / 1347*	Positive effect
	Ceratopogonidae	ns	0,5*	ns	
	Oligochetea	ns	ns	470 / 2852*	
	Tanypodinae	ns	ns	47 / 300*	

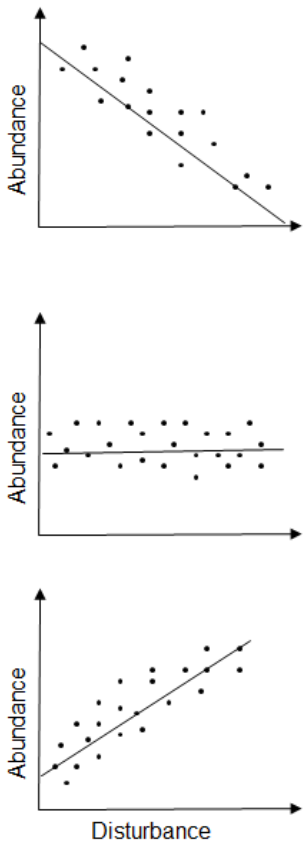


Table 2: Relationships between abundances of 22 taxa and chemical (metal or PAH) or physical (dam presence) disturbance. Chemical gradients were studied using Spearman rank correlation. For the physical disturbance, mean abundances in streams and reservoirs stations were reported when a significant difference was evidenced. (ns: not significant)

2.2. Step two: Sublethal effects - Investigation of community organisation

Impacts of environmental perturbation on spatial pattern of macroinvertebrates communities were studied through the C-score, a statistic proposed by (Stone and Roberts, 1990). It describes co-occurrence patterns among samples. (Gotelli and Entsminger, 2001). The C-score cannot be compared directly among groups. A standardized value, the SES (Standardized Effect Size, (Gurevitch et al., 1992), that allows a comparison of co-occurrence patterns, is calculated. The SES is assumed to be normally distributed. Therefore, a SES below -1.96 is typical of an aggregated community organization (i.e. high co-occurrence), while a value above 1.96 reveals a segregated organization (i.e. low co-occurrence). SES values between -1.96 and 1.96 are characteristic of a random distribution of species. Relationships between competition (SES) and disturbances levels were explored by Spearman rank correlation and Wilcoxon-Mann-Whithney tests.

2.3. Step three: Sublethal effects - Patterns and drivers of realized niches shifts

The third step aims to describe changes in the realization of ecological niches according to the spatial, trophic and body size dimensions. We first select the species with high variations of distribution among the four substrate categories on the 14 studied stations, basing on the chi-square distance. General patterns are first explored for spatial niche breadth. The realized spatial niche is determined for each taxon by measuring their abundance in the four habitat types (litter, vegetation, erosion and sedimentation) in each station. This matrix enables to calculate p_k, the proportion of the habitat k used by the species *i* in each station and thus, allows to compute the Levins index (B) of niche breadth (Levins, 1968) as follows (n=4, the total number of habitat type):

$$B_i = 1 \Big/ \sum_{k=1}^{n} p_k^2$$

The amphipod *Gammarus pulex* and the Ephemeroptera *Ephemerella ignita*, belonging to the sensitive taxa group and occurring on the 14 sites with high abundances, were selected to

describe body size niche shifts. Thus, their body size distributions were examined in five stations selected on the disturbance gradient. The measured individuals came from samples realized during the field campaign in the same microhabitat. The number of measured organisms was determined according to their total abundance recorded in the station (at least 15% of the abundance). Each organism was measured to the nearest 0.1mm from the tip of the rostrum to the base of the telson for *G. pulex* and from the end of the last abdominal sternum to the base of antenna for *E. ignita*, using a stereo microscope equipped with a lens and measured directly using software image analysis.

Finally, *G. pulex* was specifically chosen to study the trophic niche according to a technique of gut content analysis previously described (Shapas and Hilsenhoff, 1976; Dangles, 2002; Felten et al., 2008b). Six stations along the disturbance gradient were selected for the analysis. For each station, ten individuals of the same size class (10.71 mm ± 1.05 mm) and sampled in the same microhabitat were analyzed. Foregut contents were placed into a drop of water on a microscope slide. Particular attention was paid to homogenize the gut content and to slightly press the slide permitting to avoid bias due to thickness of items. Ten fields were chosen randomly at 100× magnification, and then viewed at different magnifications from 100× to 400×. Five food items were identified: (i) animal matter, (ii) leaf detritus-woody debris, (iii) microorganisms (fungi - diatoms), (iv) filamentous algae and (v) particles derived from bryophytes.

The relationships between realized niche breadth and disturbances levels were explored by Spearman rank correlation and Wilcoxon-Mann-Whithney tests.

2.4. Step four: Realized niches *vs.* fundamental niches

The last step was to measure the discrepancy between the realized and the fundamental spatial niche of each taxon and to identify whether the discrepancy between the two niches can be explained by the perturbation levels. The fundamental spatial niche is extract of the "substrate preferences" fuzzy-coded trait (Chevenet et al., 1994; Usseglio-Polatera et al., 2000) that describes the habitat use of each taxon according to the information coming from the literature. Thus, this niche corresponds to all possible strategies of habitat use expressed by each taxon in varied environmental conditions. The discrepancy between realized and

fundamental distributions was assessed using chi-squared distance for each taxon. Relationships between chi square values with the disturbance levels were explored for each taxon by Spearman rank correlation and Wilcoxon-Mann-Whitney tests.

3. Results

3.1. Lethal responses: Identification of indicator taxa

The study of the taxa' distributions along disturbance gradient elucidated three groups of taxa (Table 2). The first group is composed of 11 sensitive taxa whose abundance decreased significantly along the disturbance gradient. These decreases were mostly related to metallic contamination, except *G. pulex* whose abundances were negatively impacted by PAHs levels and Orthocladiinae that were also negatively impacted by the dam's presence. The second group consists of 7 taxa "indifferent" to disturbance gradient to the extent that their abundance was stable along the gradient selected. The last group consists of 4 beneficiary taxa that are influenced by the physical perturbation rather than the chemical one.

3.2. Sublethal responses: community and population levels

3.2.1. Community spatial organization

A first evaluation of the variation of the spatial organisation of the communities was made through the SES value associated to the C-score. The calculated C-score revealed a general pattern of aggregated communities. The SES values decrease when the contamination increase ($r_{spearman}$ = -0.64, p=0.014), but are not correlated to PAHs levels ($r_{spearman}$ = -0.08, p=0.79). Finally, more aggregated communities were found in reservoirs (W=4, p=0.012).

3.2.2. Population spatial niche breadth

The chi-square tests revealed significant variations of frequency distributions among the four substrates for 13 of the 14 studied sites. However, these differences were, in most cases, linked to one or two high differences between the observed and theoretical frequency distributions. We choose to focus on the 11 taxa that exhibited the highest variations (Table 3).

Taxon	(a) Niche breadth			(b) Niches discrepancy		
	Metals	PAHs	Stream / Reservoir	Metals	PAHs	Stream / Reservoir
Leuctra	**-0,69***	ns	ns	**0.71****	ns	ns
Esolus	ns	ns	ns	ns	ns	ns
Elmis	ns	ns	ns	**-0.65***	ns	ns
Sericostoma	**-0.66***	ns	ns	**0.58***	ns	ns
Ephemerella	ns	**0,77***	ns	ns	ns	ns
Orthocladiinae	**0,74***	ns	**1,95 / 2,76***	ns	ns	**207.52/14.92***
Tanytarsinii	ns	ns	ns	ns	ns	ns
Gammarus	ns	ns	ns	ns	ns	ns
Chironomini	ns	ns	ns	**0.77****	ns	ns
Oligochetea	ns	ns	ns	ns	ns	ns
Tanypodinae	**-0,5***	ns	ns	ns	**0.65***	**34.41/92.44**

Table 3: Relationships between niche breadth (a) and overlap with the fundamental niche (b) of 11 taxa and chemical (metal or PAH) or physical (dam presence) disturbance. Chemical gradients were studied using Spearman rank correlation. For the physical disturbance, mean niche breadth and niche overlap in streams and reservoirs stations were reported when a significant difference was evidenced. (ns: not significant)

We then search for correlation of the observed spatial niche breadth with our environmental descriptors (perturbation levels, cf. 2.1). For metals, we observed a narrowing of niche breadth for *Leuctra major*, *Sericostoma personatum* and Tanypodinae while a widening was observed for Orthocladiinae. The latter was also favored by the dam' presence, with higher niche breadth in reservoir than in streams. For PAHs, a positive relationship between niche breadth and contaminant levels was observed for *Ephemerella ignita* (Table 3a). Those various patterns of niche breadth along the metallic and PAHs gradients are illustrated by the fig. 1. We observed a specialization of *L. major* on erosion habitats (e.g. boulders, gravels, cobbles) on the most contaminated stations, while Orthocladiinae, mostly present on vegetal habitats on the least perturbed site move towards all habitats in contaminated sites. *E. ignita*, which is mostly present on vegetal when PAHs levels were low, increase its niche breadth and move to litter and erosion habitats, but always avoid sedimentary habitats.

3.2.3. Realized niches' shifts of two sensitive taxa

The effect of the metallic sediment contamination on *E. ignita* abundances was not linked to a narrowing of its spatial niche breadth. The effects on body size distribution of *E. ignita* were more pronounced (Fig. 2a). The dams effect ($p<<0.001$) have induced the selection of

organisms larger than the organisms in rivers stations, while the metallic contamination has selected organisms smaller on contaminated river stations (p<<0.001). Concerning *G. pulex* body size distribution (Fig.2b), organisms were significantly smaller (p<0.001) with the increase in PAH contamination.

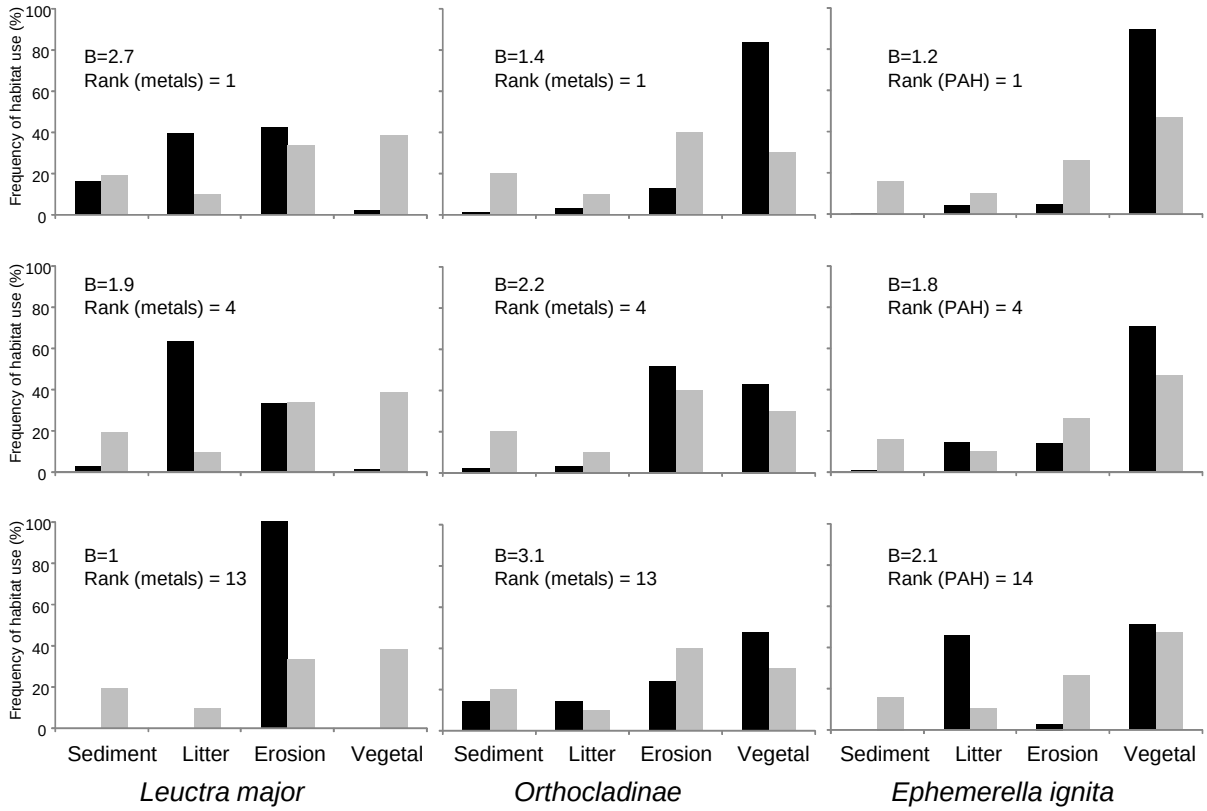


Fig. 1: Variations of realized spatial niches for (a) *L. major*, (b) Orthocladiinae and (c) *E. ignita*, and comparison with theirs fundamental spatial niche. B is the Levin's spatial niche breadth index calculated on the sites presented. Realized niche is in black, fundamental niche is in grey. Ranks correspond to mean rank of a site among all sites according to metals or PAHs concentrations in sediments.

The trophic niche breadth of *G. pulex* decreased (Fig.3) on the multiple disturbance gradient (dam presence and sediment contamination) leading to a specialization of diet on the most contaminated stations. Trophic shifts on the disturbance gradient have consisted to the decrease in Bryophytes item' feeding (p = 0.001) and microorganisms' item (p << 0.001) but conversely the increasing of leaf detritus feeding (p << 0.001) (Table 4, Fig. 4).

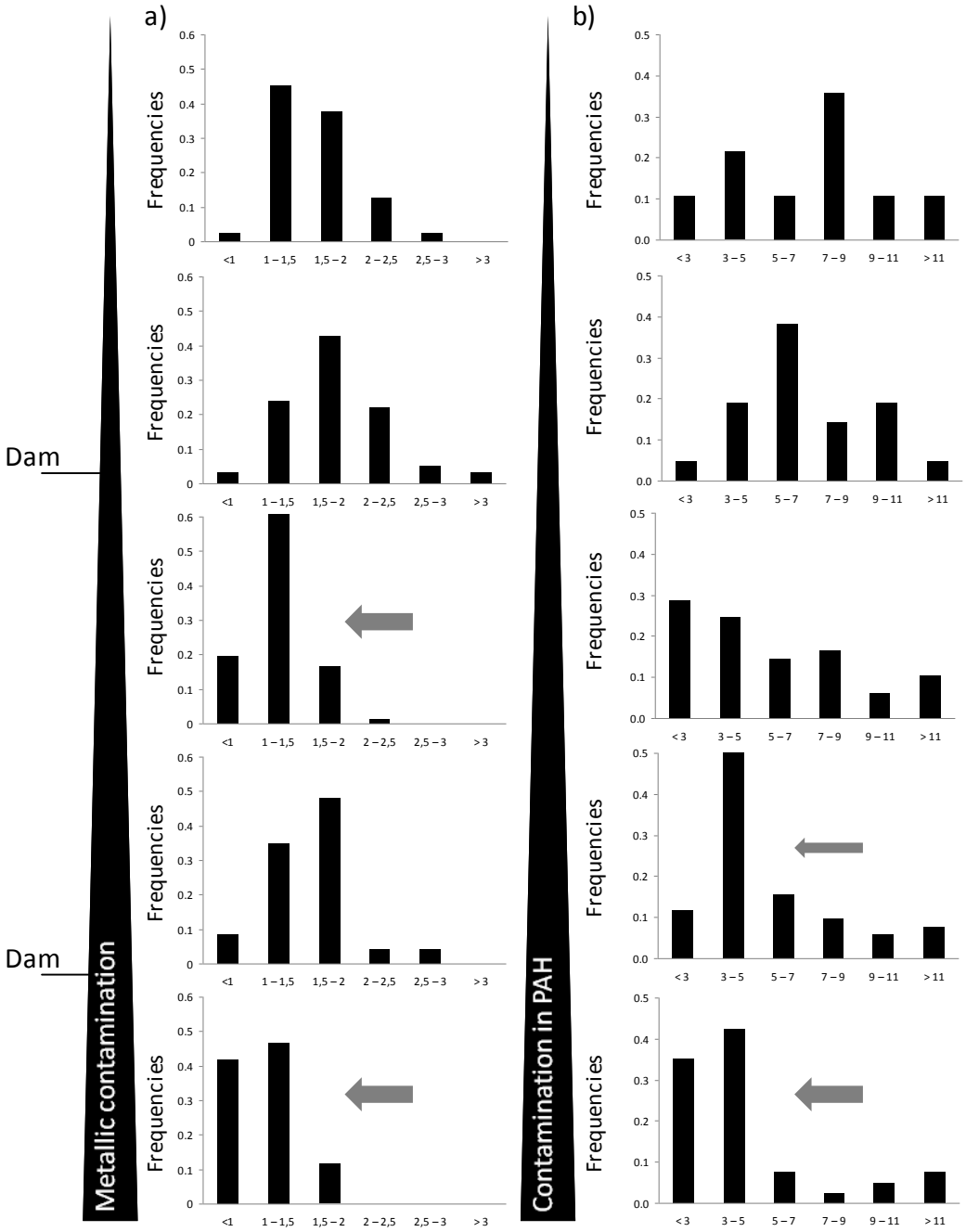
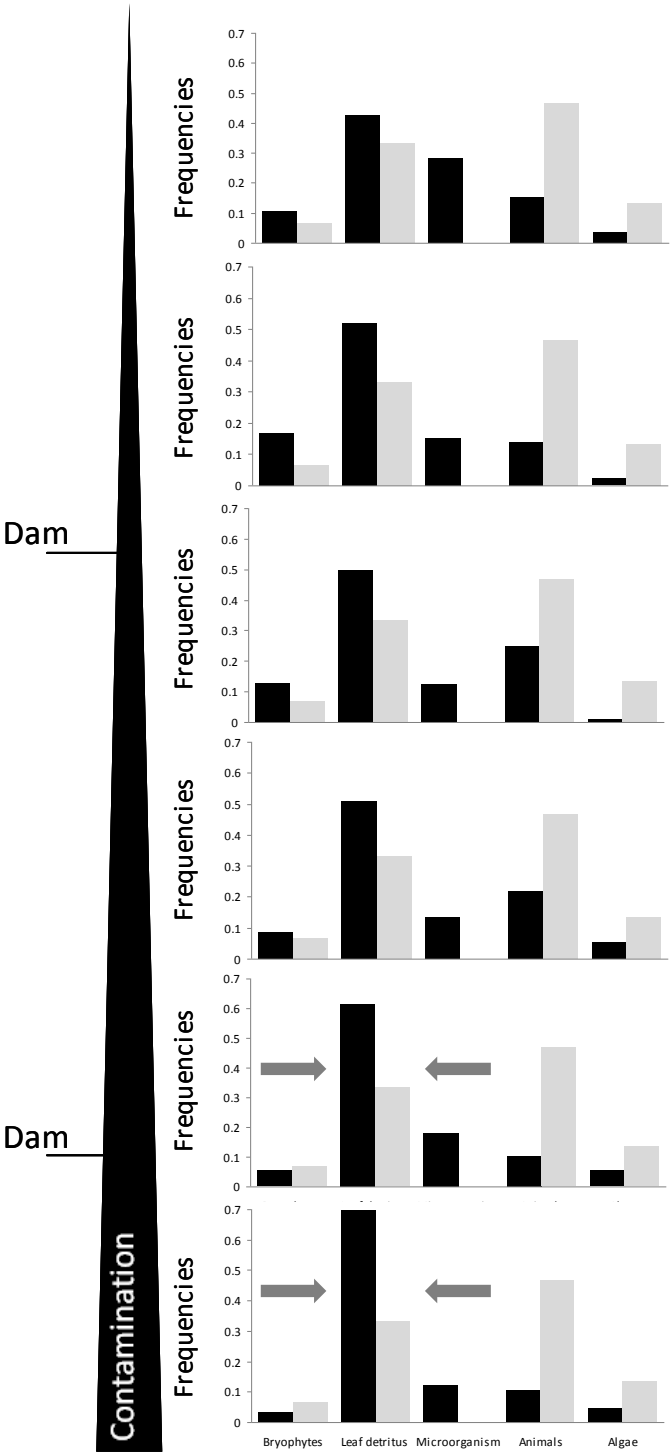


Fig. 2: Realized niche evolution along the disturbance gradient for body-size distribution of *E. ignita* (a) and *G. pulex* (b).

3.2.4. Realized niche vs. fundamental niche

For the 11 selected, among all sites, significant differences between fundamental and realized niche were found for 79% of comparisons done. This discrepancy between both niches increases significantly along metal contamination gradient for *Leuctra major*, *Sericostoma personatum* and *Chironominii sp.* The discrepancy between both niches of Tanypodinae

increases along PAH contamination gradient and in reservoirs. Conversely, the discrepancy between both niches decreases for *Elmis sp.* along metal contamination gradient and for Orthocladiinae in reservoirs (Table 3b).



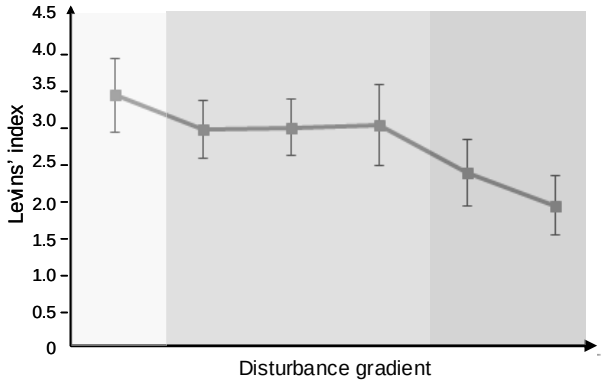


Fig. 3: *G. pulex'* trophic niche breadth along the disturbance gradient. Grey levels represents the three groups coming from a cluster analysis (complete linkage) performed on Levins' index.

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Fig. 4: *G. pulex'* realized diet niche along a PAH and dam perturbation gradient.

Realized niches Gradient	Disturbance gradient		Diet items				
	Physic	Toxic	Bryophytes	Leaf detritus	Microorganism	Animals	Algae
	Ups	1	0.104	0.427	0.280	0.152	0.037
	Dam	3	0.168	0.520	0.151	0.139	0.022
	Dow	2	0.125	0.497	0.123	0.246	0.008
	Ups	5	0.086	0.509	0.133	0.217	0.055
	Dam	6	0.054	0.612	0.179	0.103	0.052
	Dow	4	0.033	0.698	0.119	0.103	0.046
Fundamental			0.067	0.333	0.000	0.467	0.133

Table 4: Frequencies of diet items identified in *G. pulex* gut content along the disturbance gradient and according the fundamental niche coming from scientific literature. Ups and Dow corresponds to river upstream and downstream sites of associated dams, along a watercourse. Toxic gradient corresponds to mean rank of a site among all sites according to metals and PAHs concentrations in sediments.

4. Discussion

4.1. Direct effects of disturbance gradient: lethal response

The observed distributions of taxa along the disturbances gradient are consistent with several studies that reported a metal-sensitivity for Ephemerellidae (Pond et al., 2008), and Leuctridae (Beasley and Kneale, 2003) and conversely a metal-tolerance for Chironomidae (Winner et al., 1980; Gower et al., 1994; Gray, 1998; Groenendijk et al., 2002). These results also confirm a previous study that had identified, among the indicator species of reservoirs, *Ephemerella* as indicator of metal contamination in sediments (Colas et al., 2012 unpublished data), independently of habitat type (i.e. river and reservoir) while Tanypodinae abundances are related to sediment contamination only in reservoirs, probably because it is more abundant there ("beneficiary taxa" of reservoir presence). Contrary to studies that reported the metals sensitivity of *Gammarus pulex* (Güven et al., 1999; Felten et al., 2008a; Alonso et al., 2010), we did not observed lethal response associated with metal contamination of sediments along the disturbance gradient. However, metal sensitivity of *G. pulex* is mainly based on laboratory-tests with water rather than sediment contamination. We can hypothesize that metals in sediments are not sufficiently bioavailable and that concentrations in organisms are not sufficient to observe a lethal effect. Unlike metals, the population abundance of *G. pulex* has significantly decreased with the increase in PAHs contamination in sediments. Some studies have reported that PAHs are toxic to aquatic organisms (Sepic et al., 2003; Schuler et al., 2006; Sorensen et al., 2007). However, a reduced population-size of a species at a contaminated site, in comparison with a population at a reference site, is not necessarily

indicative of adverse effects of contamination on the population (Preston, 2002). Recent studies suggest that mortality is an inappropriate toxicity response, as alterations of physiological and ecological processes, as well as behavioral changes, can already happen at low concentrations that did not induce mortality (De Lange et al., 2006; Mills et al., 2006; Alonso et al., 2009).

4.2. Realized niche responses to disturbance gradient

Sediment contamination has led the sensitive taxa to modify their habitat and food preferences. Changes in habitat preferences were elucidated by the avoidance of sedimentary habitats and the aggregation in more favorable habitats, probably to reduce exposure to pollutants. Avoidance behavior has been already shown for invertebrates in response to contaminated sediment (De Lange et al., 2006), and this easily detected response of individuals exposed to contaminants could be a useful test to explore more widely (Hellou, 2011). Feeding behavior also determines also external exposure to pollutants. The increase in PAHs contamination of sediment was associated with the decrease in dietary diversity of *G. pulex* and a specialization to leaf detritus. This can be explain by three non-exclusive hypothesis: (i) a vacant niche (Dangles, 2002) due to the lethal effects of the metal contamination on shredder competitor (e.g. *L. major*), (ii) a compensatory feeding (Gessner, 2010) due to a potential alteration of litter quality, evidenced by the decrease of microorganisms (fungi's hyphae) in the gut of *G. pulex* despite a higher proportion of leaf detritus and (iii) a decrease of movements, unrelated to feeding, with the increase of contamination (Mogren and Trumble, 2010). The resource quality seems particularly important and should be evaluated insofar as toxicant effects could be exacerbated when organisms feed on a bad-quality resource. In addition to external exposure due to habitat occupancy or feeding behavior, the body size also influence toxicants intake.

Some studies suggest that species with large, massive body shape presented the lowest ratio of toxicants intake, while small individuals presented higher values (Dolédec and Statzner, 2008; Ippolito et al., 2012). However, this community-level pattern is not observed at the population level, where we observed smaller organisms for *E. ignita* and *G. pulex* along the metallic and PAHs contamination gradients, respectively. This response is more probably due to a change in population structure. Combined to the abundance patterns observed for these

two species, we can conclude that, along the contamination gradients, juveniles exhibited low survival rates, with a rarefaction of the last larval stages for *E. ignita* and of adult for *G. pulex*. That will result in higher population sensitivity (Ippolito et al., 2012) and vulnerability. Thus, these niches shifts in response to environmental pressures reveal the population vulnerability of the concerned species and can impact biotic interaction and ecosystem processes *via* changes in species performance.

Niche-based explanations suggest that a species' niche breadth determines its abundance and occupancy. Consequently, one population with a reduced niche is supposed to have lower environmental tolerances than a broad niche population, leading to a lower abundance and a higher risk of extinction (Lawton, 1993; Gaston, 1999; Chessman, 2012). However, niche narrowing was not a response we observed frequently, due to its high variability. Niche breadth is influenced by numerous factors, and contamination is not always the principal one, species interactions being also determinant. We showed that the studied perturbations, either chemical or physical, are accompanied by a modification of spatial organization of species, with more aggregated communities in reservoir and in metal-contaminated sites. This aggregation can increase competition, predation, pathogens dissemination and modify (amplify or reduce) the response of the populations to the sole physical and chemical effects. Monti and Legendre (2009) suggest than in rivers with high energy flow, the driving forces for species coexistence are mostly environmental, whereas in rivers with low-energy flow, biotic interactions are prevalent.

The homogeneous environment encountered in reservoirs can increase competition; leading to communities more vulnerable to chemicals stress than in rivers (Filser et al., 2008; De Lange et al., 2010). Yet, studies in species traits changes can be useful to link the toxicant induced disturbance of structure (i.e. populations and communities) and ecosystem functioning. For instance, modification in spatial occupancy of *L. major* may probably reduce its performances for the leaf litter breakdown as well as population structure and dietary changes of *G. pulex*. More research were needed on the link between chemicals contamination, niche shifts and their consequences on species interactions and ecosystem functioning.

4.3. Realized niche *vs*. Fundamental niche

Contrary to a density-based approach, a traits-based approach enables to reach greater sensitivity to environmental modifications insofar as trait expression can demonstrate a substantive change before the occurrence of lethal effects (Culp et al., 2010). Indeed, some studies reported that the chemical concentrations that induce changes in traits are considerably lower than concentrations causing mortality (Weis et al., 2001; Relyea and Hoverman, 2006). With the condition to select suitable response traits, these variations can be useful to diagnose a particular environmental stressor and could constitute ecologically relevant endpoints. In this study, the discrepancy between spatial niches of several taxa was indicative of sediment contamination and dam presence.

The benefit to compare both niches is to determine a constraint level of a sensitive population compared to a reference situation, defined here as the widest range of species possible responses to environmental conditions (i.e. fundamental niche). This constraint level could inform on the population vulnerability, insofar as it should determine the potential of the population to modulate its response to stressors. More researches would be necessary to explore the response of other traits including respiratory strategies, dispersal capacity, life cycle duration or reproductive performance (Rubach et al., 2011; Ippolito et al., 2012) to environmental changes at specific level, and their effects on trophic interactions and ecosystem functioning. The link between fundamental niche and realized niche could be explored experimentally and could be a relevant indicator of population response to incorporate into the environmental risks assessment.

Finally, the comparison between both niches elucidates significant differences between the theoretical / potential traits from the scientific literature and realized traits of taxa in a considered environment. These differences in the traits expression can profoundly modify the appropriateness of potential traits in determining community responses to a disturbance gradient. The increase of studies about realized traits should be helpful to refine theoretical traits databases and hence, the relevance of biotraits profiles responses of communities in ecological risk assessment.

5. Conclusion

The species' realized niches reveal abiotic and biotic constraints undergone in a given environment. This approach could discriminate the effects of environmental change on populations, identify their vulnerabilities and their extinction risk, and predict changes at the community and ecosystem levels. Future ecotoxicological researches should select traits-based indicator species to environmental changes (e.g. chemical contamination, global warming, and physical constraints) to explore the response of their niches in the field and the effects of such shifts at several organization scales. The main challenge in ecotoxicology is to identify relevant endpoints of populations sensibility transposable to significant impacts on communities and ecosystem functioning; a niche-based approach could constitute this missing link.

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Synthèse des résultats

Objectifs	Principaux résultats obtenus
O1: Caractériser le système « retenue au fil de l'eau » (en l'absence de contamination des sédiments)	✓ Forte structuration spatiale des communautés de macroinvertebrés sur le gradient berge/chenal ✓ Identification de 19 taxons indicateurs dans les habitats du chenal ✓ Importance de la contribution des berges et de l'amont des barrages dans la composition et la diversité fonctionnelle des assemblages du chenal des retenues ✓ Similarité des profils bioécologiques des milieux lotiques et des retenues ✓ Plus forte agrégation des communautés macrobenthiques dans les retenues qu'en rivière : augmentation de la compétition ✓ Plus faible richesse fongique dans les sédiments des retenues qu'en rivière ; à l'inverse plus grande richesse bactérienne
O2: Identifier les modifications structurelles et fonctionnelles associées à la contamination des sédiments dans les systèmes retenues et dans les écosystèmes rivières en aval	✓ Divergence fonctionnelle entre les communautés de retenues contaminées et celles des milieux lotiques, caractérisée par une diminution de la diversité fonctionnelle ✓ Modifications structurelles et fonctionnelles des communautés macrobenthiques jusqu'à 19 kilomètres en aval du barrage suite à la remise en suspension de sédiments contaminés ✓ Diminution de l'amplitude de niche spatiale des espèces de macroinvertebrés le long du gradient de contamination métallique des sédiments ✓ Plus forte agrégation des communautés macrobenthiques dans les retenues contaminées : augmentation de la compétition. Agrégation des espèces sensibles dans les habitats d'érosion et évitement des habitats sédimentaires ✓ Sélection des organismes de petites tailles chez *G.pulex* et *E.ignita* ✓ Spécialisation du régime alimentaire de *G.pulex* ✓ Baisse de la diversité de l'activité métabolique des communautés microbiennes

Objectifs	Principaux résultats
O3: Hiérarchiser les impacts physiques et toxiques	✓ Réponse structurelle (modification des assemblages) mais continuité fonctionnelle en l'absence de contamination. A l'inverse, la contamination des sédiments dans les retenues induit des réponses structurelles ET fonctionnelles ✓ Réponses létales et sublétales plus influencées par la contamination des sédiments que par la présence d'un barrage
O4: Sélectionner des outils de diagnose de la qualité des sédiments	✓ Meilleure aptitude du chenal à mettre en évidence le gradient de contamination ✓ Sélection de taxons indicateurs de la présence de sédiments contaminés (ex. Ephemerella ignita, Tanypodinae, Atherix) ✓ Identification de traits réponses à la contamination des sédiments au niveau des communautés (ex. taille maximale, formes de résistance, préférences de substrats) ✓ Les écarts entre niche spatiale théorique et réalisée des populations de taxons sensibles augmentent significativement avec la contamination métallique des sédiments

L'ensemble des réponses structurelles des communautés et des populations aux perturbations physiques et toxiques associées à la présence de retenue au fil de l'eau peut avoir une incidence sur la réalisation de processus écosystémiques *via* la modification des performances et de la contribution de certains taxons et/ou *via* la perte des mécanismes de complémentarité. Cette recherche des effets des modifications létales et sublétales des communautés et des populations sur le fonctionnement des écosystèmes sera restituée au chapitre suivant.

Chapitre IV

Réponses fonctionnelles aux perturbations toxiques et physiques

Préambule

L'objectif principal de ce chapitre est d'examiner si les réponses structurelles décrites dans le chapitre précédent se traduisent par des perturbations dans la réalisation de processus écosystémiques tels que les flux benthiques à l'interface eau-sédiment et la décomposition des litières végétales.

Un premier travail a été réalisé sur l'étude du fonctionnement biogéochimique des sédiments dans les retenues *via* le déploiement de chambres benthiques *in situ*, permettant la mesure des flux d'éléments (oxygène, nitrate, nitrite, ammonium et phosphate) à l'interface eau-sédiment. L'objectif de cette expérience était d'identifier les paramètres abiotiques des sédiments (contamination, quantité de matière organique…) et biotiques (communautés microbiennes et macrobenthiques) qui influencent la nature et l'intensité des flux benthiques et les conséquences potentielles sur la qualité de l'eau au sein des retenues et à leur aval (article 5).

L'étude de la décomposition des litières le long du gradient de perturbation physique et toxique a été réalisée suivant deux approches. Dans un premier temps, nous avons étudié conjointement les modifications bioécologiques des communautés de macroinvertébrés et la réalisation du processus *in situ* via la mesure des taux de décomposition de litières d'aulne (article 6). Nous avons testé l'hypothèse que les effets létaux des perturbations sur la structure bioécologique des communautés de macroinvertébrés conduisaient à une rupture du processus de décomposition des litières.

Pour autant, les perturbations peuvent également altérer le compartiment microbien associé aux litières. La modification du conditionnement de la ressource détritique qui en découle peut en retour constituer un stress additif et conduire à une perte d'efficacité (effets sublétaux) des déchiqueteurs dans la dégradation des litières. Pour tester cette hypothèse, une seconde expérience a été conduite sur le conditionnement *in situ* de litières d'aulne et par des tests de consommation en laboratoire. L'objectif de cette étude était d'évaluer l'impact de la présence de barrage et de sédiments contaminés sur le compartiment microbien et d'identifier les

conséquences potentielles sur la contribution de deux espèces de déchiqueteurs (*Gammarus pulex* et *Allogamus auricollis*) dans la réalisation du processus de décomposition et sur la production de fines particules organiques associés à la consommation des feuilles (article 7).

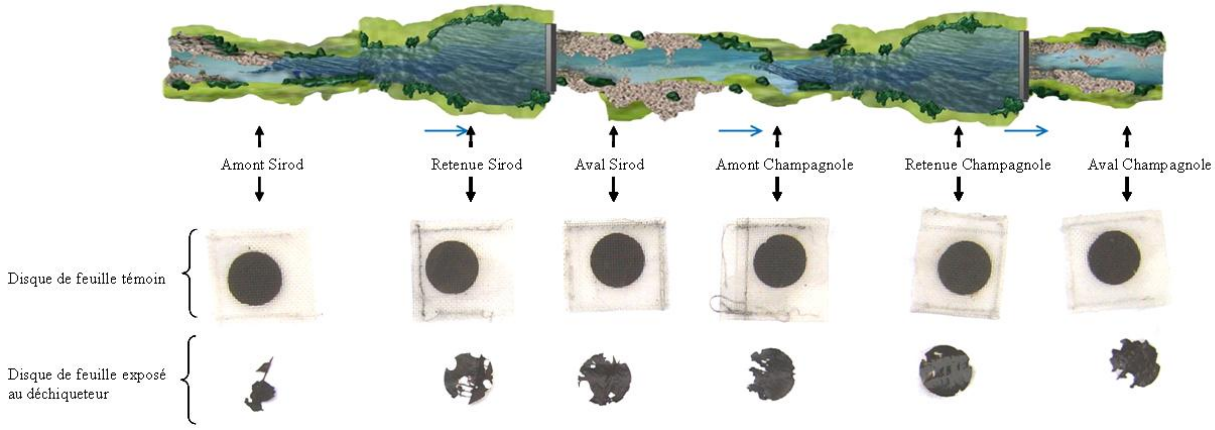

Fig.12 : Illustration de l'expérience de consommation des disques de feuilles d'Aulne exposés 45 jours aux stations de l'Ain par *G.pulex*. Source : Colas F.

Article 5: **Benthic fluxes from small run-of-river reservoirs across a gradient of sediment contamination**

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En préparation pour soumission à Hydrobiologia

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Abstract

Small run-of-river reservoirs store a large amount of sediments and detrital organic matter which entrap pollutants leading to potential alteration of nutrient fluxes at the water/sediment interface. Nonetheless the benthic fluxes of sediments from small reservoirs are rarely studied despite their importance for water quality downstream. Using *in situ* benthic chambers, we examined oxygen consumption and nutrient fluxes (nitrate, nitrite, ammonium and phosphate) of four small reservoirs along a gradient of sediment contamination. Benthic fluxes are greatly dependent on both sediment physicochemical characteristics and biological resident communities (microbial and macrobenthic). Contaminants stored in sediments may affect microbial and macroinvertebrates communities and consequently disturb nutrients and oxygen benthic fluxes. We aimed to determine what sediment characteristics influence nutrient retention or release and whether impacts of contaminated sediment on resident biota elucidate benthic fluxes changes. Benthic fluxes in reservoirs were mainly influenced by organic matter, nutrient contents and levels of contamination in sediments. High organic matter contents have promoted ammonium releases. Significant relationships between sediment contamination and nutrients fluxes were elucidated, probably due to negative effects of contamination on resident communities. In addition to adverse effects of sediments contamination, the disturbances of nutrient fluxes (e.g. ammonium release) could also impact aquatic communities. The nutrient retention in reservoirs and inversely release of reduced compounds or pollutants from sediments might have severe consequences for downstream communities already under physical constraints due to the presence of dam. More research is needed on the understanding of sediment biogeochemical functioning in small reservoirs that

accumulate numerous pollutants and, on their potential effects on water quality in reservoirs as well as in downstream ecosystems.

Keywords: small run-of-river reservoirs – benthic fluxes – sediment contamination – nutrient release and retention

1. Introduction

Run-of-river reservoirs represent a depositional zone along the river watercourse. Sediment accumulation in reservoirs can act as efficient sinks for phosphorus and to a lesser degree for nitrogen (Garnier et al. 1999; Lebo 1991; Wang and Li 2010), leading to a disruption of natural biogeochemical cycles potentially altering the amount of nutrients transported by the river and in turn, ecological functioning of reservoir and their downstream. Thus, these reservoirs can potentially modify the chemical form of nutrients and/or lead to a temporal shift in their delivery (Baldwin et al. 2010), depending of sediment geochemical or physicochemical characteristics. Nonetheless, the biogeochemical functioning of sediments is scarcely studied in small run-of-river reservoirs, yet these systems are widespread and constitute a real challenge to understand effects of dams on the downstream ecosystem integrity. Indeed, more than, 60,000 reservoirs exist in France and many are impounded by dams that are aging and in disrepair (70% are without economic use).

Adsorption and desorption capacities of nutrients are mainly determined by environmental parameters such as dissolved oxygen and pollutant concentrations, nutrient and organic matter content, temperature or the redox potential. The strong accumulation of organic matter content, commonly observed in reservoirs, is known to increase sediment oxygen demand and nutrient fluxes (Callier et al. 2009; Dahlbäck and Gunnarsson 1981; Heilskov and Holmer 2001). With the depletion in dissolved oxygen, nutrients and potentially hazardous pollutants may be released from the sediments. For instance, nitrogen release from sediments occurs predominantly by the reduction of nitrate as ammonium. This transformation of ammonium to ammonia increases when pH and water temperature increase (Camargo and Alonso 2006). In addition, high nutrient loads may also alter the major pathways by which nutrients are recycled, for example by inhibition of nitrification and preferential release of ammonium

(Burford and Longmore 2001; Jorgensen and Richardson 1996). It was a widely accepted fact that aerobic conditions at the sediment water interface prevent phosphorus and nitrogen release to the overlying water, whereas anoxic conditions support their release (Hupfer and Lewandowski 2008). Redox potential and phosphorus content (Boström et al. 1988; Nowlin et al. 2005) appears also to regulate the release of dissolved phosphorus from sediments (mostly as phosphate, PO_4^{3-}). Furthermore, geophysical properties such as particle size distribution of sediment can greatly influence nutrients retention. For instance, many studies reported an exponential increase in phosphorus adsorption with decreasing particle size (Walter and Morse 1984; Wang and Li 2010; Zhang and Huang 2007).

Accumulated sediments in reservoirs also have a strong adsorption capacity of pollutants (Cairns et al. 1984; Chapman 1990; Estebe et al. 1997). To date, there is very little data available about the effects of sediment contamination on benthic fluxes measured *in situ*. Pollutants stored in sediments may profoundly alter the biological compartments associated with biogeochemical functioning, and in turn, the form and amount of nutrients that are mobilized to the overlying water. Numerous studies have demonstrated the importance of microbial communities in nutrient cycling and transfer of a part of the primary production towards upper trophic levels (Azam et al. 1983; Sherr and Sherr 1987). These microbial transformations of dissolved and particulate nutrients have been shown to influence macroinvertebrate assemblages, which constitute also an essential compartment in nutrient cycling and primary production. Indeed, macrofauna-induced particle mixing (bioturbation) and solute transfer (bio-irrigation) stimulate mineralisation (Mermillod-Blondin et al. 2004), increase nutrient turnover and therefore renew the pool for primary production (Blackburn 1988; Braeckman et al. 2010). Changes in the resident microbial and macroinvertebrates communities induced by sediment contamination may thus affect benthic mineralization processes and therefore water quality in reservoirs and downstream dams.

This study examines benthic fluxes at the water-sediment interface of four small run-of-river reservoirs according to a gradient of sediment contamination, using benthic chambers providing an *in situ* method of measuring biological processes and resulting nutrient fluxes. The main objectives were (i) to examine effects of sediment contamination on oxygen and nutrients fluxes (nitrate, nitrite, ammonium, phosphate) at the water/sediment interface, (ii) to determine whether fluxes changes are related to sediment characteristics and to microbial and

macroinvertebrates communities' responses to contamination, and consequently (iii) to elucidate potential risks for surface water quality of reservoirs and downstream of dams.

2. Materials and methods

2.1. Study site and sediment collection

Ain and Bienne are two rivers in the Jura mountain (France, Northern Prealps ecoregion) fragmented by multiple run-of-river dams. Etables (Re4, maximum depth, 6.5m; surface area, 7 ha) and Lavancia (Re2, maximum depth, 4m; surface area, 3.7 ha) reservoirs are associated with two dams along the Bienne watercourse, while Sirod (Re1, maximum depth, 3m; surface area, 2 ha) and Champagnole (Re3, maximum depth, 3.5m; surface area, 3 ha) reservoirs are associated with two dams along the Ain watercourse. The physicochemical characteristics of the sediments (Table 1) were assessed in samples realized during the spring field campaigns (sampling depth of 20 to 30 cm) and sent to a specialized laboratory (LDA26, Avignon, France). Concerning sediment contamination, the levels of 11 metals, 7 PCBs and 10 polycyclic aromatic hydrocarbons (PAHs) were measured. PCBs were below the quantification limit in all samples (5 µg.kg^{-1} DM). Levels of contamination were defined according to the mean ranks of pollutant concentrations.

	Granulometry (%)			
	Clay	Silt	Sand	TOC
Re1	1.7	27.4	71	12.9
Re2	1.9	24.4	73.7	8.6
Re3	1.0	24.5	74.6	43.4
Re4	2.2	39.5	58.1	26.9

	Metals concentrations (mg kgDW^{-1})									
	Al	Cd	Cr	Co	Cu	Hg	Ni	Pb	Zn	Rank
Re1	3.72×10^3	0.1	21.3	3.4	4.1	0.01	9.4	9.1	26.9	1
Re2	2.08×10^3	0.2	14.9	2.3	24	0.02	10.8	32	52.4	2
Re3	3.70×10^3	0.3	27.5	3.3	28.7	0.03	11.8	18.9	84.5	3
Re4	4.39×10^3	0.3	32.8	3.4	32.2	0.03	16.9	23.9	78.2	4

	PAH concentrations (µg kgDW-1)								
	Anth	BaP	BaA	BkF	BgP	Chry	Ind	Phen	Rank
Re1	10	23	20	12	5	25	21	25	1
Re2	10	535	649	206	43	483	395	25	4
Re3	10	62	46	28	47	25	29	25	2
Re4	31	286	233	121	133	166	118	180	3

Table 1: Principal physicochemical parameters that characterize sediments of study sites.

2.2. Benthic chambers

Three fabricated Plexiglas dark benthic chambers that isolate a sediment surface of 1600 cm^2 (Fig.1) were used for the fluxes study. For each reservoir the three chambers were placed near to dam, on a sedimentary area. The chambers were carefully deposited on the bottom using all precautions required to not disturb the superficial sediment and deployed along a transect of three to five meters long. The average depth of penetration of the chambers to the sediment was 15 centimetres. Chambers were deployed at 08:30 a.m., for 6 to 8 hours, in order to avoid hypoxia conditions within the chambers (the lowest saturation measured at the end of an experiment was 52.7%). The water enclosed was mixed by a stirrer only in the surface to avoid disturbing the sediment.

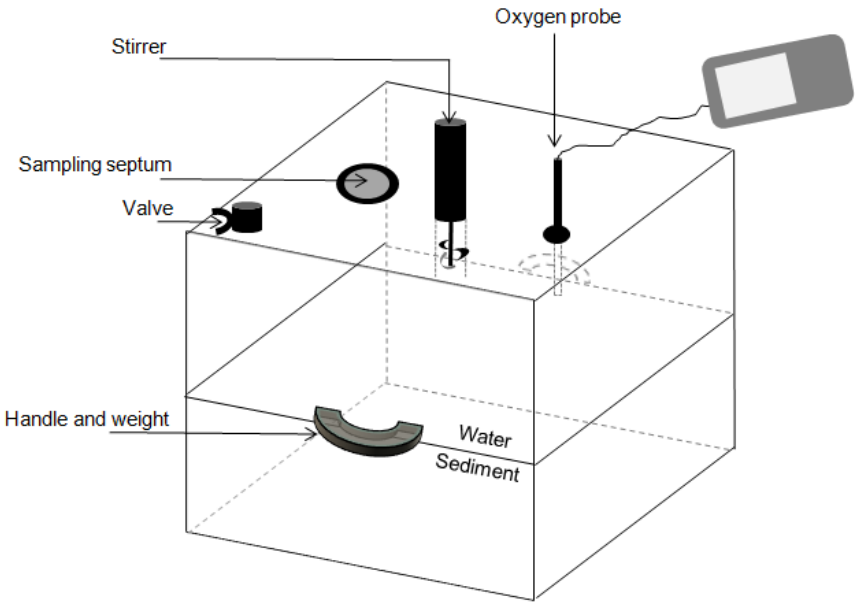

Fig.1: Schematic diagram of the benthic chambers used in the study

Dissolved oxygen concentration and temperature were measured inside the chambers with an oxygen probe (HQ40d multi - HACH) every half hour. A sample volume of 60 ml was collected every hour from each chamber by syringes through the septum and replaced by ambient water, by opening a valve during the sampling. The first sampling was done immediately after deployment of the chambers i.e. at time 0. The samples were filtered through GF/F 0.22 µm diameter syringe filters and placed on ice before return to the laboratory, where filtrates were frozen before analysis for NH_4^+, NO_2^-, NO_3^+ and $P0^4_{3-}$ (UV spectrophotometry). . At the end of experiments, 50 ml sediments were collected in the area

covered by each chambers and in an area next to the chambers and homogenized by sieving (2 mm mesh size). In laboratory sediment samples were analysed to determine organic matter, nitrogen, carbon and phosphorus content. For sediment organic matter content, samples were frozen (-20°C) before being dried at 60°C for 48-72 h to attain a constant weight, weighted, burned for 5h at 500°C, and reweighed to calculate sediment ash-free dry weights (AFDW). Sediment organic matter content is expressed as % loss of total sediment weight following combustion. Organic Carbon and Nitrogen concentrations were determined with a Carlo Erba (NA 2100) CHN analyser and total Phosphorus by acid mineralization and spectrophotometry (NFT 90-023).

2.3. Microbial communities' analysis

For each station, three sediment samples homogenized by sieving (2-mm mesh size) were collected on about 20 centimetres deep with a shovel for sediment on littoral areas. A part of samples was stored at -80°C for DNA extraction and PCR-DGGE analysis and the other part was analysed using the BIOLOG GN2 MicroPlateTM. For each sample, three replicates were analysed. Sediment DNA extractions were performed using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA) according to the manufacturer's instructions. Primers 341F-GC and 907R (Muyzer et al. 1993) were used for partial PCR amplification of bacterial 16S rRNA genes as described by Muyzer and Smalla (Muyzer and Smalla 1998). Fungal partial 18S rRNA gene fragments were amplified using a two-step PCR protocol. The first amplification used primers NS1 and EF3. Diluted amplicons (1:500) from first step were used as template for the second amplification with primers NS1 and FR1-GC as described by Oros-Sichler (Oros-Sichler et al. 2006). The amplification products were controlled on 1% (w/v) agarose gel and separated with the DCODE Mutation Detection System (Bio-Rad, Hercules, CA). The vertical electrophoresis was performed with a denaturing gradient from 40 to 60% for bacterial communities and with one from 25 to 40% for fungal communities (100% denaturant corresponds to 40% (v/v) formamide and 7 M urea). DGGE were run for 16 h at 100 V and 60°C (bacteria) and at 180 V and 58°C (fungi). The gels were stained with SYBR Green I and were imaged with a STARION FLA-9000 scanner (Fujifilm Life Sciences FSVT, Courbevoie, France). Secondly, community-level physiological profiles were assessed using the BIOLOG GN2 MicroplateTM (Biolog Inc., Hayward, CA). 5 g of each fresh replicates

were homogenized in 45 ml of sterile physiological water and shaken 30 minutes at 150 rpm. After decantation, 150 µl of supernatant for each replicate were inoculated into wells of three plates. Each Microplate™ contains 95 wells of different sole-carbon-sources. Plates were incubated at 25°C in the dark and OD600nm were recorded every 12 h during 60 h using an Expert Microplate Reader (ASYS, Eugendorf, Austria). Data were normalized by the average well colour development (AWCD) following (Weber et al. 2007). Kinetic of microbial activity was assessed through the Area Under the absorbance versus time Curves (AUC) (Guckert et al. 1996).

2.4. Macrobenthic communities' analysis

For macroinvertebrates sampling, reservoirs were subdivided into three zones, termed "tail", "middle" and "dam" reflecting their various hydraulic and hydro-morphological conditions. Three samples for each areas defined above were sampled by dredging from a boat perpendicular to a transect. All samples were preserved in 4% formalin in the field and transferred to the laboratory where they were sieved and sorted. Organisms were mainly identified at genus level (using (Tachet et al. 2000), except for some groups, which were identified at higher taxonomic level [i.e. Diptera (family or tribe level) and Oligochaeta or Nematoda]. From taxonomic data, we calculated site community mean biotrait profile, thanks to twenty two fuzzy-coded biological and ecological traits (Chevenet et al. 1994) (called biotraits hereafter) described from literature for each taxon. Biological traits reflect the life history of taxa (e.g. 'number of cycles per year'), their resistance and resilience abilities (e.g. 'resistance forms'), and general morphological ('body form') or physiological (e.g. 'respiration', 'feeding habits') features of organisms (Usseglio-Polatera et al. 2000). Ecological traits mainly describe habitat preferences of taxa at different spatial scales (e.g. substrate, current velocity, temperature, pH, saprobity, longitudinal distribution). Each trait is described by a set of categories (= modalities). The mean weighted (by log-transformed abundances) trait profiles of site assemblages were calculated and expressed as relative abundance distributions of trait categories within the assemblages (Thioulouse et al. 1997).

2.5. Data analysis

The plot between concentrations against time was found to be linear (cf. additional content) and thus benthic flux F was calculated as follows (Pratihary et al. 2009):

$$F(\text{mmol.m}^{-2}.\text{d}^{-1}) = \left(\frac{V}{A}\right)\left(\frac{dc}{dt}\right)\left(\frac{t}{24}\right)$$

Where V is the volume of the water in the chamber; A is the surface area of the sediment enclosed in the chamber; dc/dt is the slope of the linear regression of concentration (µM) versus time.

As per the convention, negative values of F denotes flux from overlying water to sediment and positive values of F denotes flux from sediment to overlying water. One-way analyses of variance (ANOVA- normal distribution and homoscedasticity were respected) were used to test for differences of sediments characteristics and benthic fluxes between stations. Stepwise multiple linear regressions were used to identify predictors (abiotic components of sediments, e.g. organic matter content, contamination levels) of benthic flux. Gradient of contamination was clarified using complete linkage clustering analysis based on Euclidean distances between sites according their concentrations in metals and PAHs. Growing levels of contamination were defined according the mean ranks of pollutant concentrations. Co-inertia analyses were performed to reveal co-structure between benthic fluxes, sediment contamination (PAHs and metals), macroinvertebrates (assemblages and community biotrait profiles) and microbial communities (assemblages and community-level physiological profiles). Co-inertia analyses were based on Principal component analyses for flux, contamination and Biolog data, Factorial Component analysis for taxonomic data (macroinvertebrates and microbial) and Fuzzy Coding analysis for macroinvertebrates biotrait profiles. We used R software (Team 2008) and the ADE4 library (Chessel et al. 2004) for all statistical analysis.

3. Results

3.1. *In situ* sediment characteristics

A classification on pollutants concentrations in sediments of sites reveals the gradient of contamination (Fig.2). According to the metal contamination, highest concentrations were associated with stations whose sediments have larger contents in organic carbon and in fine particles (Re4 and Re3) (Table 1). This contamination is mainly characterized by high concentrations of metallic pollutants such as chromium, copper, nickel and zinc.. Re2 was the site the more impacted by PAH contamination. This contamination is mainly characterized by high concentrations in Benzo(a)pyrene (BaP), Benzo(a)anthracene (BaA), Benzo(k)fluoranthene (BkF), Chrysene (Chry) and Indeno(1,2,3-cd)pyrene. The chosen sites thus represent the followong gradients of sediment contamination: Re1 (relative reference) < Re2 < Re3 <Re4 for metallic contamination and Re1 (relative reference) < Re3 < Re4 < Re2 for PAH contamination.

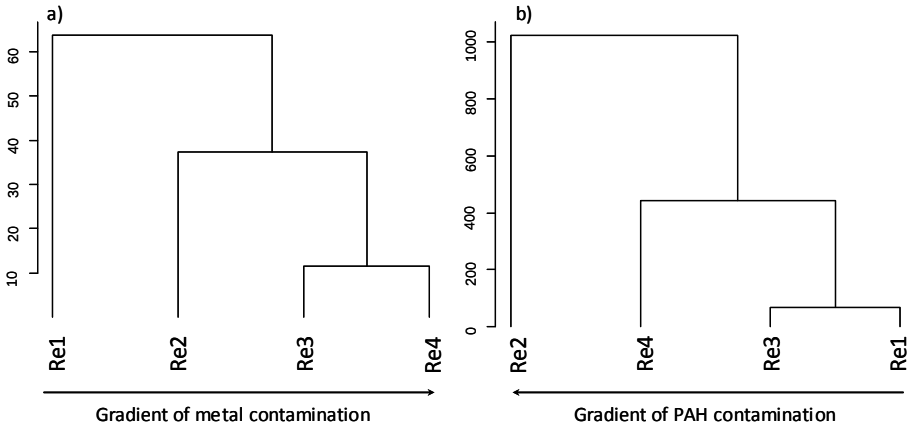

Fig.2: Hierarchical clustering dendrogram performed on the Euclidean distances between the four stations based on their a) metals and b) PAH concentrations in sediments.

Phosphorus, nitrogen, carbon and organic matter contents in sediments differed significantly between run-of-river reservoirs (Fig.3). Elementary contents of sediments have shown three groups of stations, Re3 and Re4 for which the nitrogen and phosphorus contents of sediments are higher, in contrast with the lower elementary contents of Re2 sediments, Re1 occupying an intermediate position. The organic matter content in the sediments showed similar patterns, with highest organic matter in Re3 and Re4 (maximum value: 10.05% ± 0.38) than in Re1 and Re2 (minimum value: 0.75% ± 0.02).

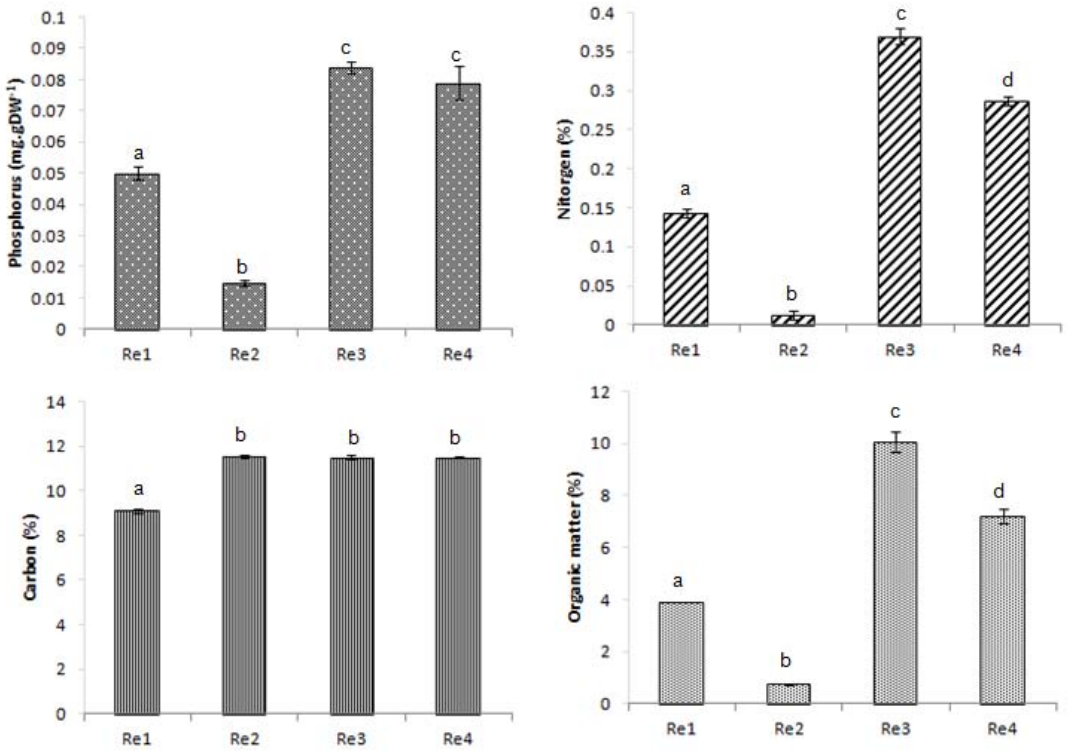

Fig.3: Mean content in phosphorus, nitrogen, carbon and organic matter in sediments of sites. Different letters indicate significant differences between sites.

3.2. Biogeochemical fluxes

Sediment oxygen fluxes varied between -0.28±0.24 at Re2 and -2.1± 0.34 at Re4) mmol.m^{-2}.d^{-1}, ammonium (NH4) fluxes ranged from 6±14.14 at Re1 and 104.33± 18.38 at Re4 µmol. m m^{-2}.d^{-1}, phosphate (PO4) fluxes varied between 1.23 (±0.6; Re2) and -38.2 (±4.2; Re4) µmol. m^{-2}.d^{-1} and nitrate (NO3) fluxes varied between 0.01 (± 0.001; Re2) and -0.13 (±0.01; Re4) mmol.m^{-2}.d^{-1} (Fig.4). All these fluxes varied significantly among run-of-river dams (Fig.4) with Re4 that was very different from the other stations particularly by higher oxygen consumption, ammonium release and phosphate retention. Although similar trend for ammonium release was apparent, this parameter was not significant for Re3, probably because of a great between-chambers variability. Denitrification was evidenced for all stations except for Re2 which sediments have released low concentration of nitrate.

The multiple linear regression analysis has clarified the importance of sediments characteristics for explaining the benthic measured fluxes (Table 2). For dissolved oxygen fluxes, the selected model explained 93% of the total variation. The best predictors were the

phosphorus and organic matter contents in sediments and then nitrogen content and PAH contamination. For nitrate fluxes, the selected model explained 84% of the total variation.

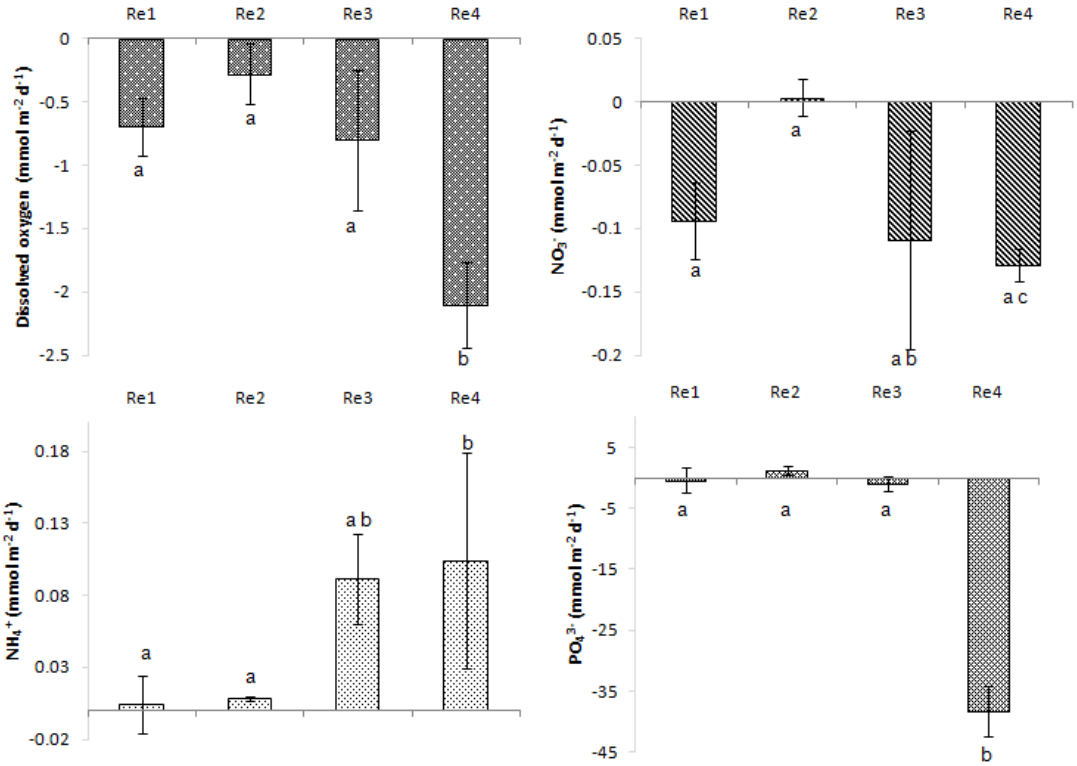

Fig.4: Mean oxygen consumption and nutrient fluxes (nitrate - NO_3, ammonium – NH_4 and phosphate – PO_4) (±SE) measured at the water sediment interface of benthic chambers. Different letters indicate significant differences between sites.

The best predictors were nitrogen content, organic matter content and metals levels of contamination. Model selected for ammonium fluxes explained 83% of the total variation. The best predictors were phosphorus content, organic matter content and total organic carbon. Finally, the selected model for phosphate fluxes explained 99% of the total variation. The best predictors were metals levels of contamination and phosphorus content.

3.3. Confrontation with the biotic compartment

Factorial planes resulting of multivariate analyses performed on microbial and macroinvertebrates communities evidenced sites differences according to faunistic and functional characteristics of assemblages (Fig.5). Biolog excepted, all the analyses evidenced

taxonomic and functional features very specific for the lowly contaminated site, Re1. The most metal-contaminated site, Re4, is better discriminated by macroinvertebrates (either taxonomic or functional features) and Biolog responses. None of these factorial planes exhibited a site structure that fit exactly to PAHs or metallic contamination gradients.

Dependent variable	Overall r^2	Overall p-value	Independent variable	Coefficient	p-value
O^2 flux -(mmol.m^{-2}.day^{-1})	0.93	< 0.001	PAH levels	-0.33	*
			Phosphorus	-1.49	**
			Nitrogen	-2.88	*
			Organic matter	3.74	**
NO_3 flux - (mmol.m^{-2}.day^{-1})	0.84	< 0.001	Metals levels	0.03	*
			Nitrogen	-0.48	***
			Organic matter	0.41	**
NH4 flux - (µmol.m^{-2}.day^{-1})	0.83	0.004	Metals levels	-0.13	
			PAH levels	0.10	
			Total organic carbon	0.38	*
			Phosphorus	0.48	**
			Organic matter	-0,62	*
PO4 flux - (µmol.m^{-2}.day^{-1})	0.99	< 0.001	Metals levels	-17.57	***
			Organic matter	18.50	
			Total organic carbon	15.97	.
			Phosphorus	27.85	**

Table 2: Multiple linear regression analyses of measured benthic fluxes against sediment characteristics at the four study sites. Variables shown for each multiple regression were conserved using a stepwise procedure of variable selection. Overall r^2 and P-values are based on the selected multiple regressions.

However, co-inertia analyses performed between biological compartment and either pollutants concentrations in sediment or benthic fluxes enables to validate similarities between biotic and abiotic responses. Significant co-structures were found between sediment contamination by metals and PAH and the taxonomic and functional responses of macroinvertebrates and microbial communities (Table 3).

Table 3: P-values from results of Co-inertia analyses between microbial or macroinvertebrates assemblages and functional diversity, and sediment contamination (in metals and in PAH) and benthic fluxes. Letters correspond to used methods of multivariate analysis as follows a) Factorial Components analysis, b) Principal Component analysis and c) Fuzzy Coding analysis.

	Microbial			Macroinvertebrates	
	Bacteria[a]	Fungi[a]	Biolog[b]	Diversity[a]	Traits[c]
Metals[b]	0.001	0.002	0.02	0.018	0.001
PAH[b]	0.001	0.002	0.001	0.016	0.003
Flux[b]	0.045	0.016	0.05	0.015	0.015

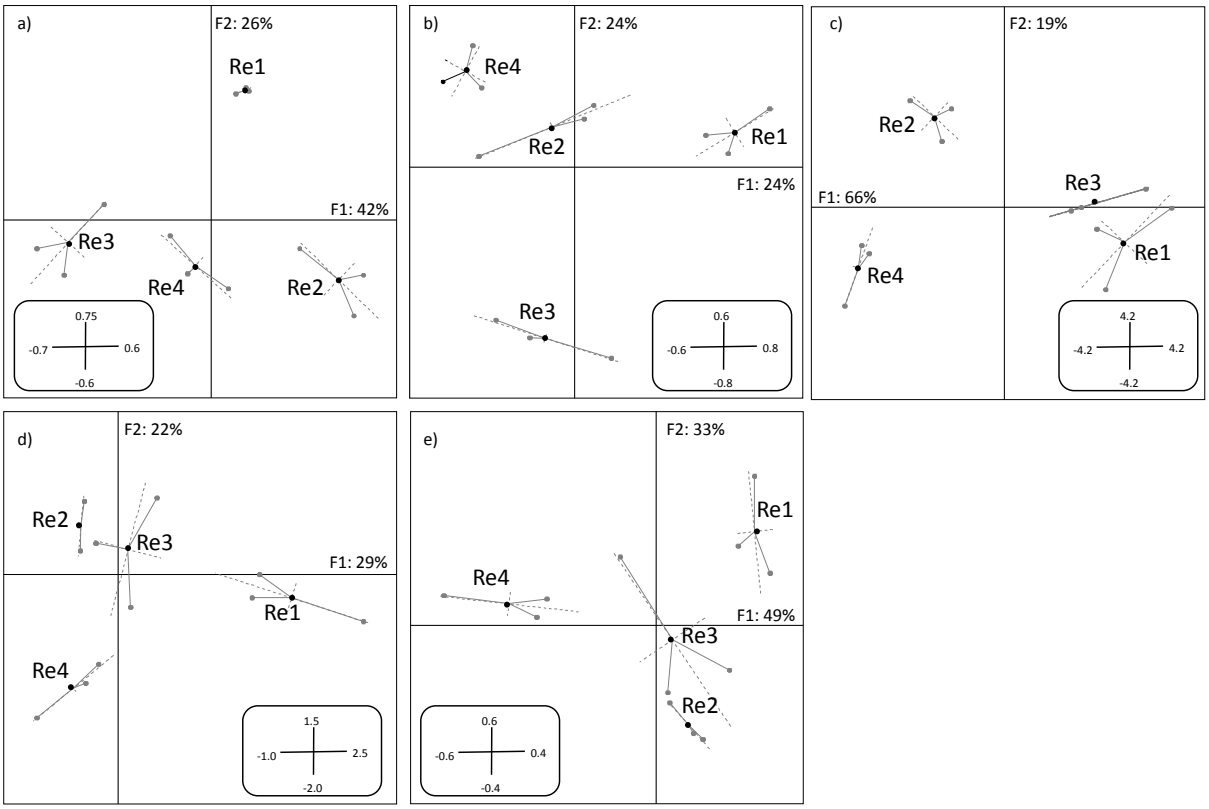

Fig 5: Factorial planes of the mulitvariate analysis performed on bacterial (a - FCA) and fungal (b - FCA) communities, on microbial community-level physiological profiles (c - PCA), on macroinvertebrates communities (d - FCA) and on macroinvertebrates biotraits profiles (e - Fuzzy coding analysis)

Significant results were identified between benthic fluxes and biotic compartment, especially for the fungal and macrobenthic assemblages and the macroinvertebrates biotraits profiles.

4. Discussion

The use of benthic chambers *in situ* is a suitable approach to understand what happens in nutrient cycling in low oxygen condition, a phenomenon that frequently occurs in organic rich waters such as reservoirs. Contrary to more current laboratory studies where exported sediments are destructured, the use of benthic chambers integrates the overall geochemical and biological processes at the sediment-water interface. Previous studies have shown that obtained rates are a good representation of natural fluxes (Nicholson et al. 1999; Reay et al. 1995). In addition, such approach is quite easy to realize and inexpensive, consequently it could be useful in seasonal management of water quality in reservoirs as well as for the risk assessment of dams' impact on water quality downstream. If it is essential to investigate

benthic nutrient fluxes in run-of-rivers dams' reservoirs, contrary to our study, pollutant fluxes should be assessed in the same time insofar as they also influence surface water quality.

4.1. Effects of sediments characteristics on benthic fluxes

Benthic fluxes in the four small run-of-river reservoirs are mainly influenced by organic matter and nutrient contents and levels of contamination in sediments. High denitrification rates are mainly associated with organically-rich sediment which could limit lateral penetration of dissolved oxygen. The denitrification rates of the small studied reservoirs are relatively similar except for the reservoir Re2 where sediments are more sandy. Nitrate influxes are also associated with nitrogen content in sediments. Previous studies have shown also that denitrification rates in a reservoir were limited by nitrate availability (Baldwin et al. 2010; Mitchell and Baldwin 1999). Contrary to nitrates, high organic matter contents promote ammonium releases. In addition, phosphorus content in sediments seems also associated with ammonium desorption. That could be explained by the high affinity of phosphorus for fine sediments. Indeed, fine sediments are expected to have greater surface area for adsorption of SRP (soluble reactive phosphorus) as well as for ammonium. Many studies showed that the amount of phosphorus adsorbed increases exponentially with decreasing particle size (Walter and Morse 1984; Wang and Li 2010; Zhang and Huang 2007) due to the larger cumulative reactive surface area. The relationship found between pollutants stored in sediments and the measured fluxes may be associated with (i) a confounding factor insofar as the organic matter entraps nutrients as well as contaminants and / or (ii) the effects of contamination on the biological activities and assemblages associated with cycle nutrients.

4.2. Relationship with the biotic compartment

Our results identify relationships between communities responses (microbial and macrobenthic) to contaminants stored in sediments and on the other hand to the measured fluxes. Because the sediment contamination significantly affects the assemblages and the functional diversity of communities, it is likely that these changes affect in turn processes at

the water-sediment interface. In addition to adverse effects of sediments contamination, the disturbances of nutrient fluxes (e.g. ammonium release) could also impact aquatic communities. Indeed, even if it is accepted that ammonium is not toxic, its products, particularly ammoniac (NH3), is very toxic (Alonso and Camargo 2003; Russo 1985; Scott and Crunkilton 2000). The potential risk of toxicity associated with ammonium release is greater in high pH conditions, as it is the case here (pH >8). In their study, Berenzen et al. (2001) have shown in laboratory conditions of neutral pH (7-8), that 3 $mg.l^{-1}$ of ammonium product 0.15 $mg.l^{-1}$ of ammoniac and 0.91 $mg.l^{-1}$ of nitrite leading to the decrease of 98% in abundance of populations of amphipod *Gammarus pulex*. Ammoniac is very toxic for all aquatic animals and particularly for fish causing an increase in gill ventilation, hyperexcitability, convulsions and finally, death (Alonso and Camargo 2003; Russo 1985). Moreover, ammoniac can cause toxicity to Nitrosomonas and Nitrobacter bacteria, inhibiting the nitrification process (Anthonisen et al. 1976; Russo 1985). This inhibition can also result in increased accumulation of ammonium, and so favour ammoniac production, in the aquatic environment, intensifying the toxicity to bacteria and aquatic animals (Camargo and Alonso 2006; Russo 1985). This condition of elevated pH is thus crucial to consider in the case of sediment contamination. Indeed, adsorption capacity for cationic heavy metals (e.g. Zn, Cd, Ni, Cu and Pb) commonly decreases with pH (Benjamin and Leckie 1981), resulting in an increased solubility of these metals (van den Berg et al. 1999). Consequently, it seems important to consider the potential synergistic or additive effects of the compounds (nutrients and pollutants) released from sediments on the resident communities but also downstream dams.

4.3. Implications for water quality and ecosystem integrity

It is admitted that reservoirs can act as efficient sinks for phosphorus and to a lesser degree for nitrogen (Garnier et al. 1999; Uhlmann et al. 1995) leading to a depletion downstream. This depletion might cause changes in the food webs and thus induces severe alterations of communities downstream, already under strong physical constraints due to the presence of dam. In addition, potential resuspension of sediments, contaminants and reduced compounds might induce chronic disturbances on downstream ecosystems. These negative effects of the sediment and water quality in reservoirs could be exacerbated in summer where oxygen

depletion conditions are more frequent in reservoirs. Furthermore, changes in trophic status in reservoirs and downstream ecosystems could enhance or slow down other processes such as leaf litter breakdown, depending on the balance between nutrient dependence and the effects of toxic substances (Baldy et al. 2007). In reservoirs, which entrap a large amount of organic matter, contamination of sediments, by affecting microbial and macrobenthic communities, could limit the degradation of this organic matter. Undegraded organic matter accumulates and favours anoxic conditions in sediments and thus the denitrification and the phosphorus retention and, conversely the release of ammonium hence probably exacerbating the impact of dam on downstream ecosystems integrity.

5. Conclusion

For effective and cost-efficient management of river water quality, more effort in ecological assessment of small run-of-river reservoirs must be made. The study of biotic and abiotic mechanisms that influence biogeochemical functioning of sediments in reservoirs is essential in the monitoring the quality of surface waters and in particular in the risk assessment associated with the presence of run-of-river dam. In spite of the relatively small number of reservoirs in this study, common patterns of nitrogen and phosphorus retention and ammonium release are exhibited cross all sites that may have adverse and additive effects on aquatic communities. Accumulated sediments with high load in nutrients and pollutants can have serious consequences in the case of dam management (e.g. drawdown, draw-off) or in the case of restoration of ecological continuity (e.g. removal of dam) leading to resuspension of sediments. This lack of consideration of the quality of stored sediment could affect downstream communities and induce a lag between dam removal and the reestablishment of suitable habitat for aquatic communities and thus compromise the success of restoration. The deployment of benthic chambers might be a relevant approach to examine nutrients and pollutants fluxes during pre-dam removal studies. More researches are need to confirm patterns observed in this study and to investigate potential effects of anthropogenic disturbances (e.g. chemical) on the biogeochemical functioning of small reservoirs and these potential repercussions on downstream ecosystem integrity.

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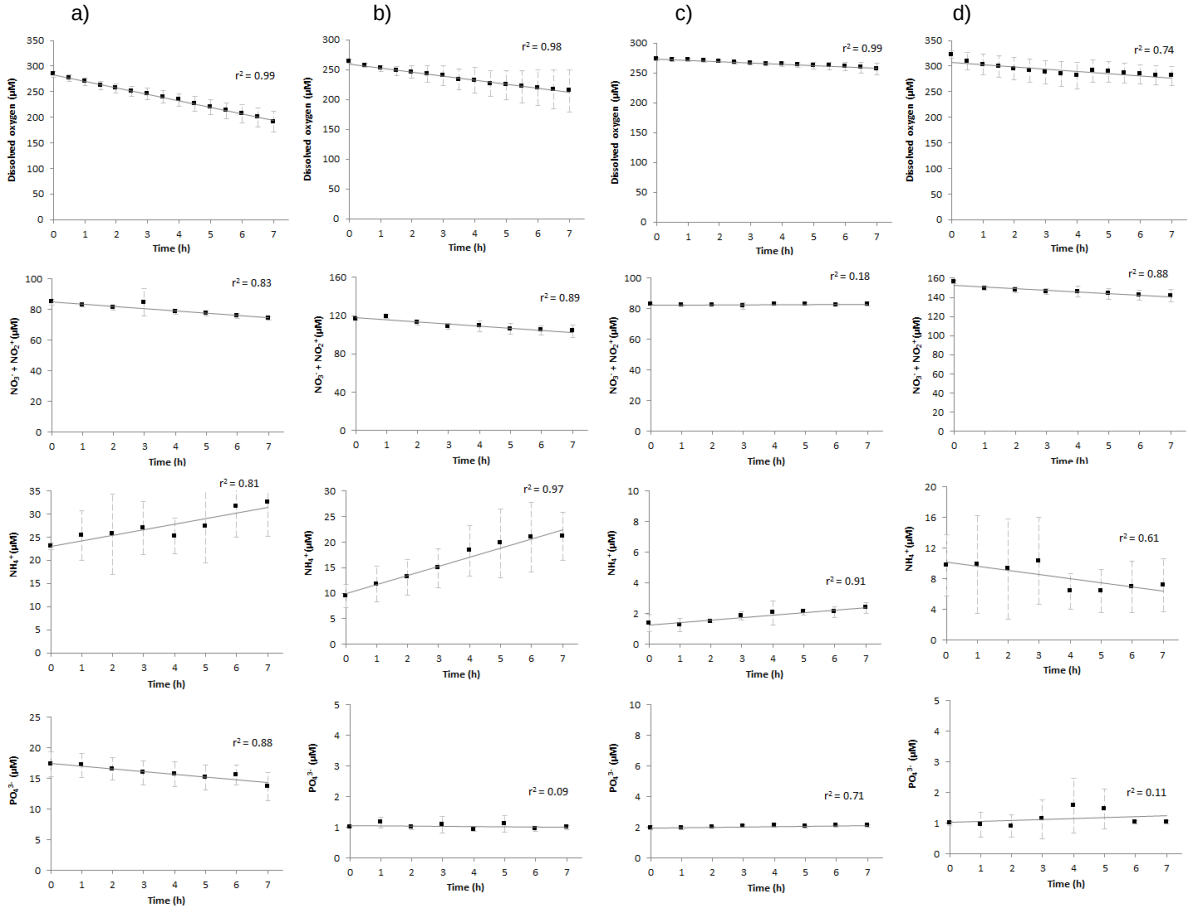

Additional content: Linear regression of mean concentration in oxygen and in nutrients with time inside the chambers for a) Re4, b) Re3, c) Re2 and d) Re1 sites.

Article 6: **Synergistic impacts of sediment contamination and dam presence on river' functioning**

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Abstract

1. Dam presence is commonly associated with strong accumulations of polluted sediments. In spite of this context of multiple stressors, physical effects are often solely considered in the ecological assessment of the dams impacts.

2. We studied four “reservoir/downstream reach” systems differing in levels of sediment contamination in reservoirs. Using assemblages and biotrait - i.e. ecological or biological attribute - responses of macroinvertebrate communities and leaf litter breakdown of *Alnus glutinosa*, we examined the individual effects and potential interactions between sediment contamination and dam presence along the gradient of ecotoxic pressure.

3. Leaf breakdown rates ranged from 0.0044 degree day^{-1} in the most contaminated reservoir to 0.0120 degree day^{-1} in the reference reservoir. Comparisons of community trait profiles among reservoirs highlighted a gradient of trait responses to sediment contamination.

4. In the absence of toxic contamination, the dam-induced modifications in biotraits of invertebrate’ assemblages were not related to a reduction of leaf litter breakdown. Conversely, contaminated sediment in reservoir induced strong functional disturbances (i.e. bioecological shifts and reduction of leaf litter breakdown) downstream of dams.

5. Key biotrait categories positively related to leaf litter breakdown rate, have been identified as “effect trait” categories. They corresponded mainly to shredders and/or small-sized (< 0.5 centimetres) insects, using aquatic (e.g. crawlers) or aerial (e.g. fliers) active dispersal strategies. In addition, trait categories, positively correlated to contamination level have been considered as “response” traits. They corresponded to large-sized (> 4 centimetres) species,

having several generations per year (polyvoltin) , using asexual reproduction and/or disseminating by drift (aquatic, passive)

6. In the current context of ecological continuity restoration, this study has identified the risks associated with the presence of historical contamination in the run-of-river reservoirs for downstream ecosystem health.

Keywords: multiple stressors - biotraits – breakdown rates –ecological continuity - macroinvertebrates

1. Introduction

The proliferation of industries in the 20th century has induced a strong increase in metal inputs in rivers which have led to large-scale degradation in freshwater communities. Despite increasing severity in environmental legislation and recent decrease of metal discharges, high concentrations of metals are still present in sediment, especially those that are fine grained (Cairns et al., 1984, Chapman, 1990, Brumbaugh et al., 2007). In addition to this permanent toxic pressure, the increasing need of water has led to river hydromorphology management including an excessive dams and weirs construction (Malmqvist and Rundle, 2002). These infrastructures drastically disturb sediment transport and resident biota, impair the physical and biological features of river channels (Petts, 1984, Stanford et al., 1996, Poff et al., 1997) and favour pollutant accumulation. Contaminated sediment are a significant, diffuse source of toxic contamination, and represent a serious threat to freshwater ecosystem ecological integrity and human health (Neal et al., 2005, Byrne et al., 2010). Even if the biological impacts of physical alterations on freshwater communities have been increasingly taken into account in the last decade, the ecological risk related to sediment contamination remains far less considered. However, in functional terms, sediments are an important part of bottom mosaics where invertebrates are involved in organic matter decomposition, nutrient cycling, carbon sequestration, and pollutant degradation (Groffman and Bohlen, 1999, Adams and Wall, 2000, Austen et al., 2002). Contaminated sediment could impair not only resident invertebrate communities, but also communities far from dams as toxicants can be transferred downstream during reservoir flush-outs or dam removal, leading to physical (e.g. interstitial space clogging) and chemical (e.g. metal toxicity) disturbances (Larsson, 1985, Asare et al., 2000, Coulthard and Macklin, 2003).

Sediment toxicity has been currently assessed by biotests which do not account for responses at the community level (Lafont et al., 2007). Traditionally, stream bioassessment methods have focused on benthic macroinvertebrate communities (Rosenberg and Resh, 1993) mainly involving taxonomy-based metrics that describe assemblage structure (Hering et al., 2006, Friberg et al., 2009). However, both “structure” and “function” should be simultaneously considered to efficiently assess the ecological integrity of rivers (Minshall, 1996, Gessner and Chauvet, 2002). Functional metrics can significantly contribute to a better assessment of stream ecosystem health because they (i) respond to many abiotic and biotic parameters, (ii) integrate environmental conditions over time and space, (iii) are more directly and easily translated in terms of ecosystem functioning than taxonomic metrics, (iv) simultaneously cover several habitats within streams and (v) are comparable at large spatial scale even across ecoregions that differ in their taxonomic composition (Feio et al., 2010).

One of the most common methods for assessing the pollutant impacts on ecosystem functioning is the measurement of leaf litter breakdown which can give evidence of functional changes in bacterial, fungal and invertebrate community composition and activity (Gessner and Chauvet, 2002; Woodward et al, 2012). It has been widely reported that leaf litter decomposition is reduced in waters impaired by metal contamination (Burton et al., 1985, Maltby and Booth, 1991, Carlisle and Clements, 2005). Biotraits-based approaches can also fundamentally improve diagnosis of anthropogenic impacts by (i) mechanistically understanding and inferring potential cause-effect relationships between stressors and biological impairments (Dolédec and Statzner, 2008, Verberk et al., 2008, Archaimbault et al., 2010, Culp et al., 2010) and (ii) partially resolving effects of multiple stressors (Statzner and Bêche, 2010, Schäfer et al., 2011). Moreover, the influence of macroinvertebrate trait combinations on leaf litter breakdown has been insufficiently explored, although they likely to be more powerful than taxonomic metrics in detecting and understanding the mechanistic basis of community diversity effects on decomposition processes (McKie et al., 2009, Schindler and Gessner, 2009, Gessner et al., 2010). The joint study of functional processes and biotrait changes in benthic communities would allow identifying the best response (to pressures) and effect (on ecosystem processes) traits to include into ecological and ecotoxicological risk assessment procedures for contaminated sediments of rivers.

Despite the ecological and ecotoxicological risks on resident and downstream communities, the run-of-river reservoirs have been very little studied. Yet, studying these systems provides an opportunity (i) to elucidate the mechanisms of community and ecosystem responses to

multiple (i.e. physical and chemical) stressors and (ii) to improve predictions about downstream impact of dams, especially in the case of contaminated sediment. The main objectives of this study were: 1) to distinguish functional changes specifically related to sediment contamination from those related to dam presence, 2) to identify effects of multiple stressors (i.e. physical constraints and toxic contamination) on downstream communities and 3) to compare taxonomic (taxa identity-based approach), functional (trait-based approach) and ecosystems (functional process approach) responses to these stressors. We hypothesized that sediment contamination in reservoirs enhances the impact of physical constraints on ecosystem functioning in the reservoirs but also in the downstream reaches due to downstream propagation.

2. Material and methods

2.1. Study sites

Four “reservoir/downstream reach” systems on the “Ain” and “Bienne” rivers belonging to the same ecoregion (Fig.1, Northern Jura-Prealps, France, Wasson et al., 2003) were selected to examine leaf litter breakdown rates and variation in assemblages and mean biotrait profiles of macroinvertebrate communities in response to both dam presence and contaminated sediment. According to the French National Agency for Water and Aquatic Environments (ONEMA), studied reservoirs are small (2 to 7 hectares) and come from weirs along the watercourse. In spring, the average flow of the Ain and Bienne rivers at the study sites were 7.80 m3s-1(± 3.44) and 5.27 (± 3.80) m3s-1, respectively. For the reference system (S1: Up1/Re1/Do1), we added an upstream site (Up1) to isolate the physical impact from the effects of sediment contamination on both the reservoir and downstream communities. The mean wet width of the study sites ranged from 19 to 35 metres in rivers and from 39 to 112 metres in reservoirs. The average depth of study sites ranged from 29 to 49 centimetres in rivers and from 69 to 141 centimetres in reservoirs. Although the watershed of both rivers is mainly forested (Ain: 57.3% and Bienne: 72.6%) and agricultural (Ain: 36.0% and Bienne: 22.0%; dairy exploitations), historical industrial activities, mainly in the upstream sector of the Bienne river, and paper mills along the Ain river, have led to the construction of dams and

to the discharge of many industrial effluents. The physico-chemical characteristics of sediments (Ekman grab, sampling depth of 20-30 centimetres) and water were measured by a specialized laboratory (LDA26, Valence, France) on samples collected during the spring field campaign according to international or national standards: for metals [ISO 11885 (Fe, Al, Mn, Zn) ; NF EN ISO 17294-2 (Cd, Cr, Co, Cu, Ni, Pb, As) and NF EN 1483 (Hg)] and for PAHs and PCBs (XP X33012 method). Concentrations of eleven metals, eight PCBs and ten PAHs were investigated in sediments. PCBs were always below their quantification limit (5µg/kg DM). The level of sediment contamination in a given reservoir was defined according to its mean rank for each pollutant concentration (mol.g-1). A higher rank represents a higher contamination level. The selected systems represented a significant gradient of sediment contamination in metals and PAHs (Friedman' test – $p < 0.001$), from the reference reservoir (Re1) to the most contaminated reservoir (Re4). Table 1 summarizes the main environmental characteristics of study sites.

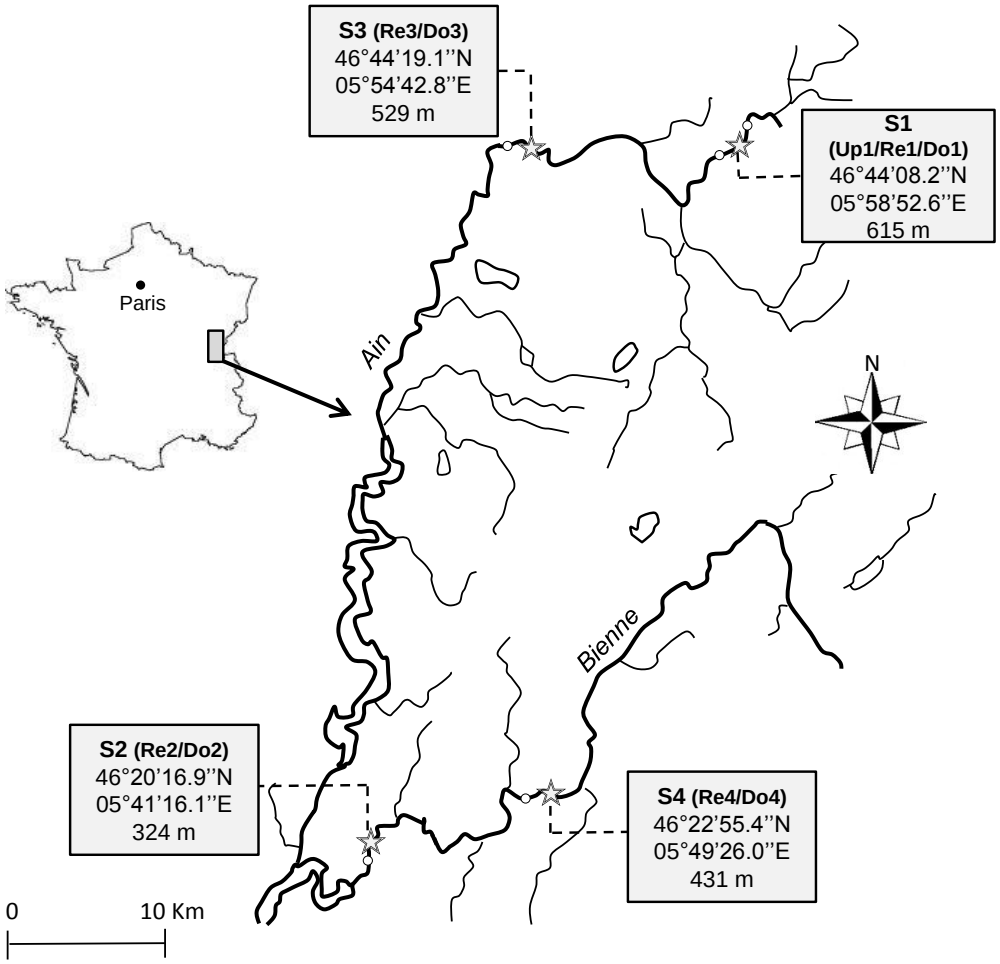

Fig.1: Location of the study systems in the Jura Mountains, eastern France. Stars correspond to the reservoir sites and circles represent river sites upstream or downstream from the dams.

		Reservoir sites (n=4)				River sites (n=5)				
		Re1	Re2	Re3	Re4	Up1	Do1	Do2	Do3	Do4
Water Chemistry	pH	8.10	8.50	8.10	8.20	8.10	8.20	8.15	8.35	8.20
	Dissolved oxygen	12.40	12.50	11.90	11.40	11.30	11.30	11.00	9.80	10.50
	Conductivity ($\mu S.cm^{-1}$)	416.00	329.00	305.00	364.00	412.00	411.00	347.00	361.00	325.00
	Calcium ($mg.L^{-1}$)	82.00	68.00	64.00	74.00	82.00	82.00	70.00	75.00	65.00
	Magnesium ($mg.L^{-1}$)	7.20	3.90	2.90	4.20	7.30	7.52	4.00	4.20	3.30
	Dissolved organic carbon ($mg.L^{-1}$)	1.40	1.70	1.80	1.80	1.50	1.40	1.70	1.70	1.80
	Biological Oxygen Demand ($mg.L^{-1}$)	<0.50	<0.50	0.60	<0.50	0.50	<0.50	0.50	0.70	0.60
	Phosphorus ($mg.L^{-1}$)	0.006	0.01	0.01	<0.005	<0.005	0.01	0.02	0.01	0.02
Metal contamination in sediments (mg $kgDW^{-1}$)	Aluminum (Al)	3.7×10^3	2.5×10^3	2.1×10^3	4.4×10^3	0.8×10^3	1.2×10^3	1.0×10^3	0.7×10^3	0.7×10^3
	Cadmium (Cd)	<0.20	<0.20	0.20	0.30	<0.20	<0.20	<0.20	<0.20	0.30
	Cobalt (Co)	3.40	2.50	2.30	3.40	2.10	2.50	1.90	1.40	1.40
	Iron (Fe)	9.9×10^3	4.9×10^3	3.9×10^3	7.0×10^3	4.5×10^3	7.3×10^3	4.4×10^3	1.7×10^3	2.2×10^3
	Lead (Pb)	9.10	11.50	32.00	23.90	4.90	4.70	16.10	82.90	18.80
	Arsenic (As)	10.60	4.60	4.90	5.90	8.70	11.40	3.50	4.10	3.30
	Chromium (Cr)	21.30	14.90	32.80	12.80	9.20	12.90	6.30	4.90	5.00
	Copper (Cu)	4.10	24.00	32.20	45.30	2.10	1.70	5.50	21.60	2.90
	Nickel (Ni)	9.40	10.80	16.90	6.50	5.10	5.90	4.90	4.30	3.10
	Zinc (Zn)	26.90	52.40	78.20	85.70	17.50	13.90	22.30	55.50	30.60
PAH Contamination in sediments (µg $kgDW^{-1}$)	Benzo(a)pyrene (BaP)	23.00	62.00	535.00	286.00	< 10	197.00	46.00	67.00	44.00
	Benzo(a)anthracene (BaA)	20.00	46.00	649.00	233.00	<10	<10	44.00	68.00	55.00
	Benzo(k)fluoranthene (BkF)	12.00	28.00	206.00	121.00	< 10	90.00	22.00	36.00	31.00
	Benzo(ghi)perylene (BgP)	5.00	47.00	43.00	133.00	< 10	153.00	28.00	46.00	36.00
	Fluoranthene (Fluo)	46.00	127.00	1919.00	545.00	< 40	443.00	105.00	161.00	130.00
	Indeno(1,2,3-cd)pyrene (Ind)	21.00	29.00	395.00	118.00	<10	108.00	18.00	36.00	33.00
	Phenanthrene (Phen)	<50	<50	<50	180.00	<50	119.00	<50	<50	63.00
General information	Surface (ha)	2.0	3.7	3.0	7.0					
	Dam types	Broad-crested	Broad-crested	Broad-crested	V-notch					
	Exploitation	out of use	in use	in use	in use					

Table 1: Main environmental characteristics of the selected study sites

2.2. Leaf litter breakdown

Senescent alder (*Alnus glutinosa*) leaves were collected from trees just before abscission in autumn 2009. Litter bags were made by placing 4 g (± 0,026) of air-dried leaves into mesh bags (15 x 20 cm, 5 mm mesh size) to allow stream biota access. In each site one iron bar was anchored to a sedimentary habitat and four bags were fastened to each bar during spring field campaign (2010). Data loggers were placed with the litter bags on each site to record water temperature every thirty minutes during the experiment. Bags were retrieved after 40 days and returned to the laboratory. The leaves were individually rinsed with water from the corresponding stream to remove fine particulate matter and invertebrates. The remaining leaf material was oven-dried to constant mass (105°C, 48h) and weighed to the nearest 0.1 mg. Subsamples (500 mg) were ignited in a muffle furnace (550°C, 4h) to relate dry mass to ash-free dry mass (AFDM). Four additional leaf bags were kept in laboratory before starting the experiment to estimate the initial oven-dried mass and AFDM of all leaf bags.

2.3. Macroinvertebrate communities

Taxon	Up1	Re1	Do1	Re2	Do2	Re3	Do3	Re4	Do4
*Allogamus**	+	+	+	+		+	+	+	
*Amphinemura**	+	+	+	+	+	+	+	+	+
Ancylus	+	+	+		+	+	+	+	+
Antomyidae*	+	+	+	+	+	+	+	+	+
*Asellus aquaticus**		+		+	+		+	+	
Atherix	+	+	+	+	+	+	+	+	+
Baetis	+	+		+	+	+	+	+	+
*Brychius**			+	+	+				
*Caenis**			+	+	+	+	+		
Ceratopogonidae	+			+	+	+	+	+	+
Chironomini*	+	+	+	+	+	+	+	+	+
Clinocerinae	+	+		+	+	+	+	+	+
Dendrocoelum			+	+					
*Drusus**						+			+
Dugesia	+	+		+		+	+	+	
Dytiscidae*	+	+	+	+	+	+			+
*Ecdyonurus**	+	+	+	+	+	+	+	+	+
*Elmis**	+	+		+	+	+	+	+	+
Epeorus	+						+		
*Ephemera**	+	+	+	+		+	+	+	+
Ephemerella	+	+	+	+	+	+	+	+	+
Erpobdella			+	+		+	+		
*Esolus**	+	+	+	+	+	+	+	+	+
*Gammarus**	+	+		+	+	+	+	+	+
Glossiphonia		+		+	+	+	+	+	+
Glossosoma	+	+		+	+				
Gordius	+	+				+			
*Halesus**	+		+		+	+	+		
Helobdella						+			+
Hemerodromiinae	+	+	+	+	+	+	+	+	+
Heptagenia									
Hydra	+	+	+			+			
Hydracarina*	+	+	+	+	+	+	+	+	+
*Hydraena**	+		+	+		+		+	+
Hydropsyche	+	+	+	+	+		+		
Hydroptila	+	+		+	+	+	+		+
*Lasiocephala**				+	+	+	+		+
*Lepidostoma**				+		+	+		
*Leptophlebia**		+	+	+	+	+	+		
*Leuctra**	+	+	+	+	+	+	+	+	+
*Limnephilus**		+	+			+	+		
*Limnius**	+	+	+	+	+	+	+	+	+
Limoniidae*	+	+	+	+	+	+	+	+	+
Liponeura			+	+					+
Lymnaeidae*		+		+	+	+	+	+	+
Micronecta				+	+	+	+	+	
*Micropterna**	+	+	+	+	+	+		+	
Nematoda	+	+		+		+	+	+	+
Oligochaeta	+	+		+	+	+	+	+	+
*Odontocerum**	+		+				+		+
Orthocladiinae	+	+		+	+	+	+	+	+
*Oulimnius**	+	+	+	+	+	+	+	+	+
*Paraleptophlebia**	+			+		+	+		
Perlidae*	+	+	+				+		
Perlodidae*	+	+	+			+	+		
Polycelis	+	+	+	+	+	+	+		
Polycentropus	+	+		+	+	+	+	+	+
*Potamopyrgus**			+				+		
*Protonemura**	+		+	+	+		+		+
*Psychoda**	+	+		+	+	+	+	+	+
Psychomyia	+	+	+	+	+	+	+	+	+
Rhithrogena	+	+		+	+	+	+		+
Rhyacophila	+	+	+	+	+		+		+
*Riolus**	+	+	+	+	+	+	+	+	+
*Sericostoma**	+	+	+	+	+	+	+	+	+
Sialis		+				+			
Simuliidae	+	+	+	+	+		+		+
Siphlonurus				+	+	+	+	+	+
Sphaerium	+		+			+	+	+	
*Stenophylax**			+			+	+		+
Tanypodinae	+	+		+	+	+	+	+	+
Tanytarsini*	+	+	+	+	+	+	+	+	+
Tipulidae*		+		+		+		+	
Torleya	+	+	+	+	+	+	+		+
Total abundance of shredders									
0.2 < frequency < 0.5	165	787	1194	595	718	870	485	94	484
0.5 < frequency < 0.7	425	611	46	132	74	216	164	44	68
frequency > 0.7	552	882	33	112	238	435	569	32	223

Table 2: Lists of the taxa identified in study sites. Taxa with a star correspond to taxa considered as shredder for at least 20% of their feeding habits. The site abundances of shredders were given according to three categories: 'strict' shredders (relative frequency of 'shredding' > 0.7 in the taxon feeding habit profile) to 'occasional' shredders (0.2 < relative frequency <0.5).

Macroinvertebrates were sampled during the spring campaign (2010) following two protocols. In reservoirs, macroinvertebrates were sampled using an original protocol (Colas *et al.*, 2011). Reservoirs were subdivided into three zones, termed "tail", "middle" and "dam" reflecting their various hydraulic and hydro-morphological conditions. Communities of the banks and of the channel were sampled separately. Three to four samples were performed on the left and right banks of each zone using a Surber net. Macroinvertebrates in the channel were sampled by dredging from a boat perpendicular to a transect in each of the three areas defined above. In river sites, macroinvertebrates were sampled according to a normalized protocol (Multi-Habitat Sampling, norm XP T 90-333 in AFNOR, 2009) designed to fulfil the European Water Framework Directive (WFD) requirements. All samples were preserved in 4% formalin in the field and transferred to the laboratory where they were sieved and sorted. Organisms were mainly identified at genus level (using Tachet *et al.*, 2000), except for some groups, which were identified at higher taxonomic level [i.e. Diptera

(family or tribe level) and Oligochaeta or Nematoda]. Individuals within each taxon were then counted. The rare taxa - with less than 3 individuals catch during the sampling program - were not included in the analysis of faunal data. Due to the heterogeneity of site sampling protocols (see above), the abundances of taxa were transformed in densities taking into account the sampled area for each sample unit, in order to allow between-sample and between-site comparisons. From taxonomic data (Table 2), we calculated site community mean biotrait profiles, thanks to twenty two fuzzy-coded biological and ecological traits (Chevenet *et al.*, 1994; named biotraits hereafter) described for each taxon from literature. The biological traits reflect the life history of taxa (e.g. 'number of cycles per year'), their resistance and resilience abilities (e.g. 'resistance forms'), and general morphological ('body form') or physiological (e.g. 'respiration', 'feeding habits') features of organisms (Usseglio-Polatera *et al.*, 2000). Ecological traits mainly describe habitat preferences of taxa at different spatial scales (e.g. substrate, current velocity, temperature, pH, saprobity, longitudinal distribution). Each trait is described by a set of categories (named modalities). The mean weighted (by log-transformed abundances) trait profiles of site assemblages were calculated and expressed as relative abundance distributions of trait categories within the assemblages (Thioulouse *et al.*, 1997).

2.4. Statistical analyses

Leaf breakdown rates (k) were estimated by fitting the AFDM data with the exponential model: $k = \frac{1}{t} \times \ln\left(\frac{M_t}{M_0}\right)$ where (i) M_t is the leaf litter AFDM (g) remaining at time t, (ii) M_o is the initial AFDM at the beginning of the experiment and (iii) t is the sum of the mean daily temperatures (in degrees) during the whole experiment. The degree days model was used to account for potential differences in temperature between the reservoir and river sites. During the experiment, temperature ranged from 10.56 °C (± 0.03) for S1 to 13.27 °C (± 0.43) for S3 on the Ain river and from 12.46 °C (± 0.13) for S2 to 12.61 °C (± 0.66) for S4 on the Bienne river. Partial least-squares (PLS) regression (Abdi, 2003) analysis was carried out to identify abiotic factors significantly controlling leaf litter breakdown rates in reservoirs and downstream river reaches, independently. The generated variable importance in the projection (VIP) values reflects the importance of each variable in the model, with VIP > 0.7 indicating

important predictors (Eriksson *et al.*, 1999). Synthetic variables concerning sediment contamination in metals and PAHs in reservoirs were added in the PLS analysis for leaf breakdown rates at downstream sites to examine importance of contamination of associated reservoirs sites for leaf breakdown rates downstream. These synthetic variables correspond to mean concentrations in PAHs and in metals (mole.g^{-1} sediment) for each reservoir. The AFDM remaining were compared between stations by a one-way ANOVA and a Tukey's HSD post-hoc test (after testing normality and homoscedasticity). In addition, simple linear models were built to examine the relationship between the metallic and the organic contaminations and leaf litter breakdown rates across all the stations. Contamination levels were determined using the mean concentrations (mole.g^{-1} sediment) in "metals" and "organic pollutants" that emerged from the PLS analysis. To explore taxonomic responses, a complete-link clustering analysis was performed based on the Bray-Curtis similarity calculated between site assemblages. "Between-sites" comparisons of trait' category utilization was performed with one-way ANOVAs after arcsin ($\sqrt{p}$) transformation (normality and homoscedasticity being respected). Significant differences were evaluated after Bonferroni correction of p-values. Percentages of similarity (Jaccard distance) used for complete-link clustering analysis were calculated on the basis of trait categories exhibiting a significant "between-sites" difference. Finally, Spearman correlation coefficients were used to explore relationships between trait categories, sediment contamination and leaf litter breakdown rates. We used Simca-P 9.0 (Umetrics AB) for the PLS analyses and R software (R development Core Team, 2008) for the other analyses.

3. Results

3.1. Leaf breakdown rates

3.1.1. Site comparisons

Leaf breakdown rates ranged from 0.0044 degree day-1 in the most contaminated reservoir (Re4) to 0.0120 degree day-1 in the reference reservoir (Re1). Significant "between-sites" differences ($p < 0.001$) in breakdown rates were evidenced, independently of the habitat type (i.e. reservoirs vs. streams) but probably related to the sediment contamination level (Fig.2). Three groups of sites were distinguished. The first group corresponded to the sites with the highest breakdown rate including the reference sites (S1) and the reservoir with an intermediate contamination level (Re2). The second group gathered the sites with lower

breakdown rates (28% ± 10 of remaining AFDM) that are the three reaches downstream from contaminated reservoirs (Do2, Do3 and Do4) and one contaminated reservoir (Re3). The reservoir subjected to strong sediment contamination (Re4) exhibited a very low breakdown rate (55% of remaining AFDM).

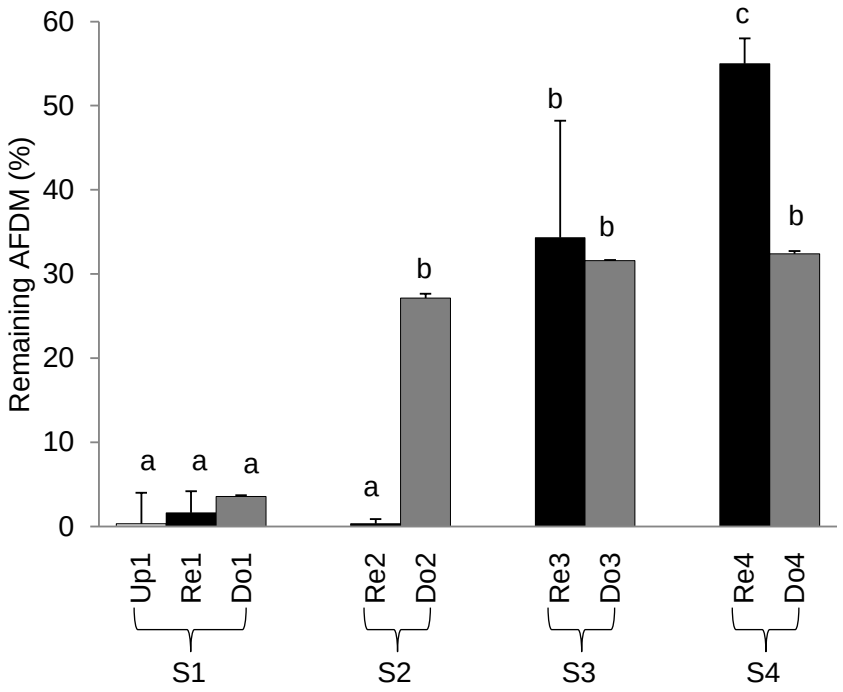

Fig.2: Mean percentages of leaf litter mass remaining after the 40 days litter bag experiment. Black bars correspond to reservoir stations, dark grey bars to downstream stations and for the first couple, the clear grey bar to the upstream station. Letters correspond to significantly different groups identified by one-way ANOVA and Tukey's HSD post-hoc test.

3.1.2. Physico-chemical predictors of leaf litter breakdown rates

Although no clear pattern was evidenced between leaf litter breakdown rate and habitat type, the best physicochemical predictors of leaf litter breakdown differed in reservoirs vs. downstream reaches (Table 3). In reservoirs, the best predictive descriptors were dissolved oxygen, zinc, benzo(ghi)perylene, magnesium, copper, water conductivity and calcium concentration. In downstream reaches, the parameters that best explained leaf litter breakdown rates were the Biochemical Oxygen Demand (B.O.D), magnesium concentration, dissolved oxygen, water conductivity and benz(a)anthracene concentration. Only five and three contaminants for the reservoirs and their downstream reaches respectively were selected by the PLS for having an influence on leaf litter breakdown rates. However, dam contamination (both metals and organic compounds) exhibited high influence on breakdown rates observed downstream reaches. Considering the nine sites, leaf litter breakdown rates

exhibited a strong negative relationship with metal contamination levels in sediments (n=9, R2 =0.74, p <0.001, Fig.3). No significant relationship was found with the PAH contamination levels.

Variables	Loadings VIP	Component 1 (R^2 = 54%)	Component 2 (R^2 = 24%)	Loadings VIP	Component 1 (R^2 = 74%)	Component 2 (R^2 = 13%)
Copper	1.11	-0.32	-0.23			
Nickel	0.68	-0.25	0.33			
Zinc	1.27	-0.36	-0.22	0.84	-0.30	0.25
Metals in dams				1.04	-0.33	-0.20
Benz(a)anthracene				1.01	-0.33	0.09
Benzo(ghi)perylene	1.23	-0.39	0.10			
PAHs in dams				0.79	-0.26	0.19
Calcium	1.00	0.36	-0.31	0.95	0.34	-0.36
Conductivity	1.00	0.36	-0.30	1.03	0.36	-0.19
Biological oxygen demand				1.20	-0.33	-0.42
Magnesium	1.12	0.38	-0.16	1.12	0.37	0.00
Dissolved oxygen	1.34	0.37	0.20	1.07	0.23	0.65
Phosphorous				0.89	-0.32	0.47

Table 3: Loadings of the two PLS performed for reservoirs and downstream stations predicting leaf litter breakdown rates from physico-chemical variables. Predictors with a negative sign contribute negatively to litter decomposition.

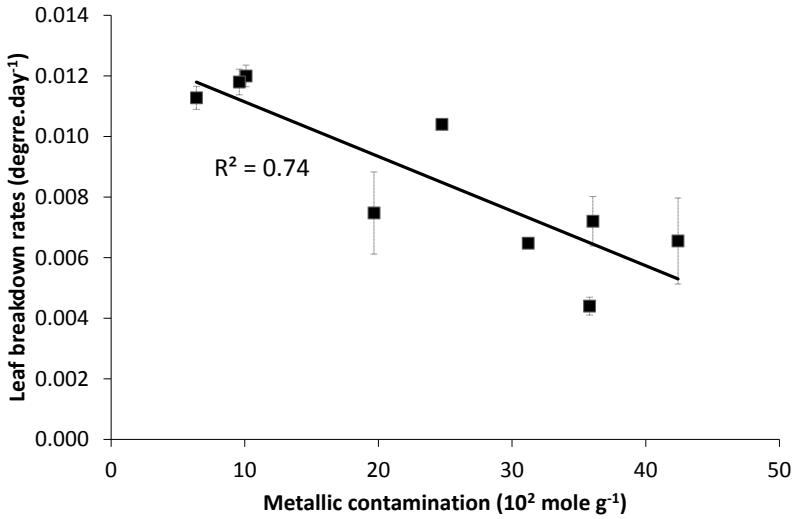

Fig.3: Linear relationship between leaf litter breakdown rates and mean concentration in metals in sediments (mole.g-1).

3.2. Taxonomic and functional responses of macroinvertebrate communities

The cluster analysis (Fig.4a) performed on the Bray-Curtis dissimilarity matrix between the assemblages of sites highlighted five groups of sites. The first group evidenced the similarity between assemblages found upstream the reference reservoir (Up1), downstream the most

contaminated reservoir (Do4) and downstream the reservoir with an intermediate contamination (Do2). The second group associated assemblages of two contaminated reservoirs (Re2 and Re3) and of a site downstream a contaminated reservoir (Do3). The three last groups isolated assemblages of reference reservoir (Re1), of the most contaminated reservoir (Re4), and of site downstream the reference reservoir (Do1), respectively. The cluster analysis (Fig.4b) performed on the Jaccard distance matrix between the mean biotrait profiles of stations highlighted three distinct groups of sites. The first group corresponded to the reference system, with a higher similarity between Up1 and Re1 than between Up1 and Do1. A second group highlighted the high similarity between the three reaches located downstream from contaminated reservoirs gathered with sites located in two intermediately contaminated reservoirs (Re2 and Re3). Finally, the third group isolated the most contaminated station, Re4.

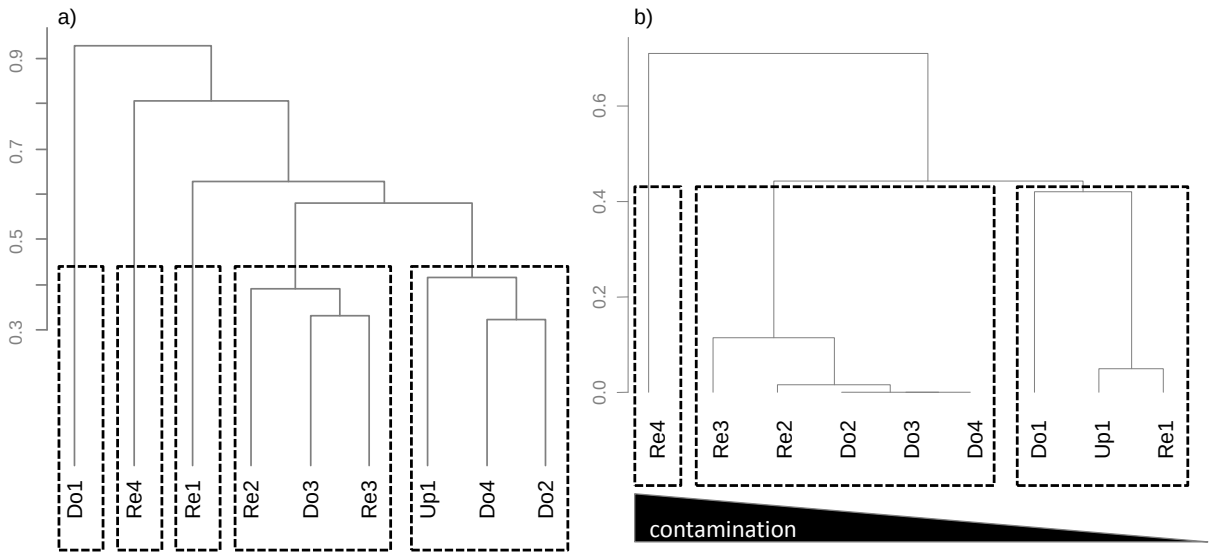

Fig.4: Dendrograms illustrating the results of the classification analyses performed on nine study site macroinvertebrate assemblages according to their (a) taxonomic abundances using the complete-link method on a Bray-Curtis dissimilarity index matrix, (b) mean trait profiles using the complete-link method on a Jaccard distance matrix. .

For precisely elucidating the bioecological shifts identified by the cluster analysis, we compared the trait profiles of:

- Re1 vs. Re2/Re3 and Re1 vs. Re4 to evaluate shifts related to the contamination gradient in reservoir sediment and similarly Do1 vs. Do2/Do3/Do4 to compare downstream stations (see section 3.2.1).

- Up1 vs. Re1 and Up1 vs. Do1 to evaluate shifts only related to physical disturbance (see section 3.2.2).

3.2.1. Bioecological responses to contamination levels

Comparisons of community trait profiles among reservoirs (Table 4a) highlighted a gradient of trait responses to sediment contamination. If few significant differences were observed between the reference and the two moderately contaminated reservoirs (similarity = 0.74), clear contrasts were evidenced between the reference and the highly contaminated reservoir (similarity = 0.44). Nevertheless, in contrast with leaf litter breakdown investigations, Re2 was associated with the biotrait profiles of stations exhibiting an intermediate contamination level (Fig. 4b). The reference reservoir community was characterized by a higher proportion of shredders and/or organisms without resistance forms exhibiting affinity for gravel and living in the river channel of oligotrophic habitats. In contrast, faunal assemblages from the two moderately contaminated reservoirs consisted of a higher proportion of organisms that were thermophilic, deposit-feeders, reproducing by free eggs or clutches, producing statoblasts or using larval diapause as resistance stages in harsh environmental conditions and/or disseminating by drift. The benthic assemblage of the most heavily impaired reservoir was composed of more organisms that were large-sized (> 4 cm) with tegumental respiration. The relative abundance of parasites, limnophilic, polysaprobic organisms or species using cocoons as resistance stages were higher than in other reservoirs. Taxa found in these reservoirs are often described as colonizing lentic (e.g. ponds) and eutrophic habitats. Finally, in both moderately and heavily contaminated reservoirs, shredder abundance significantly decreased, as well as organisms without resistance form or living in the river. Sediment contamination also reduces the proportion of organisms with active dispersal.

The “between-sites” comparison of the downstream stations revealed significant differences between the reference station vs. stations downstream contaminated reservoirs. The functional similarity (1.0) of impaired downstream reaches was already observed in leaf decomposition rates. The benthic assemblages of impaired downstream reaches included many deposit feeders and acidification sensitive organisms (Table 4b). In contrast, the invertebrate assemblage of the reach downstream reference reservoir contained more shredders and predators, and more eurythermic organisms.

Traits	Categories	Re1	Re2	Re3	Re4	Re1 *vs* Re2/Re3	Re1 *vs* Re4
Aquatic stages	Larva	0.38 (0.03)	0.43 (0.04)	0.40 (0.04)	0.31 (0.07)	NS	↘
Current velocity	Fast	0.21 (0.04)	0.16 (0.01)	0.16 (0.03)	0.11 (0.05)	NS	↘
Current velocity	Medium	0.32 (0.04)	0.33 (0.03)	0.32 (0.06)	0.26 (0.04)	NS	↘
Current velocity	Null	0.14 (0.07)	0.15 (0.05)	0.19 (0.09)	0.28 (0.05)	NS	↗
Dispersal	Aerial active	0.22 (0.11)	0.21 (0.06)	0.13 (0.07)	0.12 (0.06)	NS	↘
Dispersal	Aerial passive	0.04 (0.03)	0.13 (0.06)	0.13 (0.07)	0.12 (0.06)	↗	↗
Dispersal	Aquatic active	0.27 (0.08)	0.23 (0.05)	0.23 (0.07)	0.17 (0.05)	NS	↘
Feeding habits	Deposit feeder	0.28 (0.24)	0.51 (0.12)	0.43 (0.19)	0.44 (0.24)	↗	NS
Feeding habits	Parasite	0.01 (0.02)	0.03 (0.02)	0.03 (0.02)	0.28 (0.31)	NS	↗
Feeding habits	Scraper	0.29 (0.13)	0.25 (0.06)	0.23 (0.10)	0.14 (0.11)	NS	↘
Feeding habits	Shredder	0.35 (0.16)	0.10 (0.07)	0.17 (0.11)	0.06 (0.06)	↘	↘
Food	Dead animal	0.04 (0.03)	0.01 (0.008)	0.02 (0.02)	0.009 (0.01)	↘	↘
Food	Vegetal detritus	0.14 (0.08)	0.14 (0.06)	0.11 (0.06)	0.03 (0.04)	NS	↘
Food	Macroinvertebres	0.08 (0.05)	0.05 (0.03)	0.07 (0.04)	0.28 (0.30)	NS	↗
Food	Microphytes	0.31 (0.10)	0.27 (0.04)	0.27 (0.07)	0.20 (0.07)	NS	↘
Locomotion	Crawler	0.52 (0.21)	0.50 (0.15)	0.44 (0.20)	0.27 (0.12)	NS	↘
Locomotion	Fixed	0.04 (0.05)	0.05 (0.03)	0.08 (0.05)	0.17 (0.12)	NS	↗
Locomotion	Flier	0.03 (0.02)	0.01 (0.01)	0.008 (0.007)	0.003 (0.007)	↘	↘
Longitudinal distribution	Hyporithron	0.17 (0.03)	0.18 (0.01)	0.18 (0.03)	0.13 (0.03)	NS	↘
Longitudinal distribution	Metarithron	0.21 (0.04)	0.19 (0.02)	0.17 (0.02)	0.13 (0.03)	↘	↘
Longitudinal distribution	Outside system	0.07 (0.02)	0.13 (0.03)	0.11 (0.03)	0.14 (0.04)	↗	↗
Maximal size	≥ 4 cm	0.15 (0.21)	0.14 (0.14)	0.18 (0.19)	0.43 (0.19)	NS	↗
Reproduction	Free cluctches	0.03 (0.04)	0.12 (0.08)	0.10 (0.09)	0.09 (0.11)	↗	NS
Reproduction	Ovoviviparity	0.19 (0.21)	0.04 (0.02)	0.15 (0.16)	0.02 (0.03)	↘	↘
Resistance forms	Cocoons	0.09 (0.13)	0.09 (0.08)	0.12 (0.12)	0.26 (0.11)	NS	↗
Resistance forms	Diapause	0.04 (0.03)	0.15 (0.05)	0.12 (0.05)	0.10 (0.06)	↗	NS
Resistance forms	Egg statoblasts	0.07 (0.07)	0.21 (0.06)	0.16 (0.08)	0.03 (0.04)	↗	NS
Resistance forms	None	0.79 (0.11)	0.57 (0.09)	0.64 (0.09)	0.60 (0.11)	↘	↘
Respiration	Gill	0.39 (0.22)	0.39 (0.13)	0.38 (0.18)	0.12 (0.09)	NS	↘
Respiration	Plastron	0.08 (0.06)	0.03 (0.02)	0.02 (0.02)	0.008 (0.02)	↘	↘
Respiration	Tegument	0.51 (0.23)	0.54 (0.13)	0.56 (0.20)	0.86 (0.09)	NS	↗
Saprobity	Mesotrophic	0.41 (0.05)	0.46 (0.05)	0.45 (0.05)	0.34 (0.09)	NS	↘
Saprobity	Oligosaprobic	0.32 (0.06)	0.30 (0.03)	0.31 (0.06)	0.24 (0.06)	NS	↘
Saprobity	Xenosaprobic	0.13 (0.05)	0.12 (0.03)	0.08 (0.04)	0.06 (0.04)	NS	↘
Saprobity	α-mesosaprobic	0.18 (0.09)	0.19 (0.05)	0.24 (0.07)	0.29 (0.06)	NS	↗
Substrate preferences	Gravel	0.18 (0.02)	0.13 (0.02)	0.14 (0.02)	0.16 (0.02)	↘	NS
Substrate preferences	Litter	0.11 (0.04)	0.09 (0.009)	0.09 (0.02)	0.05 (0.02)	NS	↘
Substrate preferences	Mud	0.06 (0.04)	0.09 (0.03)	0.09 (0.05)	0.12 (0.02)	NS	↗
Substrate preferences	Roots	0.09 (0.03)	0.11 (0.03)	0.11 (0.04)	0.04 (0.03)	NS	↘
Substrate preferences	Sand	0.10 (0.02)	0.10 (0.02)	0.10 (0.03)	0.13 (0.02)	NS	↗
Temperature	Eurythermic	0.68 (0.05)	0.65 (0.03)	0.68 (0.07)	0.48 (0.15)	NS	↘
Temperature	Warm	0.07 (0.05)	0.19 (0.04)	0.17 (0.04)	0.14 (0.03)	↗	↗
Transversal Distribution	Channel	0.34 (0.11)	0.21 (0.04)	0.23 (0.09)	0.12 (0.03)	↘	↘
Transversal Distribution	Ponds	0.07 (0.02)	0.08 (0.03)	0.09 (0.04)	0.20 (0.08)	NS	↗
Trophic status	Eutrophic	0.09 (0.10)	0.15 (0.06)	0.17 (0.09)	0.24 (0.07)	↗	↗
Trophic status	Oligotrophic	0.49 (0.09)	0.38 (0.03)	0.37 (0.06)	0.42 (0.013)	↘	NS

4a)

Table 4: Relative frequencies of biotrait categories (with standard deviation) identified as significantly different by one-way ANOVAs and Tukey's HSD post-hoc tests performed a) on reservoir biotrait profiles (Re1 vs. Re2/Re3 and Re4) and b) on downstream biotrait profiles (Do1 vs. Do2/Do3/Do4). Each trait category utilization frequency in Re2/Re3 and Re4 or Do2/Do3 and Do4 was compared to that in the 'reference reservoir' (Re1) or 'downstream reach' (Do1) community, respectively. The difference was illustrated by an arrow, when the p-value (after Bonferroni correction) was significant: upward = "increasing in comparison with Re1 or Do1" or downward = "decreasing in comparison with Re1 or Do1".

Traits	Categories	Do1	Do2	Do3	Do4	Do1 *vs* Do2/3/4
Food	Dead animal	0.06 (0.03)	0.02 (0.02)	0.02 (0.01)	0.009 (0.01)	↘
Feeding habits	Deposit feeder	0.11 (0.04)	0.31 (0.16)	0.33 (0.14)	0.39 (0.17)	↗
Locomotion	Flier	0.04 (0.02)	0.01 (0.01)	0.006 (0.007)	0.01 (0.01)	↘
Number of reproductive cycle/year	< 1	0.11 (0.05)	0.03 (0.02)	0.03 (0.03)	0.01 (0.02)	↘
Feeding habits	Predator	0.18 (0.11)	0.04 (0.03)	0.08 (0.05)	0.03 (0.01)	↘
Feeding habits	Shredder	0.36 (0.09)	0.16 (0.17)	0.13 (0.09)	0.10 (0.10)	↘
Low pH sensitivity	> 4 to 4.5	0.04 (0.01)	0.09 (0.02)	0.09 (0.02)	0.09 (0.02)	↗
Low pH sensitivity	> 5 to 5.5	0.17 (0.02)	0.21 (0.02)	0.21 (0.02)	0.21 (0.02)	↗
Low pH sensitivity	> 6	0.46 (0.06)	0.30 (0.05)	0.30 (0.03)	0.29 (0.03)	↘
Temperature	Eurythermic	0.74 (0.05)	0.64 (0.09)	0.65 (0.05)	0.59 (0.05)	↘

4b)

3.2.2. Bioecological responses to dam presence

The macroinvertebrate bioecological trait profile of reference upstream (Up1) and reference reservoir (Re1) were highly similar (similarity = 0.98), even if flow reduction in the reservoir induced a significant decrease of macroinvertebrate taxa sensitive to low pH (Table 5). The dam induced a decline of taxa from springs (i.e. crenon) and a drastic decrease in organic contamination sensitive taxa (oligosaprobic) and organisms sensitive to low pH without resistance forms and/or living in cold water. In contrast, an increase in species tolerant to organic contamination (α-mesosaprobic) and/or living in lowlands reaches, potentially using diapause or dormancy and feeding as predator, was observed in downstream site. The global similarity proportion with the upstream station was 0.82.

Traits	Categories	Up1	Re1	Do1	Up1 *vs* Re1	Up1 *vs* Do1
Altitude	Lowlands	0.55 (0.08)	0.60 (0.09)	0.72 (0.04)	NS	↗
Feeding habits	Predator	0.04 (0.02)	0.04 (0.03)	0.18 (0.11)	NS	↗
Longitudinal distribution	Crenon	0.12 (0.02)	0.11 (0.02)	0.75 (0.01)	NS	↘
Low pH sensitivity	> 4 to 4,5	0.09 (0.03)	0.05 (0.02)	0.03 (0.01)	↘	↘
Low pH sensitivity	> 6	0.29 (0.05)	0.34 (0.04)	0.46 (0.06)	NS	↗
Resistance forms	None	0.78 (0.09)	0.79 (0.01)	0.59 (0.12)	NS	↘
Resistance forms	Diapause	0.06 (0.04)	0.04 (0.02)	0.19 (0.08)	NS	↗
Saprobity	α-mesosaprobic	0.11 (0.01)	0.18 (0.04)	0.23 (0.03)	NS	↗
Saprobity	Oligosaprobic	0.37 (0.05)	0.32 (0.06)	0.28 (0.05)	NS	↘
Temperature	Cold	0.33 (0.06)	0.25 (0.04)	0.15 (0.04)	NS	↘

Table 5: Relative frequencies of biotrait categories (with standard deviation) identified as significantly different by one-way ANOVAs and Tukey's HSD post-hoc tests performed to describe the impact of flow modification on the reservoir community (Up1 vs. Re1) and the impact of dam presence on the downstream river community (Up1 vs. Do1). Each trait category utilization frequency in Re1 or Do1 was compared to that in the upstream community (Up1). The difference was illustrated by an arrow, when the p-value (after Bonferroni correction) was significant: upward = "increasing in Re1 or Do1" or downward = "decreasing in Re1 or Do1".

3.3. Towards response and effect biotrait categories

The study of the relationship between trait categories, sediment contamination and leaf breakdown rates has allowed identifying response and effect trait categories (Table 6). First, key biotrait categories related to the functional processes, i.e. negatively correlated to contamination and positively correlated to breakdown rate, have been identified. These trait modalities were: “shredder”, “channel” and “metarithron” as habitat features, “< 0.5 centimetres” as maximal potential size, and “aquatic active” or “aerial active” as dispersal strategies. All these traits categories are some bio/ecological attributes of key invertebrate taxa participating in the leaf litter decomposition processes. In addition, a combination of trait categories was more indicative of disturbance, i.e. was positively related to contamination and negatively related to leaf breakdown rate including “large-sized” (i.e. maximal size > 4 cm), “polyvoltin”, “asexual reproduction”, “aquatic passive” dispersal, “tegumental” respiration mode and “microorganism” as food. These trait categories mainly corresponded to taxa more tolerant to toxic and organic contamination, such as Chironomidae, Oligochaeta and Nematoda.

		Response categories		Effect categories
		metals	organic	rates
Maximal size (cm)	< 0.5	-0.76*	-0.67	0.76*
Maximal size (cm)	> 4	NS	0.81*	-0.70
Number of reproductive cycles	> 1 per year	0.72	NS	-0.88**
Aquatic stages	Egg	-0.71	NS	0.73
Reproduction	Asexual	0.73	0.74	-0.72
Dispersal	Aquatic passive	NS	0.76	-0.69
Dispersal	Aquatic active	-0.73	-0.84*	0.83*
Dispersal	Aerial active	-0.69	-0.81*	0.84*
Respiration	Tegument	NS	0.85*	-0.75
Respiration	Plastron	-0.93**	NS	0.92**
Locomotion	Flier	-0.89*	NS	0.90**
Locomotion	Crawler	-0.71	-0.77	0.83**
Locomotion	Attached	NS	0.78	-0.86*
Food	Microorganism	0.76	0.69	-0.68
Food	Dead plant	NS	-0.69	0.67
Food	Dead animal	-0.72	NS	0.73
Feeding habits	Shredder	-0.79*	NS	0.82*
Transversal distribution	River channel	-0.79*	-0.76	0.88**
Longitudinal distribution	Metarithron	-0.73	-0.75	0.86*

Table 6: Spearman’ correlations between biotrait categories and sediment contamination (response categories) and leaf litter breakdown rates (effect categories). Trait categories with a positive sign increase with the contamination for response trait categories and contributed positively to litter decomposition for effect trait categories. * p-value < 0.01; ** p-value < 0.001; NS = no significant.

3.4. Sensitivity of the different approaches in detecting disturbances

The different approaches used in this study allowed us to highlight the impacts of the different stressors independently (Table 7). The study of macroinvertebrate community structure did not evidence any structuring effect of the levels of sediment contamination and the presence of dam. In contrast, the similarity of sites according to biotrait profiles has permitted to distinguish dam impacts from those of sediment contamination as well as cumulated impacts of dam presence and contaminated sediment. Although dam presence did not significantly impacted leaf litter breakdown, sediment contamination and the synergy of both perturbations led to disturbance in achievement of this ecosystem process.

	Approaches		
	Communities		Ecosystem
	Taxonomic	Functional	Leaf breakdown
Physical perturbation	No	Yes	No
Ecotoxic perturbation	No	Yes	Yes
Multiple stressor	No	Yes	Yes

Table 7: Synthetic table summarizing the abilities of each approach applied in this study to detect individual effects of the physical and ecotoxic perturbations, in a multi-stressor context.

4. Discussion

Examining the ecological impact of selected dam on running rivers allowed to discriminate between physical effects related to flow alteration and toxic effects due to toxicant accumulation in sediment. In particular, investigating biotrait profiles of benthic invertebrate assemblages has elucidated i) the response of invertebrate communities to dam presence, ii) the significant modifications in benthic assemblage biotraits due to sediment contamination and iii) the cumulated effects of dam and sediment contamination on both biotraits and an ecosystem process, leaf litter breakdown.

4.1. Functional disturbances related to dam presence

The dam only slightly impaired reference reservoir communities (Re1), mainly leading to a decrease in acidification-sensitive taxa. Despite the changes in flow regime, the upstream reach assemblage trait was not significantly modified. In these small run-of-river reservoirs, the hydrological and hydromorphological constraints may be balanced by a greater availability in littoral habitats. In contrast, in the downstream reference reach (Do1), the dam impact was more pronounced. First, the dam presence induced an increase in predators in the downstream community that may be related to an increase in Chironomidae below the dam (Bredenhand and Samways, 2009). In addition, the biotrait profiles in the downstream reach underlined a decrease in cold water organisms that could indicate alteration in the seasonal temperature regime. The observed increase in the ability of organisms to develop resistance forms and to tolerate pollution revealed also the impact of dam on downstream reach communities. Dam presence was supposed to impair leaf litter breakdown in the reservoir and in the downstream reach by the modifications of (i) the availability and quality of detrital resources and (ii) the assemblages (i.e. invertebrates and microorganisms) involved in leaf litter decomposition. Indeed, flow changes in reservoirs have been assumed (i) to reduce the colonization (Bärlocher, 1992, Chauvet, 1992) and activity (Ferreira and Graça, 2006) of microbial communities, potentially reducing leaf litter palatability to shredders and (ii) to increase litter clogging and burying in sediments (Naamane et al., 1999, Benfield et al., 2001). Despite these constraints, leaf litter breakdown rates measured in the reference reservoir (Re1) were not significantly different from those of its upstream reach (Up1). Similarly, in coherence with other previous studies (e.g. Casas et al., 2000, Muehlbauer et al., 2009), no physical impact on leaf litter breakdown rates was evidenced downstream the dams, in the absence of sediment contamination.

4.2. Functional disturbances associated to contaminated sediment

Intense siltation due to flow reduction and high historical contamination of sediment should lead to clearer trait-based responses of benthic communities to sediment contamination in reservoirs than in downstream reaches. This community response was characterized by a selection of adaptations in terms of feeding habits, resistance forms, dispersal, respiration and

reproduction modes. In particular, deposit feeders were more abundant in contaminated reservoirs and in the more heavily contaminated reaches, parasites took the place of some shredders and scrapers. Feeding habits strongly determine organisms' exposure risk and sensitivity to toxicants (Vaal et al., 2000, Ducrot et al., 2005, Rabení et al., 2005). The vulnerability of shredders has been related to the direct impact of meta toxicity (Niyogi et al., 2001, Carlisle and Clements, 2005)because this trophic group was composed of sensitive species (e.g. Ephemeroptera Plecoptera Trichoptera) or indirectly, because the contamination may alter the resource quality through microbial community alterations (Sridhar et al., 2001, Baudoin et al., 2008, Fernandes et al., 2009) and accumulation of contaminants in microorganisms on leaf litter (Farag et al., 1998, Schaller et al., 2011). This alteration of food quality used by macroinvertebrate communities under toxic conditions may have bottom-up effects on leaf breakdown process although many compensatory phenomena may exist; e.g. (i) shredders tolerant to toxic contamination or to poor quality resources, or (ii) diet plasticity of other feeding groups making it possible to use (in the absence of major competitors) leaf litter as complementary resource (Callisto et al., 2007). Our study evidenced a reduction of leaf litter breakdown rates with the increase in sediment metal contamination. Numerous studies have already reported impacts of river metal contamination on leaf litter decomposition (e.g. Carpenter et al., 1983, Maltby and Booth, 1991, Maltby and Crane, 1994, Carlisle and Clements, 2005). In addition to sediment contamination, dissolved oxygen availability could significantly influence leaf litter decomposition rate. Dissolved oxygen concentration may be a limiting factor in reservoirs (because of low flow and low current velocity), especially in interstitial habitats, influencing sediment pollutant bioavailability, bacterio-fungal colonization and biological activity (Medeiros et al., 2009). Oxygen depletion leads also to qualitative and quantitative changes in macroinvertebrate and microbial assemblages (Ward et al., 1998) and then may impair leaf litter decomposition. Finally, because contamination by heavy metals occurs also through external contact (Paul and Meyer, 2001), the maximal size of organisms has been expected to be related to contamination level. Thus, the relative abundance of small-sized organisms should decrease at high metal concentrations due to a higher surface/volume ratio (Dolédec and Statzner, 2008). The higher frequency of large-sized organisms (> to 4 cm) in the most contaminated sites was consistent with this hypothesis. The biotrait shifts associated with flow modification and sediment contamination can potentially reduces the resilience of resident communities to disturbances. For example, the strong reduction of the dispersal abilities of organisms towards downstream

may reduces resilience of downstream site communities and can affect the life cycles of many organisms (Brasher, 2003).

4.3. Cumulated impacts on downstream reach communities

Our results suggested that sediment contamination might induce a loss in resilience and resistance potential of reservoir communities (e.g. a decline in reproductive performances, reduced dispersal abilities, and a loss in resource harvesting efficiency) and to some extent, a weaker resilience of downstream reach communities already subjected to physical constraints related to dam presence. Regardless of the level of sediment contamination in the reach, the biotrait profiles of reach communities sampled downstream a contaminated reservoir were similar and clearly different from reach communities sampled downstream the reference reservoir. In addition to changes in traits related to local physical constraints, communities located downstream contaminated reservoirs were characterized by changes in a combination of traits (i.e. less K-strategists, more deposit-feeders, less shredders and predators), assumed to be related, like litter breakdown alteration, to the cumulative impact of both dam presence and reservoir contamination.

4.4. Complementarity of approaches used

The structural changes (i.e. bioecological and taxonomic) related to physical and chemical impairment can affect ecosystem functioning by cascading effects (McGill et al., 2006, Zavaleta et al., 2009, Menezes et al., 2010), especially if the impaired traits are the main contributors to ecosystem functional properties (i.e. functional traits). The taxonomic study of faunal assemblages did not reveal the presence of any physical and ecotoxic disturbances and potential cumulated impacts of these two perturbations. In contrast, studying community biotrait profiles allowed us to identify trait categories responding both to dam presence and sediment contamination. These “response traits” might be correlated with the stressor effects on functional processes. Trait categories within communities that respond to metal contamination of sediments were identified and correlated to leaf breakdown rate. Examining

biotrait profiles also allowed identifying constraints (i.e. physical impact and low toxic contamination) that had no significant effects on leaf breakdown rate. Nelson et al. (2000) demonstrated that community structure provided more information on stressor impacts (e.g. dam and metals) than did measurements of leaf litter breakdown rates because of (i) feedback mechanisms such as the replacement of intolerant shredders by tolerant ones (Schindler, 1987) and/or (ii) resistance of microorganisms to the stressors. Due to the high sensitivity of trait-based approaches for detecting the effects of physical and chemical stressors, we can assume that observed biotrait shifts are potential predictors of a disruption of functional processes (including leaf litter breakdown) in rivers. Because of increasing functional redundancy, a higher functional diversity of communities is considered as more contributing to ecosystem resistance and resilience. However, we hypothesized the existence of a threshold in community biotrait changes. When such threshold is exceeded, the functional changes in benthic communities could become irreversible. The identification and definition of such ecological and functional thresholds, thanks to biotrait-based approaches and leaf litter decomposition monitoring, seems necessary in risk assessment of contaminated sediments and dam presence. It could certainly help to predict and to ensure ecosystem recovery, especially in the case of restoration practices (e.g. dam removal). Finally, our results lead us to wonder about the definition of a “functionally disturbed” ecosystem, i.e. must we consider that ecosystem functioning is disturbed if changes in biotraits within invertebrate assemblages can potentially induce a significant loss in community resilience even if such changes do not still affect measured functional processes (e.g. leaf litter breakdown rate) or only when measuring a significant effect on functional processes despite the level of changes in community trait combinations?

5. Conclusion

Even if the ecological impact of dam has been increasingly studied in the last decades, those inherent to the cumulative effects of contaminated sediments have been scarcely and poorly examined. We have demonstrated that in the absence of contaminated sediments, changes in biotrait profiles do not generate negative effects on ecosystem functioning processes. Sediment contamination alters the reservoir functioning and by propagation of the effects might reduce the resilience of downstream communities. Sediment contamination may induce

also significant modifications in upper trophic level composition (Fleeger et al., 2003). This study has allowed highlighting the relevance of simultaneously using benthic invertebrate trait-based approaches and leaf breakdown process. These approaches combining the monitoring of both biotrait shifts and functional processes should be integrated in the ecological and ecotoxicological risk assessment related to contaminated sediments and should be helpful to predict the effects of multiple stressors. Run-of-river reservoirs constitute a relevant study framework for combined effects of physical and chemical stressors. In addition, the "good ecological potential" of such systems, potentially defined by their sediment quality, must maintain both high biotrait diversity and ecosystem processes expected in good ecological conditions, the guarantee for downstream reach integrity already under physical stress. This definition of their "good ecological potential" is particularly important in the context of ecological continuity restoration policy, including contaminated sediment resuspension risk evaluation. Omitting to assess the ecological and ecotoxicological risk related to sediment contamination in run-of-river reservoirs could lead to unexpected ecological consequences of ecological continuity restoration (e.g. dam removal). Indeed, the negative effects of contaminated sediment on habitat quality and functional processes (e.g. leaf litter decomposition), could deeply compromise ecosystem recovery (e.g. faunal recolonisation) and could lead to “physically restored” but “functionally disturbed” rivers.

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Article 7: **Importance of river continuity for detrital resource quality: implications for assessing ecosystem integrity**

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Abstract

1. Dams affect streams world-wide through shifts in hydromorphological components, retention of detrital organic matter and sediments and pollutant accumulation. Detrital organic matter, often retained in these systems, constitutes an essential resource at the basis of stream food-webs. Despite its importance for stream management and restoration, knowledge of the combined effects of physical and chemical disturbances on detritus quality and in turn on stream functioning, remain scarce.

2. We investigated the effects of physical and chemical disturbances on leaf litter quality and their consequences on leaf litter breakdown using dams as model of multi-stressed ecosystems. We hypothesized that the interaction of both disturbances reduces the quality of detrital resource that could in turn negatively impact the transfer of nutrients and energy to detritivores due to bottom-up effects. Temporal changes in resource quality according to the leaf litter stoichiometry, fungal biomass and community structure associated with decaying alder leaves were examined in four reservoirs characterized by a gradient of sediment contamination as well as in their upstream and downstream reaches. Potential effects of leaf litter quality on higher trophic levels were assessed by evaluating leaf litter breakdown rates and the production of fine particulate organic matter (FPOM) by two invertebrate shredders.

3. Dams had marked negative effects on fungal communities and leaf litter nutrient content but these effects decreased with exposure time. Conversely, negative impact of sediment contamination was marked throughout experiment

4. Consumption rates and FPOM production by Gammarus pulex were good indicators of the effects of resource quality changes. Leaf breakdown rates were clearly related to palatability and nitrogen content.

5. Synthesis and applications. Both disturbances, sediment contamination and dam presence, interactively reduced detrital resource quality and consequently on leaf litter breakdown by invertebrates. These changes in resource conditioning are likely to increase the storage of organic matter in reservoirs leading to additional stress to downstream ecosystems. Leaf litter microbial conditioning and breakdown rates seem to be powerful indicators of reservoir functioning, and could be interesting for risk assessment of multiple stressors associated with the presence of dam.

Key-words: multiple stressors, resource quality, decomposition, dam impact, contaminated sediment, fungi, leaf-shredding invertebrates, bioassessment.

1. Introduction

Worldwide, the construction of dams and reservoirs is one of the most important stressors of rivers (Sondergaard and Jeppesen, 2007). Dams induce discontinuities within the river continuum and affect ecosystems by altering biotic communities (Ward and Stanford, 1983a; Bednarek, 2001). The ecological continuity is a fundamental requirement not only for migration of aquatic species but also for nutrient exchanges and sediment transport. Indeed, in addition to strong physical impacts on hydromorphological components of rivers, the retention of sediment in reservoirs entraps many nutrients, leading to deficits ("hungry water") downstream (Kondolf, 1997). Moreover, accumulated sediments become both sink and source of contamination (Cairns et al., 1984; Chapman, 1990) posing crucial environmental risks to society.

Surprisingly, many studies have examined ecological impacts associated with large reservoirs (e.g. Gore, 1977; Petts. 1984; Ogbeibu and Oribhabor, 2002; Santucci et al., 2005; Maloney et al., 2008; Kornijów, 2010)); but very little had focused on small run-of-river reservoirs. Yet these systems are widespread and constitute a real challenge to understand effects of dams on the downstream ecosystem integrity. More than 60,000 small reservoirs exist in France and

many are impounded by dams that are aging and in disrepair (70% are without economic use). To date, the risk assessment associated with the presence of dams does not integrate the monitoring of the reservoirs (often regarded as a “black box”) including the effects associated with sediment contamination. These systems also constitute interesting models of multi-stressed ecosystems (physically and chemically). In addition, impacts of dams on important ecological processes driving the functioning of ecosystem such as the fate of detrital material have been very little documented.

In this context of multiple stressors associated to dams, leaf litter breakdown may be disturbed in several ways: 1) through direct impacts of physical and toxic disturbances inducing changes in decomposer and/or detritivore assemblages that are key actors of leaf litter breakdown, 2) through effects on food resource location, detritus being mainly stored in reservoirs, and 3) through effects on detritus quality, that modify the activity and performances of detritivore communities. Leaf litter breakdown is known to be influenced by changes in leaf litter quality such as conditioning by microbial (bacteria and fungi) decomposers and improvement of leaf elemental composition (ratios of essential elements e.g. C: N, C: P, or N: P ratios) (Bärlocher, 1992; Gessner and Chauvet, 1994; Sterner and Elser, 2002; Cross et al., 2003). It is well known that shredders may benefit from fungal colonization because aquatic Hyphomycetes associated with leaves constitute a food resource for shredders (Bärlocher and Kendrick, 1975; Arsuffi and Suberkropp, 1988) and also because through their activities, fungi increase the softness of the leaf matrix (Suberkropp et al., 1983).

These components of resource quality may be impacted by a range of natural and anthropogenic factors, notably the presence of dams, the accumulation of sediments and contaminants. Indeed, flow change due to dams may decrease fungal colonization of leaves. Current velocity is an important factor regulating the fungal assemblage structure (Chauvet, 1992), sporulation (Bärlocher, 1992) and nutrient acquisition (Ferreira and Graça, 2006). Similarly, we can hypothesize that reservoirs and dams may reduce fungal dispersion in downstream reaches. Concerning sediment contamination, a reduction in fungal diversity and activity has been already observed in streams polluted by heavy metals (Niyogi et al., 2001; Sridhar et al., 2001; Lecerf and Chauvet, 2008). Nonetheless, to our knowledge, no study has examined the effects of sediment contamination on leaf litter breakdown and microbial conditioning. Nutrient enrichment generally stimulates fungal activity and thus litter decomposition (Elwood et al., 1981; Suberkropp and Chauvet, 1995). The increase in

sedimentation in reservoirs affects nutrient distribution and availability leading to the loss of nutrients from the water column (Kennedy and Walker, 1990) and a degradation of water quality of reservoirs and downstream (Hart et al., 2002). These multiple stressors associated with the presence of dam may have additive effects, but also either larger or smaller effects than expected due to their synergistic or antagonistic interaction, respectively (Folt et al., 1999; Vinebrooke et al., 2004; Townsend et al., 2008). Because stressors usually operate in concert, resource managers need to understand how they interact (Matthaei et al., 2010).

To date, little attention has been paid to the combined effects of multiple anthropogenic stressors on detrital organic matter quality in the evaluation of ecosystem functioning. However, the quality of the detrital resource is crucial for the activity and sensitivity to disturbances of macroinvertebrates communities and, therefore, for energy transfer in detrital chains of aquatic ecosystems. Indeed, we hypothesize that a high-quality resource is more likely to reduce the retention time of organic matter in reservoirs and thus the "hungry water" effects downstream dams. In addition, food quality may modulate the response of organisms to toxicants (Heugens et al., 2001). It can be hypothesized that a higher microbial conditioning of the detrital resource is more likely to sustain ecosystem processes by i) compensating effects of diversity loss by allowing higher performances of detritivore communities and ii) enhancing resistance abilities of organisms exposed to disturbances.

The objectives of the present study were 1) to evaluate how multiple anthropogenic stressors associated to dams can affect the quality of detrital resource and 2) to identify potential consequences of such qualitative changes on leaf litter processing. We predicted that the disruption of river continuity affects the quality of the resource leading to a decrease of the efficiency of ecosystem processes due to bottom-up effects. Finally, we hypothesize that focusing on the interactions between resource quality, resource availability and the multiple anthropogenic stressors could provide important insights into the understanding of leaf litter breakdown in disturbed ecosystems. In addition, such integrative approach could be useful to predict trajectories of functional recovery after restoration practices (e.g. dam removal) and for accurate assessment of stream ecological health using functional indicators.

2. Materials and methods

2.1. Study sites

Assessing physical effects of dam presence entails two distinct comparisons. First, reservoir sites should be compared with their upstream sites in order to reveal flow modifications on resource quality. Secondly, downstream sites should be gauged against the upstream conditions in order to bring out dam impact. To enable these comparisons, four systems of reservoirs (n=4) and associated sites located upstream/downstream (n=8) were chosen on two French streams called Ain and Bienne belonging to the same ecoregion (Northern Jura-Prealps; Fig.1) and showing similar morphology and hydrology.

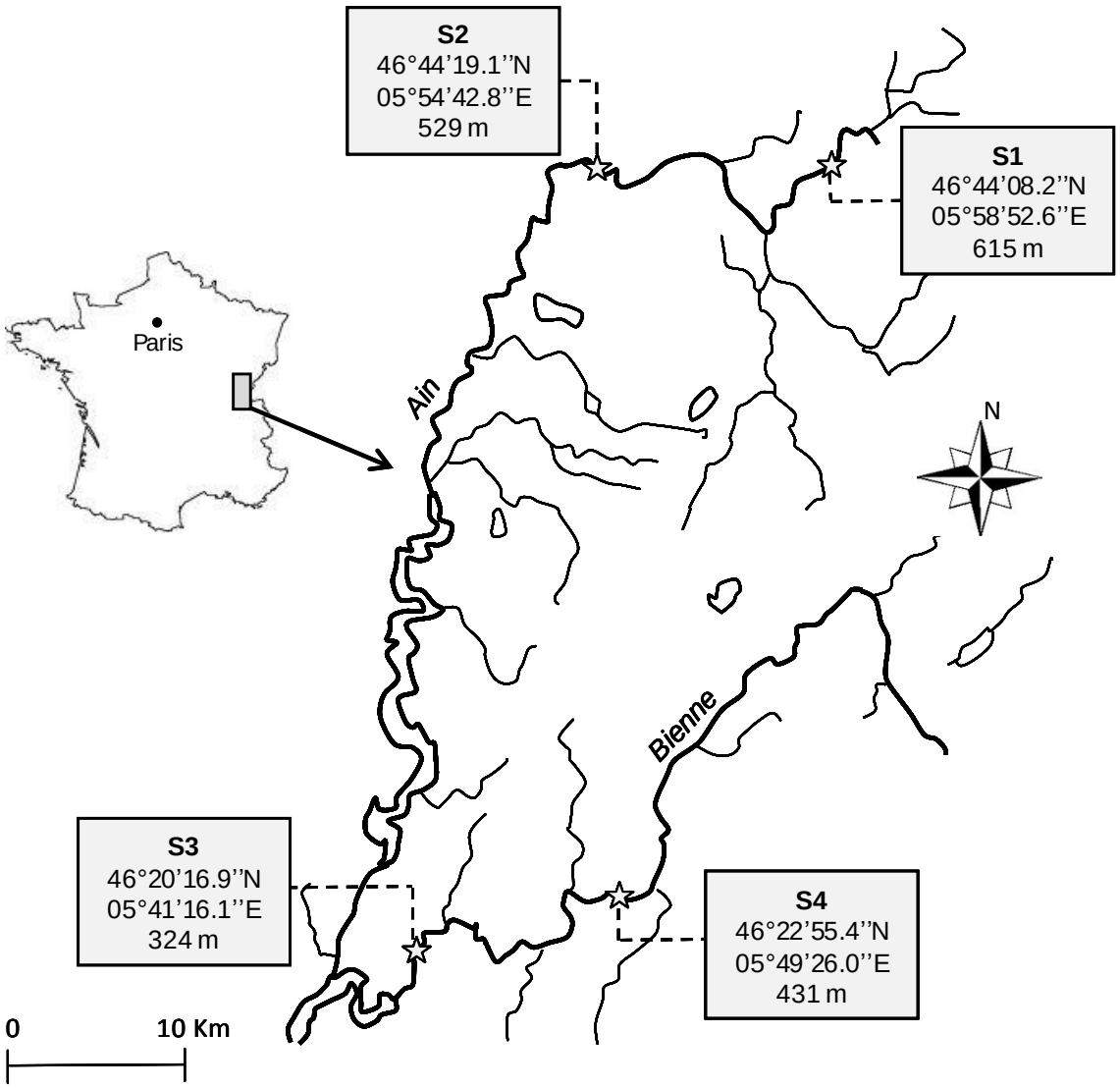

Fig.1: Location of the study systems in the Jura Mountains, eastern France

2.2. Sediments quality

Considering cumulative impact of dams in regard to pollutants stored, chosen systems represented a gradient of reservoir sediment contamination (from S1 as unimpacted sites to S4 with a strong contamination in reservoir). Levels of sediment contamination were assessed in samples obtained during the field campaigns (sampling depth of 20 to 30 cm) and sent to a specialized laboratory. Overall, the levels of 11 metals, 7 PCBs and 10 polycyclic aromatic hydrocarbons (PAHs) in the sediments were measured. A principal component analysis (Fig.2) has elucidated the gradient of sediment contamination of reservoirs sites. The first system is characterized by a reference reservoir (Re1) in comparison with three other reservoirs. Concerning the other sites, the factorial plane of the PCA analysis identified reservoirs highly and moderately contaminated in heavy metals essentially (Re4 and Re3 respectively), and a reservoir mainly contaminated in PAHs (Re2). Table 1 summarizes levels of contamination in metals and in PAH for reservoirs as well as for river sites.

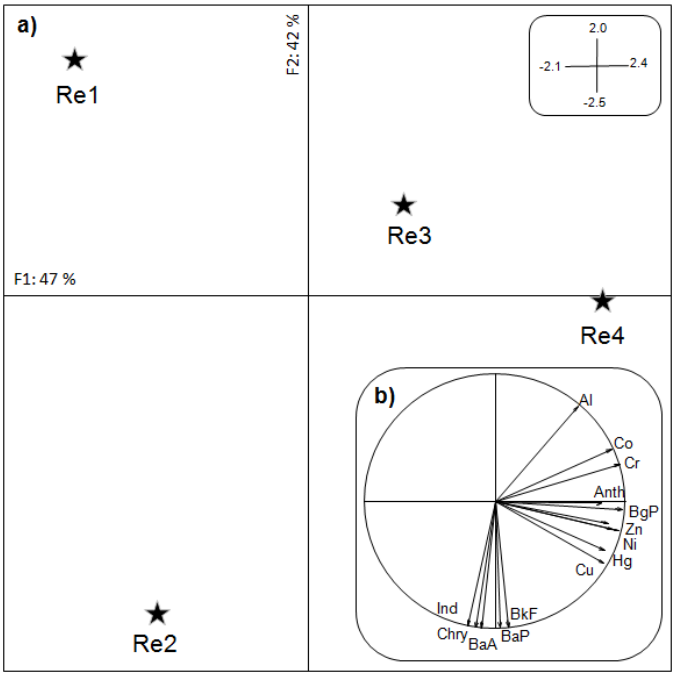

Fig.2: Principal Component Analysis performed on concentrations of metallic and PAHs pollutants in sediment of reservoirs: (a) factorial plane of study sites, and (b) correlation circle for pollutants.

2.3. *In situ* leaf litter conditioning

Alder (Alnus glutinosa) leaves, the dominant riparian tree species, were collected from trees just before abscission in fall 2010. Leaf bags were made by placing 2 g (± 0, 02) of air-dried leaves into mesh bags (15 x 20 cm, 500 µm mesh size). In each site one iron bar was anchored on a sedimentary habitat and nine bags were fastened to each bar during winter 2010 field campaign. Three replicate bags were retrieved from the twelve sites after 14 (T1), 28 (T2) and 45 (T3) days of exposure, immediately placed in individual sealed plastic bags with stream

water and transported to the laboratory in a cool box. For each sampling date, 2 L of water of each site was collected for laboratory processing of the leaf bags (rinsing of leaves collected with water from the corresponding stream in order to remove fine particulate matter).

		Metal contamination in sediments (mg kgDW^{-1})									
		Al	Cd	Cr	Co	Cu	Fe	Ni	Pb	Zn	As
Reservoir (n=4)	Minimum	2.08	0.10	12.80	2.30	4.10	3.9×10^3	6.50	9.10	26.90	1.00
	Mean	6.93	0.15	33.88	4.10	25.10	7.9×10^3	17.67	19.46	73.53	4.82
	Maximum	19.70	0.30	83.5	9.00	45.30	15.0×10^3	54.70	32.00	108.00	10.60
River (n=8)	Minimum	0.71	0.10	4.90	1.40	1.70	1.7×10^3	3.10	4.70	13.90	0.10
	Mean	3.87	0.14	19.55	33.09	9.91	5.6×10^3	12.67	20.48	35.24	5.64
	Maximum	15.2	0.30	65.00	307.00	23.9	8.9×10^3	35.60	82.90	65.20	11.40

		PAH Contamination in sediments (µg kgDW^{-1})								
		Anth	BaP	BaA	BkF	BgP	Chry	Fluo	Ind	Phén
Reservoir (n=4)	Minimum	10.00	20.00	15.00	11.00	5.00	25.00	46.00	15.00	25.00
	Mean	13.50	159.00	163.50	65.00	49.17	124.84	463.33	100.83	50.83
	Maximum	31.00	535.00	649.00	206.00	133.00	483.00	1919.00	395.00	180.00
River (n=8)	Minimum	10.00	5.00	5.00	5.00	5.00	25.00	20.00	5.00	25.00
	Mean	19.70	97.10	74.60	48.50	67.10	78.40	220.70	52.40	85.40
	Maximum	80.00	393.00	379.00	201.00	220.00	328.00	846.00	187.00	318.00

Table 1: Main physicochemical parameters characterizing gradient of sediment contamination in metal and PAHs for reservoir and river sites.

2.4. Fungal communities associated with decaying leaves

Ergosterol was used as an indicator of fungal biomass (Gessner and Newell, 2002). At each sampling date, three replicate sets of 5 discs from the leaves retrieved after the three times of exposure were lyophilized, weighed to the nearest 0.1 mg and heated in 5 ml hot alkaline methanol (KOH, 8 g L−1) for 30 min at 80°C. The extract was purified by solid-phase extraction on cartridges (Waters Oasis HLB, 60 mg, 3 cc). Ergosterol was separated by reversed phase high performance liquid chromatography on C18 and quantified by measuring absorbance at 282 nm. Ergosterol was converted to fungal biomass using a conversion factor of 5.5 mg ergosterol g−1 mycelial dry mass (Gessner and Chauvet, 1993). A DNA extraction and a PCR-DGGE analysis were used to appreciate fungal community structure. For DNA extraction, 100 mg of leaf from each replicate, site and exposure time were crushed and total DNA was extracted using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA). ITS3GC and ITS4 primers (White et al. 1990) were used for PCR amplification of ITS2 region of fungal ribosomal DNA (Nikolcheva and Bärlocher, 2005). The amplification products were separated with the DCODE Mutation Detection System (Bio-Rad, Hercules,

CA). The electrophoresis were performed on 8% polyacrylamide gels with a denaturing gradient from 30 to 70% (100% denaturant corresponds to 40% (v/v) formamide and 7 M urea). DGGE were run for 16 h at 55 V and 56°C and stained with SYBR Green I. The gels were imaged with a STARION FLA-9000 scanner (Fujifilm Life Sciences FSVT, Courbevoie, France).

2.5. Leaf litter elemental stoichiometry

Three replicate sets of 4 mg (± 0.31 mg) of leaves for each site and exposure time and 3 mg (± 0.29 mg) of each macroinvertebrate species used for the three feeding trials were used to quantify the percentage of carbon and nitrogen contained in this organic matter using a CHN elementary analyzer (Carlo Erba NA 2100). Similarly, organic phosphorus content was determined in leaves and macroinvertebrates species after persulfate digestion, as already described by Danger et al. (2007). C: N: P ratios were expressed as molar ratios.

2.6. Leaf consumption rates

The palatability of leaves to detritivores was assessed by short term leaf consumption experiments using two abundant shredders in the study sites: the amphipod Gammarus pulex and the Trichoptera Allogamus auricollis (Limnephilidae). For each species and each exposure time, individuals were collected on a reference site. Forty liters of water from the site were also collected then filtered in the laboratory through 0.45 µm filter for feeding trials. G. pulex and A. auricollis used for each feeding trial were independently acclimated to laboratory conditions for 24h (8 ±1°C, filtered water of reference site, without food). Then, at three exposure times (i.e. 14, 28 and 45 days), ten leaf litter consumption measurements were carried out for each sites and each species. Each microcosm received 50 ml of filtered water and two leaf disks (16 mm) of corresponding site. A disk was exposed to feeding and a control disk was enclosed in a small bag (2.5 x 2.5 cm, 500 µm mesh size) rendering the disk unavailable for macroinvertebrates. Finally, one individual of G. pulex or A. auricollis was placed in each microcosm. All microcosms were placed in a thermostated chamber (8 ±1°C) during 24h for microcosms with G. pulex. and 72h for those with A. auricollis. A total of 720 measurements were performed (12 sites x 10 replicates x 2 species x 3 times). At the end of feeding trials, animals, control disk and the remaining exposed disk were removed, oven-

dried (105°C, 24h), weighed to the nearest 0.001mg and ashed (550°C, 4h). Consumed leaf mass was calculated as the difference between the control AFDM and the remaining AFDM. Consumption rates (CR) were calculated as the ratio between the AFDM ingested per day per gram of organism dry mass (Waldbauer, 1968; Findlay and Arsuffi, 1989). Water of four replicates of microcosm for each treatment was reserved for the quantification of fine particulate organic matter (FPOM) production.

2.7. Production of fine particulate organic matter

The breakdown mediated by shredders induces the production of fine particulate organic matter including feces and pseudo-feces (FPOM, 0.45 to 1 mm - (Wallace et al., 1991; Webster et al., 1999)). To quantify the production of FPOMs, water of microcosms was filtered on a 0.45 µm pore size 18-mm diameter nitrate cellulose membrane, first washed with pure water, dried at 80°C and preweighed to the nearest 0.001 mg. After filtration, the membrane was dried at 80°C for 12 hours and weighed to determine FPOM. However, the quantification of produced FPOMs by the macroinvertebrates feeding might be obscured by the production of FPOM resulting from the activity of microorganisms associated with leaf disks. Thus, three replicates of leaf disks for each sites and exposure time were placed in the same conditions but without shredders, in order to quantify FPOMs produced by microorganisms.

2.8. Data analysis

Two-way analyses of variance (ANOVA) and a Tukey's HSD post-hoc test were used to test for the effects of "exposure time" and "dam impact" on the components of litter quality (fungal biomass and richness, C: N: P ratios). Similarly, simple linear regressions were used to detect effects of sediment contamination on resource quality. Stepwise multiple linear regressions were used to summarize effects of disturbances on resource quality and to identify predictors (components of resource quality and disturbances) of leaf breakdown process (consumption and FPOM production). For all parametric analyses, normal distribution and homoscedasticity were respected. R software (R development Core Team, 2008) and Ade4 library (Chessel et al., 2004) were used for all statistical analyses.

3. Results

3.1. Fungal richness and biomass

Fungal richness was strongly correlated to retention time (Fig.3). The multiple linear regression analysis (Table 2) clarified the importance of variables explaining the fungal richness response. The selected model explained 50% of the total variation. Best predictors of fungal richness were the metallic contamination, the exposure time and the dam presence. Fungal richness decreased with the increase in metallic contamination of sediments (regression coefficient= -0.906, p<0.001). Regardless levels of sediment contamination, fungal richness was higher in reservoirs than in upstream and downstream sites (regression coefficient=2.565, p<0.001).

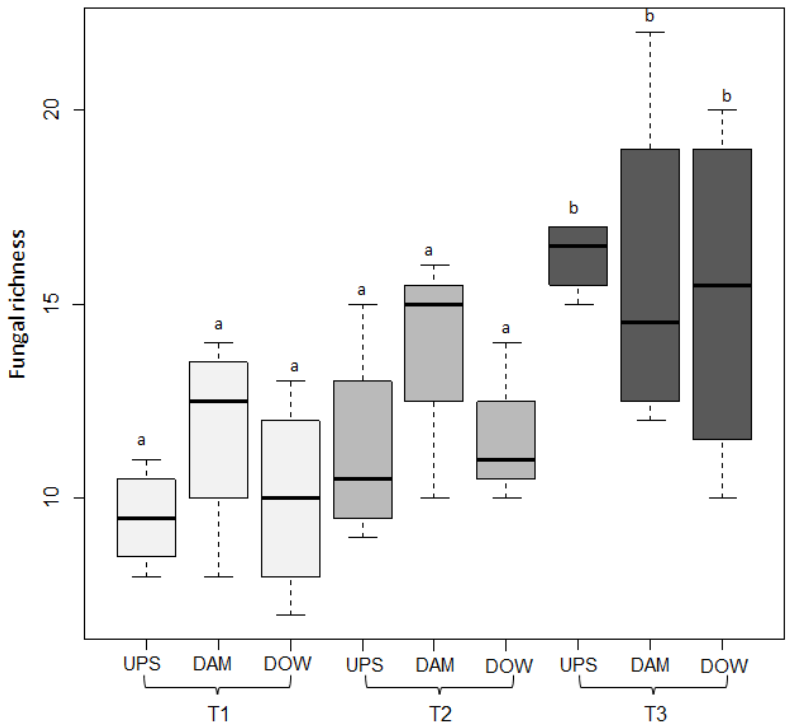

Fig. 3: Evolution of fungal community richness in decaying leaves in function of habitat types (UPS: upstream; DAM: reservoir and DOW: downstream). T1, T2 and T3 refer to the three times of exposure i.e. 14, 28 and 45 days. Box: 25% quantile, median, 75% quantile. Letters at the top of boxes indicate significant differences identified with analyses of variance.

We observed a significant effect of dam on mean fungal biomass associated with decaying leaves (Fig.4, two way-ANOVA, F= 10.077; P< 0.001). Biomasses were significantly lower in reservoir sites compared with sites located upstream (P=0.001; Tukey's HSD post-hoc test). The effects of dams on fungal biomass decreased with the exposure times of the leaves. The fungal biomass in reservoir sites were significantly different (p <0.01) compared with those observed in upstream and downstream sites after 14 days of exposure. After 28 days,

these differences were more pronounced ($p < 0.001$) with the upstream, while the downstream sites had an intermediate position with a higher fungal biomass than in the reservoirs but lower than upstream sites. After 45 days of exposure, the impacts associated with the presence of dams were no longer significant. However, the mean biomass upstream (22.02 mg.g $AFDM^{-1}$) was still higher than the mean fungal biomass of downstream sites (15.63 mg.g $AFDM^{-1}$) and of reservoirs (11.79 mg.g $AFDM^{-1}$). When looking at the dynamic of fungal colonization on all sites, the maximal biomass of fungi was reached after 28 days of exposure. It remained relatively stable for sites upstream and for reservoir sites, but decreased for downstream sites after 45 days of exposure.

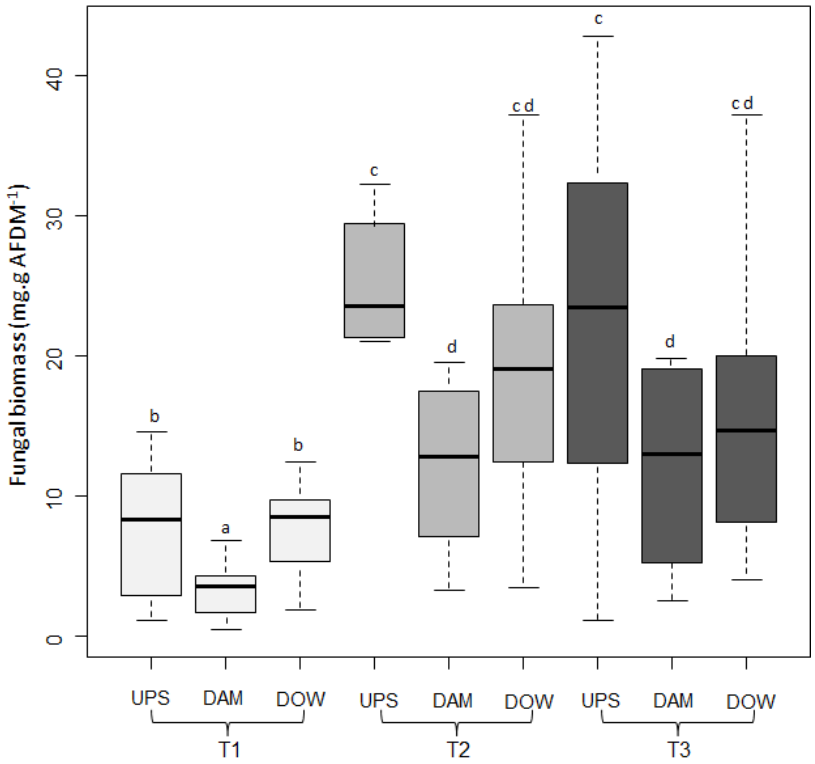

Fig. 4: Fungal biomass associated with decaying leaves in study sites (UPS: upstream; DAM: reservoir and DOW: downstream). T1, T2 and T3 refer to the three times of exposure i.e. 14, 28 and 45 days. Box: 25% quantile, median, 75% quantile. Different letters at the top of boxes indicate significant difference

A simple linear regression (Fig.5) revealed a negative relationship ($p < 0.0001$) between fungal biomass and metallic contamination in sediments of sites. The multiple linear regression analysis clarified the importance of variables explaining the fungal biomass response (Table 2). The selected model explained 48 % of the total variation of fungal biomass. The best predictors were the metallic contamination of sediments and the exposure time of leaves.

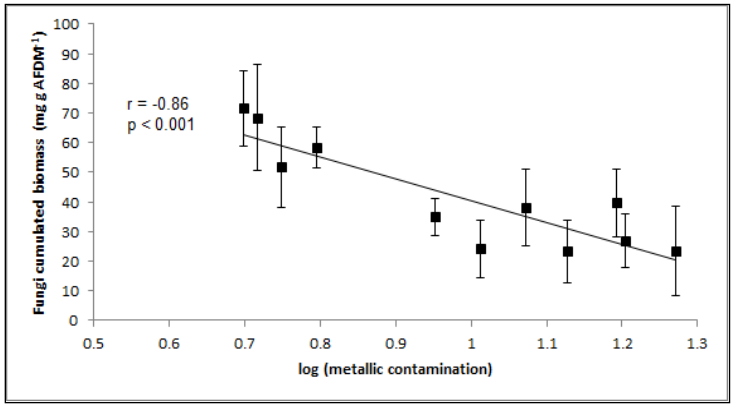

Fig. 5: Linear relationship between the fungal biomass and total metallic contamination in sediments.

3.2. Leaf litter stoichiometry

Leaf litter C: N and C: P ratios decreased with exposure time. After14 days of exposure, the impacts of dams were significant ($p < 0.01$) since in the reservoir sites leaves showed higher C: N ratios (Fig.6a). Downstream sites had an intermediate position and leaves showed higher C: N ratios than in upstream sites but lower than in leaves exposed in reservoir sites. After 45 days of exposure, the difference was reversed. The impact of dam was significant ($p < 0.01$) on downstream sites with leaves exhibiting lower C: N ratios than leaves exposed in upstream sites, whereas reservoir site occupied an intermediate position. Regarding the C: P ratios in the leaves, the impacts of dams were significant ($p < 0.01$) since at 14 days leaves in the reservoir sites showed higher ratios than in river sites (Fig. 6b).

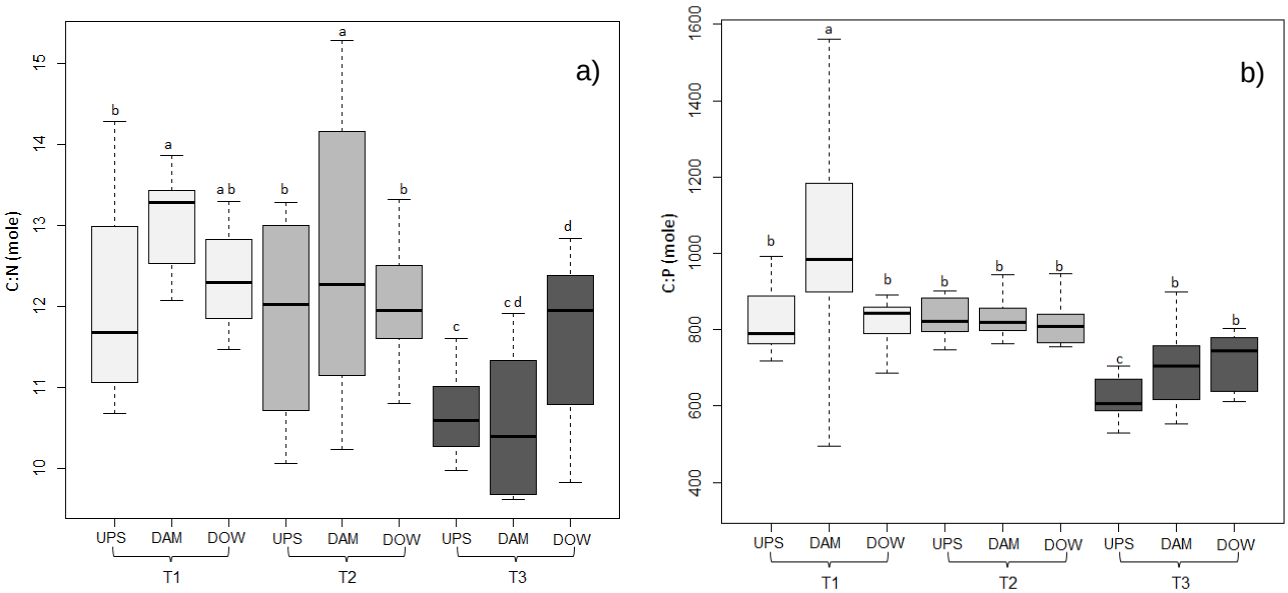

Fig. 6: Evolution of elementary ratios C: N (a) and C: P (b) in decaying leaves in function of habitat types (UPS: upstream; DAM: reservoir and DOW: downstream). T1, T2 and T3 refer to the three times of exposure i.e. 14, 28 and 45 days. Box: 25% quantile, median, 75% quantile. Different letters at the top of boxes indicate significant differences identified with analyses of variance.

Even if these differences disappeared at 45 days of exposure; the C: P ratios in the leaves remained lower in upstream sites than in reservoir sites than in downstream sites. Simple linear regressions revealed negative relationships between amount of nitrogen or phosphorus in leaves (Fig. 7, $p < 0.001$) and metallic contamination in sediments.

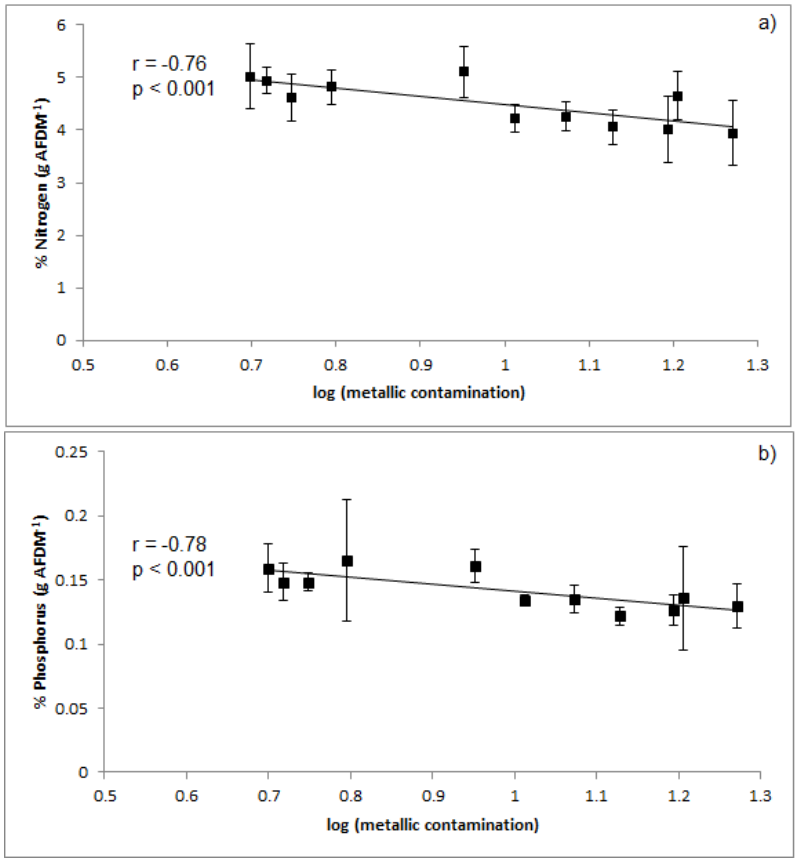

Fig. 7: Linear relationship between elementary ratios C: N (a) and C: P (b) of 12 study sites and total metallic contamination in sediments.

3.3. Leaf consumption rates and FPOM production

Multiple linear regression analyses have elucidated importance of leaf quality parameters on leaves consumption by shredders and on the associated FPOM production. Table 3 summarizes results for both shredders. The palatability of leaves for Gammarus pulex was explained at 15% by the fungal biomass and the exposure time of leaves meaning that fungal biomass and exposure time enhanced the leaves consumption of G. pulex. The production of FPOM associated with the consumption of leaves by G. pulex, was higher for leaves conditioned in upstream or contaminated (i.e. in metals) sites and for leaves with a high fungal richness. This selected model explained 38% of the total variation. In regard to the palatability of leaves based on consumption tests with Allogamus auricollis, the selected model, although significant, explained only 5% of the total variation and may be thus

considered unreliable. The study of the production of FPOMs associated with consumption of A. auricollis provided no significant results (data not shown).

Dependent variable	Overall r^2	Overall p-value	Independant variable	Coefficient	P-value
Fungal biomass	0.48	< 0.001	Metallic contamination	-4.006	< 0.001
			Physic perturbation		
			- Dam	-3.562	0.084
			-Downstream	-3.462	0.052
			Retention time		
			- 28 days	11.542	< 0.001
			- 45 days	10.137	< 0.001
Fungal richness	0.50	< 0.001	Metallic contamination	-0.906	< 0.001
			Physic perturbation		
			- Dam	2.565	< 0.001
			-Downstream	-0.194	0.746
			Retention time		
			- 28 days	1.833	< 0.001
			- 45 days	5.333	< 0.001
C:N ratios	0.51	< 0.001	Metallic contamination	0.526	< 0.001
			Organic contamination	0.284	< 0.001
			Physic perturbation		
			- Dam	-0.185	0.429
			-Downstream	0.652	< 0.001
			Retention time		
			- 28 days	-0.339	0.118
			- 45 days	-1.549	< 0.001
C:P ratios	0.40	< 0.001	Metallic contamination	44.22	< 0.001
			Retention time		
			- 28 days	-64.47	< 0.05
			- 45 days	-215.90	< 0.001

Table 3: Multiple linear regression analysis of variables associated with leaf litter breakdown against resource quality parameters (fungal and elementary quality), major stress factors (sediment contamination, physic perturbation) and the retention time at the 12 study sites. Variables shown for each multiple regression were conserved using a stepwise procedure of variable selection. Overall r2 and P-values are based on the selected multiple regressions.

4. Discussion

4.1. Multiple stressor effect on detrital resource quality

The presence of dam significantly alters fungal production in reservoirs and in sites located downstream. Even if the exposure time of the leaves reduces the impacts of dam on fungal

production, the fungal biomass remains lower in leaves exposed in reservoir sites than in upstream sites, at the end of the experiment. In reservoirs, and regardless levels of sediment contamination, the low fungal biomass may be associated with flow change, the accumulation of sediment, the decreased oxygen availability and the amount of nutrients available in the water column. Several studies have reported the influence of current velocity in structuring fungal assemblages (Canton and Martinson, 1990; Bärlocher, 1992; Chauvet, 1992). Water flow deceleration could reduce the fungal biomass through a low kinetic of colonization (low dispersion, low physical abrasion and leaching) and low sporulation rates (Ferreira and Graça, 2006). In addition to impacts directly associated with a lentic facies, a higher sedimentation may lead to a greater clogging of leaves in reservoirs than in river. This can lead to oxygen depletion on leaf surfaces and may affect aquatic Hyphomycetes metabolism and, ultimately, their growth (Pascoal and Cassio, 2004; Medeiros et al., 2009). Fungal biomass was significantly depleted in streams below dams and although this result was not significant, fungal richness showed a tendency to be also lower in leaves exposed downstream dams than those exposed upstream dams. We assume that the disruption of ecological continuity by the dams may decrease the passive dispersal of aquatic Hyphomycetes and conidia below dams. Indeed, the higher fungal richness observed in reservoirs supports this hypothesis. However, a greater availability of niches associated with the retention of a large amount of organic matter could also promote fungal richness.

To our knowledge there are no studies dealing with the effects of dam presence on the mineral quality of the detrital resource, despite reservoirs may be particularly important in retaining carbon and nitrogen (Vanni et al., 2011). In this study the amount of nitrogen in leaf litter was greater in the reservoirs than downstream. Unlike nitrogen, fungal biomass and richness, the amount of phosphorus in the leaves was not impacted by the presence of dam, but only by sediment contamination. Bärlocher (2003) and colleagues suppose that the effects of eutrophication in the enrichment of leaves could offset the impacts of moderate metal contamination on leaf litter breakdown, but no study has focused on the impacts of dam on the distribution of nutrients and its implications in the fungal and mineral quality of detrital resource. Yet, changes in leaf litter C:N:P ratios can greatly influence the fungal conditioning (Cross et al., 2005) and consequently its consumption by shredders. Future studies should examine the availability patterns of nutrients, particularly in reservoirs, due to their large retention in detrital carbon.

Dependent variable	Overall r^2	Overall p-value	Independant variable	Coefficient	P-value
Palatability for *G. Pulex*	0.15	< 0.001	Fungal biomass	0.080	< 0.05
			Retention time		
			- 28 days	-0.207	< 0.05
			- 45 days	0.277	< 0.001
FPOMs associated to *G.pulex*	0.38	< 0.001	Fungal richness	0.264	< 0.05
			Metallic contamination	0.607	< 0.001
			Physic perturbation		
			- Upstream	0.825	< 0.05
			-Downstream	0.673	0.067
Palatability for *A. auricollis*	0.05	<0.05	Fungal biomass	-0.025	< 0.05
			Fungal richness	0.019	0.057
			Metallic contamination	-0.019	0.086
			Physic perturbation		
			- Upstream	0.019	0.404
			-Downstream	-0.021	0.355
			Retention time		
			- 28 days	0.059	< 0.05
			- 45 days	0.033	0.315

Table 3: Multiple linear regression analysis of variables associated with leaf litter breakdown against resource quality parameters (fungal and elementary quality), major stress factors (sediment contamination, physic perturbation) and the retention time at the 12 study sites. Variables shown for each multiple regression were conserved using a stepwise procedure of variable selection. Overall r2 and P-values are based on the selected multiple regressions.

If the impacts of dam presence tend to be offset by the exposure time of the leaves, the effects of metal contamination of sediment on resource quality did not decrease with exposure time and affected all quality components. The effects of dams on fungal activity are exacerbated by sediment contamination. Nonetheless, the higher richness observed in reservoirs might offset to some extent (moderate contamination) the effects of sediment contamination on leaf litter breakdown, thanks to a redundancy in the fungal community that buffers its core functions against loss of biodiversity. Conversely, the cumulative effects (dam presence and contaminated sediment in reservoirs) on downstream communities seem more worrying for the stability of communities and their functions insofar both perturbations induce a species loss.

In addition to direct effects of metal contamination of sediments on the fungal compartment, the accumulation of fine sediments is more likely to impact the resource quality through clogging, depletion in dissolved oxygen, the release under reducing conditions of metals (and other reduced compounds) and the burial of litter. Clogging is frequent downstream dams

(Ward and Stanford, 1995). A lower resource quality in contaminated reservoirs might increase retention time of leaves, and consequently the risk of leaves burying. Once buried in sediment, the resource is less accessible to colonization by microbes and invertebrates, low dissolved oxygen concentrations might deter invertebrates, and potentially anaerobic conditions might hamper microbial processes (Webster and Benfield, 1986; Benfield et al., 2001; Collins et al., 2011). In addition, the longer contact with the contaminants stored can lead leaves and associated microorganisms (bacteria and fungi) to accumulate high amounts of metals and metalloids (Gadd, 2004; Schaller et al., 2011), decreasing all the more the resource quality and constituting a toxicity risks for the potential consumers..

4.2. Effects of resource conditioning on higher trophic levels

Changes of resource quality associated with anthropogenic disturbances have the potential to alter storage, transformation and export of carbon in detritus-based ecosystems. It is widely accepted that fungi increases the palatability and nutritional quality of resource to consumers (Cummins, 1974; Boling et al., 1975; Arsuffi and Suberkropp, 1989). In our study, the palatability of leaves for G. pulex was mainly governed by the fungal biomass and the retention time of the leaves. Many studies suggest that fungal conditioning and nutrient content improvement infer an advantage to Gammarus spp. by positively influencing survival, growth rates, or both (Kostalos and Seymour, 1976; Graca et al., 2001; Danger et al., 2012). Fungal conditioning of leaves influences the assimilation efficiency of the resource to amphipods (Nelson, 2011). Our results evidenced a higher production of FPOMs by G. pulex exposed to leaves of contaminated stations characterized by a lowest fungal biomass could indicate a weaker assimilation efficiency. Low assimilation efficiency may result in less matter and energy available for maintenance, growth, and reproduction, compromising performance and thus reducing resistance of G. pulex to disturbances. Contrary to G. pulex, qualitative changes in detrital resources have little affected the consumption rate of A. auricollis. The ratios C: N and C: P measured in G. pulex were higher than A. auricollis. Consequently, stoichiometric imbalances between leaf litter and the nutritional requirements for G. pulex' growth are lower than those for A. auricollis. If G. pulex is more sensitive to fungal conditioning of leaf, the Limnephilidae may be more constrained by the elementary quality of the resource. Iron and colleagues ((Irons et al., 1988)) have reported a positive

relationship between the consumption rates of Limnephilidae and the amount of nitrogen of the leaves. The weak response of consumption rates of A. auricollis to the change in the quality of the resource can be explained by: (i) the strong ability of limnephilid larvae to select richest leaf patches in fungi thus, allowing to cope with the resource quality, (ii) the ability to eat poorly conditioned and hard materials, contrary to G. pulex which is limited by its feeding apparatus (Graça et al., 1993), (iii) variations in the amount of nitrogen and phosphorus not sufficient to induce a change in feeding habits and finally, (iv) the experimental choices (i.e. plant species and the feeding trial time). Alder leaves remain palatable for consumers even in the absence of conditioning. Indeed, the amount of nitrogen and phosphorus initially present in the leaves was important and consequently, the consumption rate of A. auricollis (0.21 mg AFDM.day-1) greater than for G. pulex (0.07 mg AFDM.day-1). Choosing a refractory tree species (e.g. Oak, Beech), thus not palatable for consumers in the absence of conditioning, would have been more relevant to reveal the importance of changes in the quality of the resource in the feeding behavior of shredders.

In addition to the main components of the quality of the resource, other elements of the quality could have been taken into account that can also be affected by environmental changes and in turn explain the feeding behavior of both shredders such as fungal synthesis of micronutrients (Nelson, 2011), fungal attractants and repellents (Aßmann and von Elert, 2009), contents in fatty acids (Torres-Ruiz et al., 2007) or the adsorption of metals on leaves. In a disturbed ecosystem, the quality of the resource can be crucial to the persistence of detritivores. For instance, a longer time to reach a high-quality resource in disturbed sites can strongly affect aquatic organisms that have their life cycles synchronized with the autumnal litter supply (Bärlocher, 2000; Gulis and Suberkropp, 2004) modifying phenological patterns of use of the resources and thus inducing changes in the ecosystem processes. This impact can be more or less important depending on the adaptive capacity of shredders i.e. the plasticity of their trophic and temporal niches. It would be interesting to study the in situ realization of trophic (e.g. diet content) and temporal (development cycles) niches of both shredders in response to resource quality changes. This rupture of the phenological coincidence between the development of shredders and the availability of a high-quality resource may be more determining in the loss of shredders than the disturbance itself. In a previous study (unpublished data), leaf breakdown rates on the same study sites were investigated. This study identified no impact of dam in the absence of sediment contamination. In contrast the contaminated sediments have induced strong disturbances of leaf breakdown rates in reservoir

and in downstream sites. The leaf breakdown rates reported have been partly associated with biotrait shifts of macroinvertebrates communities (i.e. lethal effects). Changes in the resource quality may also induce additional stress leading to differential responses of litter decomposition process when combined with anthropogenic stressors. This context of multi-stressor involves many causality dilemmas and makes difficult to identify the relative importance of each variable: the direct effects of disturbances, the effects of the resource quality or the effects of the loss of shredders. The study of the interactions between the quality of detrital resources and the response of shredders to disturbances can be crucial to understand and predict fate of detritic organic matter in such systems.

4.3. Synthesis and applications

Multiple stressors of aquatic ecosystems, due to the complexity of ecological responses induced by their interactions, are not integrated in the bioassessment of water resource and therefore, constitute a large-scale challenge for freshwater scientists and managers. The study of the combined effects of dams and contaminated sediments, exemplifies the concept of multiple stressor leading to two types of disturbances: physical and toxic. The consideration and the understanding of interactive effects between these stressors on ecological responses are essential for the development of bioassessment methodologies, in defining the ecological status of water bodies and in planning and monitoring restoration programs. The study of leaf litter breakdown process is a critical issue when considering dams due to the retention of detritus in reservoirs and thus its depletion in ecosystems downstream. Moreover while many studies focus on the availability and the intrinsic quality of allochthonous inputs of organic matter in aquatic ecosystems, the impacts of disturbances on the resource quality and the effects of these changes on response of ecosystemic process are still very rare. Yet, the impacts on the quality of the resource can represent an additional stressor which can combine with other stressors. The interaction between sediment contamination and the dam presence has strong effects on resource quality and consequently on leaf litter breakdown. These changes in resource conditioning are likely to increase the storage of organic matter in reservoirs leading to additional stress to downstream ecosystems. Evaluation of microbial conditioning and leaf litter breakdown rates could be powerful indicators of reservoirs

functioning as well as for risk assessment of multiple stressors associated with the presence of dam.

In the European Union, the European Water Framework Directive (WFD; 2000/60/EC) establishes a framework for the protection of water resource which the main objective is to achieve a “good ecological status’ for all waters, by 2015. Nonetheless, the “good ecological status” does not exist for the run-of-river reservoirs. The WFD distinguishes three types of water body: natural, artificial and heavily modified water bodies. Run-of-river reservoir is defined as a heavily modified water body because it results from physical alterations by human activity. As such, the concept of “good ecological potential” for these systems is much less strict. It is replaced by the concept of “good ecological potential", whose definition is unclear. Yet, considering their elevated number, the quality of these systems has a great importance for the preservation of downstream ecosystem integrity. Our study supports that the consideration of the combined effects of disturbance and resource quality is fundamental to understand the functioning of reservoir ecosystems and in the definition of their "good ecological potential" but also in the planning of restoration projects of ecological continuity such as removal of dams. Indeed, in addition to the risks associated with the resuspension of contaminated sediments, the release of poor quality and potentially contaminated organic material could have serious consequences for the integrity of ecosystems downstream. In contrast, maintaining a high-quality of the resource could ensure the resilience of communities and of ecosystem functioning after restoration.

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Synthèse des résultats

Objectifs	Principaux résultats obtenus
O1: Caractériser le système « retenue au fil de l'eau » (en l'absence de contamination des sédiments)	✓ *Forte structuration spatiale des communautés de macroinvertébrés sur le gradient berge/chenal* ✓ *Identification de 19 taxons indicateurs* ✓ *Importance de la contribution des berges et de l'amont des barrages dans la composition et la diversité fonctionnelle des assemblages du chenal des retenues* ✓ *Similarité des profils bioécologiques des milieux lotiques et des retenues* ✓ *Augmentation de la compétition* ✓ *Plus faible richesse fongique dans les sédiments des retenues qu'en rivière ; à l'inverse plus grande richesse bactérienne* ✓ **Plus faible colonisation fongique des feuilles en décomposition** ✓ **Maintien du processus de décomposition des litières**
O2: Identifier les modifications structurelles et fonctionnelles associées à la contamination des sédiments dans les systèmes retenues et dans les écosystèmes rivières en aval	✓ *Divergence fonctionnelle entre les communautés de retenues contaminées et celles des milieux lotiques, caractérisée par une diminution de la diversité fonctionnelle* ✓ *Modifications structurelles et fonctionnelles des communautés macrobenthiques jusqu'à 19 kilomètres en aval du barrage suite à la remise en suspension de sédiments contaminés* ✓ *Diminution de l'amplitude de niche spatiale des espèces de macroinvertébrés le long du gradient de contamination métallique des sédiments* ✓ *Plus forte agrégation des communautés macrobenthiques dans les retenues contaminées : augmentation de la compétition. Agrégation des espèces sensibles dans les habitats d'érosion et évitement des habitats sédimentaires* ✓ *Sélection des organismes de petites tailles chez G.pulex et E.ignita* ✓ *Spécialisation du régime alimentaire de G.pulex* ✓ *Baisse de la diversité de l'activité métabolique des communautés microbiennes* ✓ **Plus faible richesse et biomasse fongique sur les feuilles en décomposition** ✓ **Rupture du processus de décomposition** ✓ **Altération des flux à l'interface eau-sédiment**

Objectifs	Principaux résultats
O3: Hiérarchiser les impacts physiques et toxiques	✓ *Réponse structurelle (modification des assemblages) mais continuité fonctionnelle en l'absence de contamination. A l'inverse, la contamination des sédiments dans les retenues induit des réponses structurelles ET fonctionnelles des communautés* ✓ *Réponses létales et sublétales plus influencées par la contamination des sédiments que par la présence d'un barrage* ✓ **Altération des processus dans les retenues contaminées et synergie des impacts physiques et toxiques en aval des retenues contaminées**
O4: Sélectionner des outils de diagnose de la qualité des sédiments	✓ *Meilleure aptitude du chenal à mettre en évidence le gradient de contamination* ✓ *Sélection de taxons indicateurs de la présence de sédiments contaminés (ex. Ephemerella ignita, Tanypodinae, Atherix)* ✓ *Identification de traits réponses à la contamination des sédiments au niveau des communautés (ex. taille maximale, formes de résistance, préférences de substrats)* ✓ *Les écarts entre niche spatiale théorique et réalisée des populations de taxons sensibles augmentent significativement avec la contamination métallique des sédiments* ✓ **Sensibilité des mesures de processus fonctionnels à la contamination des sédiments**

Chapitre V

Discussion générale : d'une échelle à l'autre

Préambule

Cette discussion sera structurée en deux parties. La première sera centrée sur l’échelle spatiale d’observation et la nature du système étudié, et visera à comprendre comment les retenues au fil de l’eau sont structurées, quelles sont leurs caractéristiques écologiques et comment elles influencent les écosystèmes en aval lorsque les sédiments qui y sont stockés sont contaminés. La deuxième partie s’intéressera aux différentes échelles d’intégration biologique étudiées lors de ce travail de thèse, en essayant d’identifier les paramètres qui permettraient de comprendre les transferts d’effets entre échelles.

1. Le système « retenue » : Enjeux pour la préservation du bon potentiel écologique

1.1. Caractérisation du système « retenue au fil de l'eau »

Les retenues au fil de l'eau sont peu étudiées, et de ce fait très peu d'informations sont disponibles quant à la structuration des communautés au sein des réservoirs. Les spécificités de ces communautés sont tout aussi méconnues, que ce soit simplement en réponse aux contraintes hydromorphologiques inhérentes à ce type de système ou en réponse à la présence de toxiques.

La première étude réalisée sur les retenues du Fier (article 1) a examiné l'importance de différentes échelles spatiales dans la réponse structurelle et fonctionnelle des communautés macrobenthiques, sur trois niveaux : longitudinal (queue, milieu et barrage), transversal (berges et chenal) et mésohabitationnel. Ces résultats préliminaires montrent que la **structuration longitudinale** des communautés est **négligeable** et qu'il n'y a pas de différences significatives des assemblages faunistiques dès lors que l'on se situe dans la zone d'influence de la retenue. Au contraire, une **forte structuration transversale** des communautés est mise en évidence, particulièrement en retenue contaminée. Lors de cette étude préliminaire, les communautés de berges étaient plus appropriées dans la discrimination des impacts associés à la contamination des sédiments et ce malgré l'hétérogénéité des habitats littoraux.

Si dans cette première étude, la variabilité inter-habitat était inférieure aux effets de la contamination, il est toutefois probable que cette **hétérogénéité des substrats littoraux** limite l'identification de patterns structuraux communs à plusieurs systèmes. En effet, sur l'ensemble des retenues échantillonnées (article 2), les habitats littoraux ne permettent pas l'identification et la caractérisation d'assemblages faunistiques et de profils bioécologiques indicateurs de ce type de système, **à la différence des habitats du chenal**. L'échelle des berges ne semble pas être la plus appropriée pour identifier des patrons généraux de réponse à la contamination des sédiments. Par ailleurs, du fait d'une contrainte physique moins forte, les habitats de berges peuvent constituer un habitat refuge pour les taxons les plus sensibles. Par

conséquent, une réponse plus tardive à la contamination est attendue pour les communautés de berges.

Indépendamment des niveaux de contamination des sédiments, dix-neuf taxons indicateurs ont été identifiés dans le chenal des retenues, des plus polluotolérants à l'instar de *Chironomus sp.* (Diptère) aux plus polluosensibles tels que *Leuctra sp.* (Plécoptères) et *Ephemerella sp.* (Éphéméroptères). Il apparaît clairement que le chenal des retenues abrite des cortèges faunistiques originaux et d'une diversité insoupçonnée dans la mesure où la contrainte hydromorphologique est forte. Cette forte contrainte sur l'habitat est sensiblement identique pour l'ensemble des retenues et permet la sélection **de cortèges faunistiques** partageant les mêmes caractéristiques écologiques et biologiques et par conséquent l'identification de **profils bioécologiques communs à ce type de systèmes.** Par ailleurs, il apparaît que même si, dans le chenal des retenues une **structure faunistique différente** de celle des rivières associées, est observée, **la structure bioécologique des communautés est similaire** pour les deux types de systèmes **en l'absence de contamination** sédimentaire.

Bien que le chenal semble être l'échelle spatiale la plus appropriée pour le développement d'outils d'évaluation des risques écologiques associés à la présence de sédiments contaminés dans les retenues, il apparaît essentiel de considérer la diversité des habitats de berges. Nos résultats mettent en effet en évidence la contribution des communautés de berges aux propriétés fonctionnelles des communautés du chenal. De plus, de nombreux processus écosystémiques prennent place dans les habitats littoraux (Naiman et Décamps, 1997; Rowan *et al.*, 2006; Free *et al.*, 2009). Ils influencent la qualité de l'eau et de ce fait la structuration et la résilience des communautés macrobenthiques de l'ensemble de la retenue. Par exemple, la diversité des habitats et des communautés littorales peuvent être d'une grande importance dans la réalisation du processus de décomposition des litières issues de la ripisylve adjacente ou de l'amont, et donc dans le transfert du carbone allochtone (James *et al.*, 1998). Dans une méta-analyse, Hladyz et ses collègues (2011) ont montré, sur cent rivières européennes, l'importance de la végétation riveraine dans ce processus. D'une manière générale les altérations de la qualité de la zone rivulaire affectent les communautés macrobenthiques et l'efficacité du processus de dégradation de la matière organique. Les habitats de berges constituent également une protection chimique et physique face aux apports du bassin versant en polluants et en sédiments fins.

1.2. Réponses structurelles et fonctionnelles de l'écosystème « retenue » à l'accumulation de sédiments contaminés

En l'absence de contamination des sédiments dans les retenues les **fonctionnalités des milieux lotiques associés sont préservées** (article 2). A l'inverse, la **contamination des sédiments** induit une **modification du profil bioécologique** des communautés, qui se caractérise notamment par la présence d'organismes associés à des milieux eutrophes, à faible capacité de dispersion, de grande taille et présentant des formes de résistances. Ces modifications conduisent à une **réduction de la diversité fonctionnelle** des communautés de réservoirs et de ce fait induisent **une perte de résilience** des communautés, conduisant potentiellement à des impacts sur le fonctionnement des retenues et des rivières en aval.

En plus des **effets létaux** mis en évidence par la sélection de caractéristiques bioécologiques et la diminution de la richesse et de la diversité taxonomique, la présence de barrages et de sédiments contaminés induit des **effets sublétaux** (article 4) tels que la **diminution de l'amplitude de niches spatiales** des taxons sensibles et l'**augmentation de la compétition** résultant de l'agrégation des populations vers des habitats moins susceptibles d' être impactés par les polluants (ex. habitats d'érosion). L'augmentation de cette compétition peut constituer un stress supplémentaire, particulièrement pour les populations de taxons devenues plus vulnérables par le déplacement de leur niche au-delà de leur optimum.

L'ensemble de ces modifications structurelles peut avoir des conséquences sur la réalisation de **processus fonctionnels** tels que la décomposition des litières ou les flux à l'interface eau-sédiment (article 5-6-7). En l'absence de contamination des sédiments, les modifications structurelles des populations et des communautés macrobenthiques ne sont pas suffisantes pour induire une altération du processus de décomposition des litières. **La présence de retenues au fil de l'eau n'induit donc pas nécessairement une rupture du processus de décomposition des litières**. A l'inverse, cette **rupture est observée dans les réservoirs impactés** par la présence de sédiments contaminés, et est **associée aux modifications bioécologiques** des communautés de macroinvertébrés et notamment à la perte de déchiqueteurs (article 6). Cette diminution du nombre de déchiqueteurs peut être expliquée par l'**impact toxique direct** de la contamination (ingestion de feuilles contaminées et/ou diffusion des polluants), par la présence d'une **ressource alimentaire de faible qualité**

(impact sur le compartiment fongique et les ratios élémentaires) et/ou par l'**effet combiné** des deux facteurs (toxicité et faible qualité de la ressource).

En effet, indépendamment des niveaux de contamination des sédiments, **la présence de barrage altère la production fongique** (article 7) associée aux litières. Une plus faible biomasse fongique en retenue qu'en rivière peut être associée aux modifications du régime hydrologique (faible courant, forte profondeur), à l'accumulation de sédiments fins pouvant recouvrir la surface des feuilles et à la diminution de l'oxygène dissous. Cette **plus faible qualité nutritive n'induit pas de perturbation quantitative du processus de décomposition** dans les **retenues non contaminées**. Cette absence de réponse mesurable ne signifie toutefois pas une absence de modification du mécanisme conduisant à la réalisation du processus. En effet, la faible qualité de la ressource peut être contrebalancée par la richesse et la diversité des communautés observées favorisant la compétition, et de ce fait la différenciation des niches et les mécanismes de complémentarité et/ou par des mécanismes compensatoires (ex. les déchiqueteurs mangent plus afin de compenser la perte de qualité nutritive).La présence de sédiments contaminés est un facteur de stress additionnel pour les communautés fongiques associées à la ressource détritique accumulée dans les retenues. Cet effet synergique se traduit par une **très faible production fongique** et par conséquent un **mauvais conditionnement de la ressource** pouvant induire un **stress supplémentaire pour les populations de déchiqueteurs** qui deviennent alors d'autant plus vulnérables et moins résistants à la contamination des sédiments.

Les modifications structurelles des communautés précédemment évoquées ainsi que les conséquences sur la réalisation du processus de décomposition des litières peuvent également se traduire sur le **fonctionnement biogéochimique des sédiments**, et réciproquement (article 5). En effet, les flux benthiques ont été fortement corrélés à la **quantité de nutriments**, de **matière organique** et de **polluants dans les sédiments**. Plus spécifiquement, le contenu en matière organique influence significativement les taux de dénitrification de la colonne d'eau, les taux d'absorption du phosphore, et à l'inverse le relargage d'ammonium potentiellement toxique pour les communautés aquatiques.

Cette modification du statut trophique de la colonne d'eau, et notamment de la disponibilité en nutriments comme le phosphore et le relargage d'ammonium, peut **inhiber la croissance fongique** associée aux litières et participer à la rupture du processus de décomposition. Outre

le relargage de composés réduits, il est probable que les sédiments riches en matière organique relarguent de manière épisodique des contaminants dans la colonne d'eau. Par ailleurs, la diminution en oxygène dissous est déterminante dans le devenir de la matière détritique dans les réservoirs dans la mesure où il s'agit du principal paramètre qui contrôle les taux de décomposition dans les retenues (article 6). Enfin, la quantité de **matière organique non dégradée augmente le stock de matière organique** dans les sédiments et de ce fait stimule la demande en oxygène pour la respiration bactérienne et réduit l'oxydation des produits de la respiration anaérobique. Cela conduit à des conditions d'hypoxie ou d'anoxie à l'interface eau-sédiment, à l'accumulation de composés réduits dans les sédiments de surface et à leur relargage dans la colonne d'eau, qui affecte négativement les communautés benthiques (Gray *et al.*, 2002; Viaroli *et al.*, 2004). La figure 13 synthétise les résultats obtenus sur les modifications structurelles et fonctionnelles associées à la présence de sédiments contaminés dans les retenues au fil de l'eau étudiées.

1.3. Impacts directs et indirects de la contamination des sédiments sur les écosystèmes en aval des retenues

La contamination des sédiments stockée dans les réservoirs peut profondément altérer les communautés en aval, déjà soumises aux impacts associés à la présence d'un obstacle, directement via **la remise en suspension des sédiments** et la remobilisation des contaminants dans la colonne d'eau et/ou indirectement via **les effets en cascades des réponses bioécologiques et fonctionnelles** des communautés des retenues.

La remise en suspension des sédiments stockés dans les réservoirs est relativement fréquente, lors de crues, de vidanges, de curage ou de manière plus anecdotique, lors de retrait de barrage. Cette remise en suspension induit un **stress multiple** associé d'une part, aux **perturbations physique**s relatives à l'augmentation de la turbidité puis au colmatage des habitats par exemple et d'autre part, aux **perturbations toxiques** relatives aux sédiments contaminés et à la remobilisation des polluants dans la colonne d'eau. Des modifications structurelles et fonctionnelles associées à la vidange d'un réservoir contaminé (article 3) ont été mises en évidence plus de 4 mois après la vidange et jusqu'à 19 kilomètres en aval du barrage. A la différence de l'impact physique, s'atténuant rapidement vers l'aval, l'impact toxique pourrait perdurer à plus long terme et sur de plus longues distances du fait de la remobilisation des polluants dans la colonne d'eau et de leur transfert dans le réseau

trophique, des dépôts de sédiments contaminés et du relargage saisonnier des polluants complexés.

Indépendamment de la contamination des sédiments stockés dans les retenues, la présence de barrages, en altérant l'hydromorphologie naturelle des cours d'eau, affecte les communautés aval. Pour autant ces modifications structurelles, bien qu'elles réduisent la diversité des communautés (les rendant alors probablement plus **vulnérables** à une perturbation supplémentaire), **ne se traduisent pas** nécessairement **à un niveau écosystémique**. En effet, en l'absence de contamination des sédiments dans les retenues, le processus de décomposition n'est pas altéré en aval et ce malgré un impact de la présence de barrage sur les communautés microbiennes associées aux litières (article 7). Cet impact, caractérisé essentiellement par **un retard dans la production de biomasse mycélienne sur les feuilles** par rapport à celles exposées aux stations en amont des barrages, est probablement dû aux **modifications d'écoulement** pouvant limiter le transport des spores et la colonisation fongique, au **colmatage des feuilles** (diminution de l'oxygène) ou à **la rupture de la continuité** pouvant réduire la **dispersion** des organismes et **affecter la distribution des nutriments** en aval.

La contamination des sédiments stockés dans les retenues induit une **synergie des impacts** physique et toxique qui conduit à la rupture du processus de décomposition en aval (perte de la **continuité fonctionnelle**) en altérant les communautés microbiennes et la structure taxonomique et bioécologiques des communautés macrobenthiques. Cet impact peut être associé au dysfonctionnement des retenues développé précédemment (Fig. 13) conduisant à la remobilisation épisodique des contaminants et autres composés tel que l'ammonium, à l'appauvrissement de la qualité de l'eau, à la perte de richesse et de diversité des communautés dans les retenues. Ces effets limitent le pool d'espèces susceptibles de coloniser les secteurs avals et de ce fait, conduisent à l'établissement d'une double **barrière physique et chimique**.

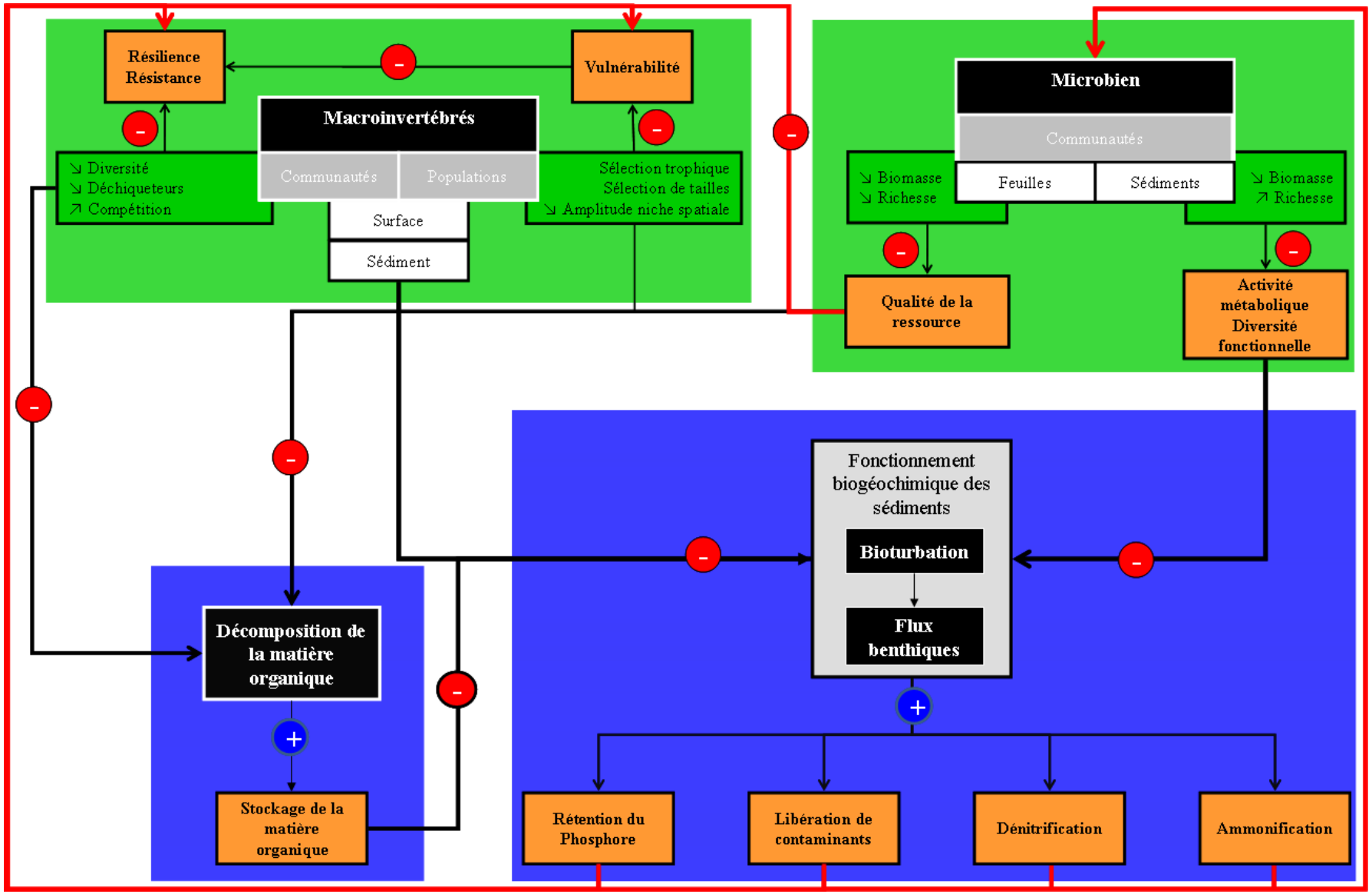


Fig.13 : Schéma général des impacts structurels et fonctionnels de la présence de sédiments contaminés dans les écosystèmes de retenues au fil de l'eau étudiés

1.4. Hiérarchisation des perturbations physiques et toxiques : importance des stress multiples

Parce que les écosystèmes sont soumis à une multitude de stress, l'évaluation des risques associée à la présence d'une perturbation ne peut être réalisée sans considérer la présence d'autres perturbations et les effets potentiellement cumulés des différents stress sur les organismes aquatiques. Cette prise en compte des facteurs de stress multiples est primordiale afin de **hiérarchiser les perturbations**, mieux comprendre les **relations « causes à effets »** et consécutivement **cibler des mesures de gestion et de restauration** efficaces des écosystèmes aquatiques (Hope, 2006; Thrush *et al.*, 2009; Burton et Johnston, 2010).

Comme nous l'avons décrit à plusieurs reprises dans ces travaux de thèse, la présence de sédiments contaminés est le plus souvent associée à des perturbations physiques. En l'absence de contamination des sédiments piégés, les impacts physiques de la présence de retenue au fil de l'eau sont compensés et ne se traduisent pas au niveau écosystémique. A l'inverse, la contamination des sédiments altère les communautés (microbiennes et macrobenthiques) et les processus écosystémiques dans les réservoirs et en aval. Pour autant, les **impacts physiques** constituent un stress additif à ne pas négliger puisqu'ils **augmentent la vulnérabilité des communautés au stress toxique**. En effet, nos résultats mettent en évidence une synergie entre les deux perturbations qui pourtant, sont le plus souvent évaluées indépendamment l'une de l'autre.

La **présence de barrage** agit comme un **filtre environnemental** sur les communautés et induit la **convergence des traits** des organismes vers des caractéristiques biologiques et écologiques qui leur permettent de se maintenir dans le milieu. En l'absence de contamination, la présence d'habitats diversifiés dans les zones littorales des retenues et en aval maintient la diversité taxonomique et fonctionnelle (« limiting similarity »), permettant de compenser l'impact physique et de pérenniser le processus écosystémique. A l'inverse, la contamination des sédiments, en induisant une perturbation chronique et persistante, maintient le filtre environnemental associé à la présence du barrage. La similarité fonctionnelle des communautés en aval de retenues perturbées illustre cet effet de filtre environnemental de la contamination des sédiments (article 6) et explique la rupture du processus de décomposition.

En conclusion, sur les retenues étudiées, les **impacts chimiques** associés aux sédiments contaminés sont **plus structurants** que les impacts physiques. Peu d'études ont examiné l'importance relative des deux types de perturbations sur les communautés aquatiques. Rogers et ses collègues (Rogers *et al.*, 2002), ont tenté de discriminer l'influence des perturbations physiques (chenalisation, dégradation de la ripisylve) et chimiques (contamination par les métaux) en utilisant des indices de conditions chimiques, physiques et biologiques. Ils ont également été confrontés à la difficulté de dissocier les effets des deux perturbations et soulignent l'importance des impacts toxiques dans la structuration des réponses biologiques. Pour autant, ils supposent que la présence d'une perturbation physique peut avoir masqué les effets de la contamination et devrait être intégrée dans l'évaluation des risques associés à la présence de métaux.

Cette hiérarchisation des impacts toxiques et physiques est particulièrement **cruciale** et d'actualité avec le développement des projets de restauration de la continuité écologique tel que le retrait de barrage. En effet, de tels projets concernent essentiellement des petites structures, telle que les retenues sur lesquelles nous avons travaillé. Même si le retrait de barrage pourrait promouvoir la récupération des communautés et de ce fait, limiter leur vulnérabilité à de nouvelles perturbations et garantir le maintien de l'intégrité des écosystèmes, il constitue également une perturbation dont les effets restent aujourd'hui, imprévisibles. Dans le cas de sédiments contaminés, il apparaît plus opportun de restaurer chimiquement, préalablement au retrait de barrage, ces écosystèmes (ex. curage des sédiments, restauration des zones littorales), afin de promouvoir leur récupération structurelle et fonctionnelle. Dans la mesure où nos résultats ne concernent que six retenues de petites tailles, d'autres recherches devraient examiner la pertinence des réponses que nous avons observé en considérant également **un gradient de perturbation physique** (ex. du seuil au grand barrage) afin d'établir des **mesures de gestion adaptées à l'intensité des deux perturbations**.

En plus des stress d'origine anthropique, certains facteurs biotiques et abiotiques peuvent également **influencer la tolérance des organismes aquatiques aux toxiques** (Heugens, 2003) tels que la **compétition** ou la **qualité des ressources alimentaires**. Lors de l'examen des réponses sublétales, nous avons mis en évidence, dans les sites contaminés, une augmentation de la compétition interspécifique associée à une agrégation des communautés

sur des habitats d'érosion (article 4). L'augmentation de cette compétition peut induire un **stress supplémentaire** pouvant se combiner à ceux déjà recensés et **augmenter encore la vulnérabilité** des populations. Par ailleurs, la diminution de la qualité de la ressource détritique peut également favoriser la compétition intra- et interspécifique (article 7). Par exemple, chez les gammares, l'augmentation de la contamination induit une homogénéisation du régime alimentaire et de ce fait peut favoriser l'augmentation de la compétition intraspécifique (article 4). Quantifier la nature de ces filtres biologiques est important mais vraisemblablement difficile (Poff, 1997). Il serait intéressant d'étudier expérimentalement et *in situ* l'importance de ces stress multiples sur les réponses biologiques et notamment d'explorer dans quelles mesures la compétition et la qualité de la ressource alimentaire influencent la vulnérabilité des populations au stress toxique.

1.5. Enjeux de la définition et de la préservation du potentiel écologique des retenues au fil de l'eau

En tant que masses d'eau fortement modifiées, les retenues au fil de l'eau ne sont pas soumises à la même obligation de suivi et à la même rigueur quant à l'accomplissement du bon état écologique, et sont de ce fait, très rarement évaluées. Bien que les masses d'eau fortement modifiées doivent atteindre le « **bon potentiel écologique** », l'absence d'un cadre réglementaire explicite quant à la définition de ce potentiel compromet **la prise en compte des enjeux de préservation et de restauration de ce type de système**.

Définir et évaluer le bon potentiel écologique des retenues au fil de l'eau est primordial pour (i) **réduire les impacts** de la présence des obstacles sur l'intégrité des écosystèmes avals et (ii) **pour garantir et promouvoir** le succès des projets de restauration de la continuité écologique. A la lumière des travaux de recherche réalisés dans cette thèse, le **bon potentiel écologique** des retenues pourrait être défini sur la base de l'**évaluation des risques associés aux sédiments** accumulés dans la mesure où la **bonne qualité** des sédiments promeut une qualité d'habitat suffisante au maintien de la **continuité des fonctionnalités** des milieux lotiques et de ce fait, **à la résilience des écosystèmes avals** à la présence de barrage. En d'autre terme, le bon potentiel écologique des retenues au fil de l'eau pourrait être évalué sur la base des potentialités de ces systèmes à ne pas dégrader les communautés et le fonctionnement des écosystèmes avals.

Dans la mesure où un très grand nombre de barrages au fil de l'eau ne seront pas retirés du fait de leur usage économique, il apparaît essentiel d'intégrer le suivi de ces systèmes pour limiter leur impact sur les communautés en aval. Par ailleurs, cette absence de prise en compte des retenues au fil de l'eau dans l'évaluation de la qualité des masses d'eau naturelles paraît **contradictoire aux objectifs de la DCE** ; l'accumulation des sédiments accumulés pouvant **compromettre l'accomplissement du bon état écologique** pour la plupart des cours d'eau européens.

La présence de sédiments contaminés accumulés dans les réservoirs peut entraver **le succès de la restauration de la continuité écologique** dans le cas de retrait de barrage. Par ailleurs, cette dernière ne devrait pas être uniquement définie comme le rétablissement des possibilités de circulation des organismes aquatiques et des flux de sédiments (circulaire DCE 2005/12 relative à la définition du « bon état »), mais également comme **la préservation et la récupération des fonctionnalités des milieux lotiques**.

Le plus souvent, les projets de restauration par le retrait de barrages sont construits sur le postulat que le rétablissement des profils hydromorphologiques naturels des cours d'eau s'accompagne, à plus ou moins long terme, de la récupération des communautés et des fonctionnalités des écosystèmes. Malheureusement, la plupart du temps la restauration physique ne suffit pas à promouvoir la récupération des écosystèmes. Cet échec de la restauration peut être associé à (i) la présence de sédiments contaminés dans les retenues, (ii) des phénomènes d'hystérésis et de ce fait à la perte des capacités de récupération des communautés et (iii) à l'absence de taxons recolonisateurs suite à des perturbations dans les secteurs amont et dans les affluents.

Afin d'établir une politique de gestion et de restauration environnementale raisonnée de la ressource en eau, il apparaît essentiel de mieux **connaître les mécanismes qui régissent la biodiversité et le fonctionnement des retenues au fil de l'eau** et leurs impacts sur les systèmes avals. Ce type d'approche devrait permettre de mieux définir la notion de « bon potentiel écologique » afin de prioriser les mesures de gestion de ces systèmes et de mieux prévoir le succès des effacements de barrages.

2. Sélection d'outils de diagnose structurelle et fonctionnelle de la qualité des sédiments : approche intégrée de la population à l'écosystème

Pendant ce travail de thèse, nous avons testé différents outils à chaque niveau d'organisation biologique, dont certains ont permis d'élucider l'impact de la contamination des sédiments. Pour autant, les outils testés à chaque niveau n'**intègrent ni ne prédisent** de manière satisfaisante **les réponses biologiques observées aux autres niveaux d'intégrations**. Pour une meilleure diagnose de l'**intégrité des écosystèmes**, nous préconisons le développement de **méthodologies** d'évaluation des risques écologiques basées sur l'**intégration des réponses biologiques sur les trois niveaux**.

2.1. Indicateurs populationnels de la contamination des sédiments stockés dans les retenues

L'étude des réponses populationnelles à la présence de toxique est le plus souvent réalisée en laboratoire sur des espèces modèles et manque de ce fait de pertinence écologique. En effet, à l'heure actuelle les taxons utilisés dans les tests écotoxicologiques ne permettent pas d'élucider et de prévoir la réponse aux perturbations toxiques aux niveaux supérieurs d'organisation biologique. Par exemple, une grande attention a été donnée aux effets de la contamination métallique des sédiments sur les larves de chironomes (*Chironomus riparius*), communément utilisées pour l'évaluation de la toxicité *via* l'étude des effets sur la croissance, la mortalité, l'émergence ou la morphologie des pièces buccales (Wiederholm, 1984; Ingersoll et Nelson, 1990; Michailova et Belcheva, 1990; Moore *et al.*, 1994; Hudson et Ciborowski, 1996; Bird, 1997; Ristola *et al.*, 1999). Pourtant, à l'instar d'autres études *in situ* (ex. Grumiaux *et al.*, 1998; Beasley et Kneale, 2003), nos résultats n'identifient pas d'effet létal de la contamination des sédiments sur *Chironomini* ; bien au contraire, ce taxon semble être favorisé dans les stations contaminées (article 4).

L'absence de réponse létale de ce taxon peut être expliquée par sa capacité d'adaptation génétique à la contamination métallique (Janssens de Bisthoven *et al.*, 1998; Groenendijk *et al.*, 2002), par la réduction de la prédation (ex. sensibilité du prédateur Tanypodinae aux métaux) et de la compétition interspécifique associée à l'augmentation de la contamination (article 4). Outre l'absence de réponse létale, la contamination des sédiments pourrait altérer la contribution des chironomes au processus de bioturbation (réponse sublétale). Nous supposons que notre étude sur l'activité de bioturbation des Chironomes n'a pas pu aboutir parce que la densité d'organismes intégrée dans les colonnes de sédiments, bien que représentative des densités moyennes identifiées *in situ*, était insuffisante pour détecter les activités de bioturbation et que la bioluminescence des sédiments riches en matière organique a pu affecter la lecture des échantillons au spectrophotomètre. Néanmoins, nous supposons que l'activité de bioturbation de C*hironomus* est plus sensible à la disponibilité et à la qualité nutritive des sédiments qu'à leur niveau de contamination. En effet, dans leur étude expérimentale sur la réponse d'espèces de macroinvertébrés à l'apport de nourriture et de contamination dans les sédiments, De Haas et ses collègues (2002) rapportent un effet positif de la quantité et qualité de la ressource alimentaire dans les sédiments (matière organique) sur *C. riparius*, et ce malgré la présence de toxique.

A la différence de ce qui est observé pour les métaux, peu de taxons ont été identifiés comme sensibles à la contamination en HAPs (effet létal significatif sur *Gammarus* seulement, article 4). Il est probable que les niveaux de contamination en HAPs n'aient pas été suffisants pour observer des effets létaux, et que la présence de métaux dans les sédiments soit plus structurante. Bien qu'il soit probable que les cocktails de contaminants métalliques et organiques dans les sédiments interagissent, l'identification d'une synergie des effets sur les réponses biologiques observées *in situ* est difficile et requiert une approche expérimentale en laboratoire ou en mésocosmes. Il est toutefois envisageable que la contamination en HAPs induise des **effets sublétaux** qui ne peuvent pas être mis en évidence par la distribution des taxa le long du gradient de perturbation. La sélection de taxons indicateurs bien que classiquement effectué sur la base des réponses létales, peut également être réalisée par l'évaluation des réponses sublétales. Par ailleurs, l'étude de ces réponses pourrait permettre d'identifier des indicateurs de perturbation toxique plus **précoces** et de ce fait, **prédictifs de la sensibilité et de la vulnérabilité** des populations *in situ*.

Les effets sublétaux des toxiques sur les populations d'espèces résistantes, qu'elles soient tolérantes ou sensibles, peuvent être élucidés par la modification de l'expression de traits biologiques et écologiques, pouvant indiquer un niveau de contrainte ou une adaptation à la contamination dans l'environnement considéré. Nous avons ainsi pu montrer que l'expression de certains traits permettait de diagnostiquer les effets des toxiques *via* leur modification le long d'un gradient de perturbation ou *via* la confrontation des amplitudes de niche théorique et réalisée (article 4). Dans la mesure où l'amplitude de niche théorique détermine la gamme de réponse possible d'une espèce à la perturbation, l'étude de la niche réalisée permet de mesurer ses réponses dans un environnement donné, et **l'écart entre les deux niches permet d'identifier le niveau de contrainte environnemental** ainsi que le risque d'extinction des populations (soit leur vulnérabilité). Ces réponses sublétales peuvent se traduire aux niveaux supérieurs d'organisation biologique (communautés et écosystème) si le stress toxique persiste et si l'espèce considérée est fonctionnellement dominante et efficace.

Le développement d'outils au niveau populationnel par la sélection d'espèces et traits indicateurs des effets des perturbations est important pour comprendre les **liens mécanistiques** entre réponse biologique et contaminants et pour améliorer **la pertinence écologique** des méthodologies d'évaluation des risques basées sur des études expérimentales. Identifier les traits biologiques et écologiques qui expliquent la sensibilité des espèces indicatrices aux contaminants pourrait permettre par exemple, de sélectionner des espèces modèles **partageant un profil bioécologique similaire** et dont le suivi des réponses en laboratoire serait alors plus **représentatif des réponses** des populations *in situ*.

Néanmoins, l'extrapolation de ces réponses aux niveaux d'intégration biologique supérieurs reste difficile et réductrice: (i) **au niveau des communautés**, comme le définit le **principe d'exclusion compétitive** (Gause, 1934), aucune espèce ne partage complètement sa niche avec une autre espèce ; par conséquent, l'existence d'une parfaite correspondance des réponses biologiques des espèces indicatrices et des autres espèces occupant le même environnement est donc peu probable ; (ii) **au niveau des écosystèmes**, cette extrapolation suppose que les espèces considérées soient des **espèces ingénieurs ou clés** et qu'elles **contribuent seules** à la réalisation des processus écosystémiques, ce qui minimise l'importance de la redondance fonctionnelle au sein des les communautés macrobenthiques (compensation des effets létaux et sublétaux sur les populations). Bien que les espèces et les traits indicateurs peuvent être choisis parce que pouvant induire un effet direct ou indirect sur

les autres espèces et sur les processus écosystémiques (ex. espèces ingénieurs, trait fonctionnel), ce type d'approche ne peut à l'heure actuelle, se substituer intégralement à l'étude des effets aux niveaux supérieurs d'intégration biologique.

2.2. Utilisation des profils de traits biologiques et écologiques des communautés

Bien que la contamination des sédiments induise une modification de la structure taxonomique des communautés de macroinvertébrés, l'étude des **profils bioécologiques** est plus appropriée pour **discriminer l'impact** de cette contamination (articles 1, 2, 3) et en déterminer les effets au niveau écosystémique (articles 5 et 6). Outre sa capacité à établir un **lien causal** entre réponses biologiques et perturbation, cette approche **intègre directement les effets létaux** des toxiques sur les populations et permet de **prédire les effets potentiels sur le fonctionnement des écosystèmes**. En effet, les traits biologiques et écologiques ont été plus sensibles aux modifications environnementales que la mesure du processus de décomposition des litières (mécanismes de compensation) en révélant l'impact de la perturbation physique sur les communautés en aval, non détecté par le suivi du processus (article 6). L'aptitude des traits biologiques et écologiques des communautés macrobenthiques à évaluer les impacts de perturbations multiples a déjà été rapportée (Statzner et Bêche, 2010; Wooster *et al.*, 2011) et, pourraient être complémentaire au suivi du processus de décomposition des litières. Par conséquent, il apparaît primordial d'explorer **la contribution des traits** des communautés **au fonctionnement de l'écosystème** et de ce fait de distinguer les traits réponse et les traits d'effet.

Nous avons par exemple identifié des traits qui varient avec la contamination des sédiments (pontes et œufs libres, formes de résistances, racleurs, parasites, α-mesosaprobe) et la présence de barrage (oligosaprobe, diapause, température) dont la variation n'induit pas d'effet sur le processus de décomposition des litières (traits de réponses) et des traits dont la variation a aussi un effet sur le processus (traits de réponses et d'effets) tels que la taille maximale, le mode de dispersion, le régime alimentaire ou encore le type de nourriture. Cette relation entre profils bioécologiques des communautés de macroinvertébrés et processus écosystémique est rarement examinée, alors qu'elle pourrait améliorer les méthodologies

d'évaluation des risques écologiques *via* la sélection et le suivi de traits d'effets qui intègrent les réponses des communautés aux perturbations et leurs conséquences sur le fonctionnement des écosystèmes. Par ailleurs, la diversité fonctionnelle, issue des profils de traits des communautés, permet d'évaluer conjointement les capacités de résilience et de résistance des communautés à la présence de perturbations et mériterait donc d'être considérée pour prédire les réponses biologiques à des projets de restauration.

L'étude des traits et de la diversité fonctionnelle des communautés peut également être développée pour le **compartiment microbien**, bien que plus difficile d'un point de vue méthodologique. Notre étude du compartiment microbien dans les sédiments nous a permis d'élucider l'intérêt d'une approche fonctionnelle dans l'évaluation des impacts associés à la contamination métallique. En effet, à la différence de l'examen de la **structure** des communautés microbiennes, l'étude du potentiel métabolique nous a permis de mettre en évidence un impact de la perturbation sur le profil fonctionnel des communautés bactérienne (article 3). Par ailleurs, la colonisation des feuilles par les Hyphomycetes pourrait être influencée par les traits des conidies en plus de la structure foliaire (Dang *et al.*, 2007). Fernandes et ses collègues (Fernandes *et al.*, 2011) examinent comment la diversité de ces traits (*via* le remplacement d'un type fonctionnel provenant d'un site de référence par celui d'un site contaminé par les métaux) affecte la production fongique et la décomposition des feuilles en présence de contamination métallique. Ils mettent en évidence une sélection de traits dans les communautés des stations contaminées qui permet de maintenir la production fongique et la réalisation du processus écosystémique et proposent d'**incorporer les mesures de diversités fonctionnelles basées sur les traits dans les études qui examinent les effets de la biodiversité sur le fonctionnement** des écosystèmes.

Du fait d'un manque d'information sur la taxonomie et l'écologie des Hyphomycetes aquatiques, l'utilisation des approches basées sur les traits pour le compartiment fongique reste aujourd'hui limitée. Bien que l'utilisation des approches moléculaire soit intéressante pour évaluer le pool des espèces présentes dans un milieu, la définition et la description des traits nécessite une **caractérisation taxonomique précise** des espèces présentes et actives par des méthodes d'identification visuelle des spores après prélèvement dans la colonne d'eau, dans l'écume ou par sporulation sur la matière organique en décomposition. Notre étude de la structure des communautés fongiques associées aux feuilles en décomposition (article 7) par les méthodes moléculaires nous a certes fourni une image globale de la richesse des

peuplements fongiques mais ne nous a pas permis d'identifier les espèces actives dans le milieu et de déterminer leur contribution au processus de décomposition (absence de lien traits-performances). L'apport conséquent d'une meilleure prise en compte de ce compartiment pour la compréhension du fonctionnement écologique des écosystèmes justifierait l'essor de recherches complémentaires sur l'écologie et la taxonomie des Hyphomycetes aquatiques, conditions *sine qua non* pour la construction d'une base de traits robuste et l'exploration du lien diversité fonction.

D'une manière générale, l'étude de l'expression des traits dans les communautés est primordiale dans la mesure où la sélection de traits en réponse à la contamination peut i) **altérer la réalisation des processus écosystémiques**, ii) **augmenter la vulnérabilité** des communautés à une nouvelle perturbation (perte de résistance) et iii) **limiter les capacités de récupération** des communautés dans le cas de retrait de la perturbation (perte de résilience). Pour autant, l'expression des traits biologiques et écologiques dans les communautés **n'intègre pas** directement les conséquences des **effets sublétaux** des populations sur le fonctionnement des écosystèmes. En sous-estimant l'importance des impacts directs de la perte de performance des populations dans la réalisation des processus écosystémiques, les méthodologies d'évaluation des risques écologiques uniquement basées sur les profils de traits dans la communauté pourraient manquer de sensibilité quant à la prédiction des effets des perturbations sur le fonctionnement des écosystèmes.

2.3. Utilisation des processus écosystémiques comme intégrateurs des réponses létales et sublétales aux perturbations

Dans la mesure où à l'heure actuelle aucun indicateur aux niveaux des populations et des communautés ne permet de prédire les effets des perturbations sur le fonctionnement des écosystèmes, il est nécessaire d'intégrer le suivi de processus écosystémiques dans l'évaluation des risques écologiques associés à la présence de sédiments contaminés. L'intérêt d'un diagnostic basé sur ce niveau ultime d'organisation biologique est l'**intégration des réponses létales et sublétales** des niveaux d'organisations inférieurs à la présence de perturbations.

La **décomposition des litières** et le **conditionnement des feuilles** par le compartiment fongique ont été des **outils sensibles pour identifier les effets de la contamination métallique des sédiments** (article 6 et 7). La sensibilité des taux de décomposition s'explique essentiellement par les effets de la contamination des sédiments sur le compartiment macrobenthique, dans la mesure où les taxons les plus sensibles sont essentiellement des taxons appartenant à la guilde des déchiqueteurs. L'étude du **conditionnement** de la ressource détritique par le compartiment fongique est quant à elle une approche intéressante dans l'**évaluation des impacts des perturbations multiples**, dans la mesure où la biomasse fongique répond de manière cumulée aux modifications d'écoulement et à la contamination des sédiments. Concernant l'étude des effets des perturbations sur le **fonctionnement des retenues**, le déploiement de **chambres benthiques** semble être l'outil le plus approprié car les flux benthiques sont **intégrateurs** à la fois des **modifications structurelles** des communautés microbiennes et macrobenthiques mais également de la **rupture du processus de décomposition**. Par ailleurs, cette approche à l'avantage d'être peu coûteuse, facile à utiliser et permet de prédire les impacts de la présence du barrage sur la qualité de l'eau des écosystèmes en aval. Cependant, le fonctionnement d'un écosystème est la résultante de nombreux processus (multifonctionnalités des écosystèmes). Puisqu' ils peuvent répondre de manière différentielle aux perturbations et que l'altération de l'un d'entre eux peut affecter la réalisation des autres, il serait intéressant d'intégrer le suivi de plusieurs processus dans les méthodologies d'évaluation des risques écologiques associés à la présence de retenues.

Par ailleurs, intégrer la mesure de processus fonctionnel dans l'évaluation des risques écologiques associée à la présence de retenues au fil de l'eau permettrait de faire le lien avec les services écosystémiques et de quantifier les pertes économiques associées aux perturbations ainsi que les gains dans le cas de restauration. Cette vision économique des écosystèmes est particulièrement importante pour la mise en place d'une gestion raisonnée, concertée et durable de la ressource en eau.

2.4. Conclusion

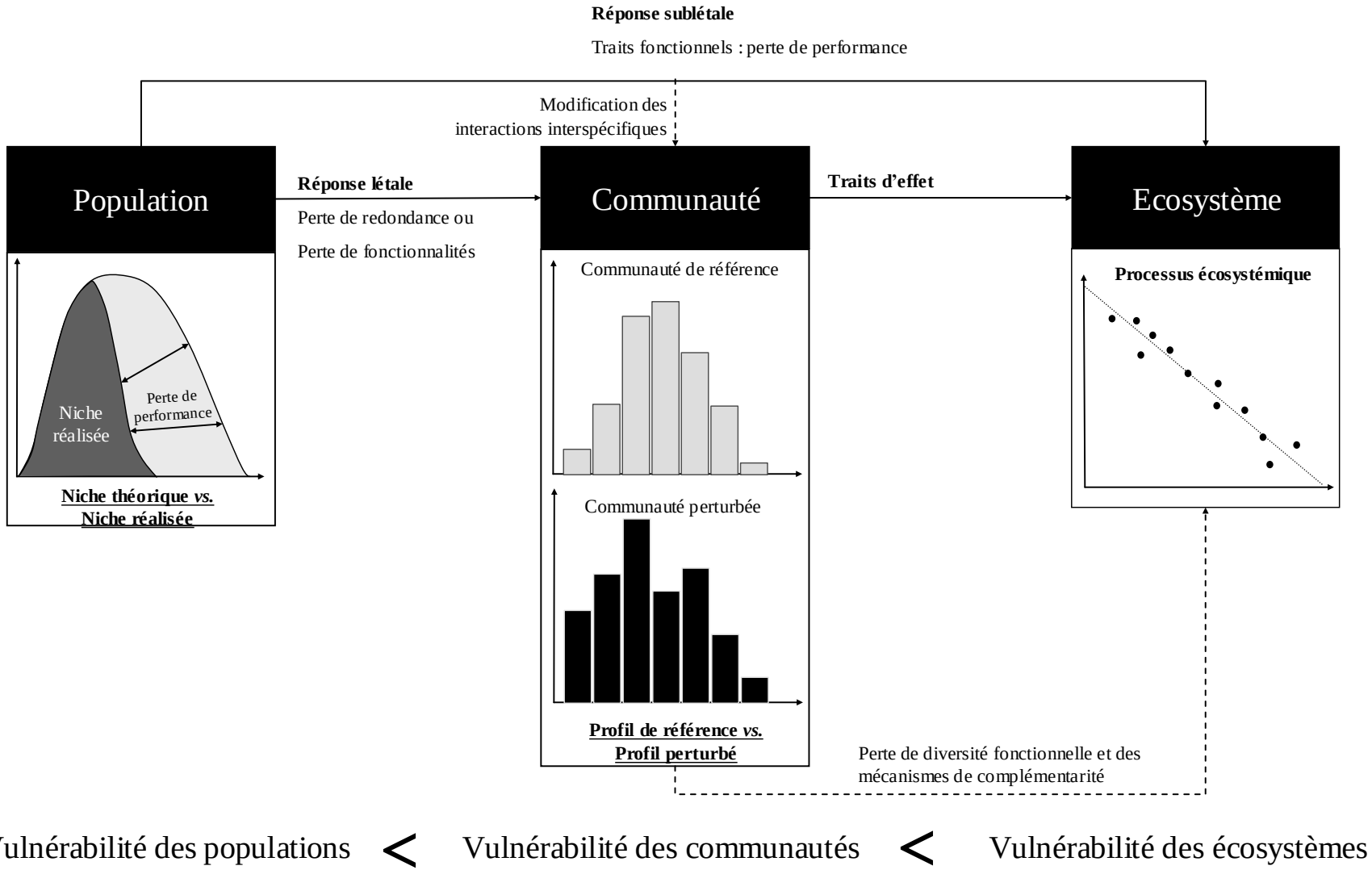
La difficulté des approches intégrées est la sélection d'indicateurs pertinents à chaque niveau qui intègrent les réponses du niveau inférieur d'organisation biologique et dont la variation induit un effet au niveau supérieur (prédictif). En permettant d'examiner et d'identifier les

liens entre les réponses des différents niveaux d'intégration biologique, le développement d'une approche basée sur les traits pourrait résoudre cette difficulté (Fig. 14).

Le niveau populationnel pourrait être intégré *via* le suivi sur des espèces indicatrices *in situ* (ex. *Ephemerella ignita*, *Leuctra major*) de réponses sublétales telles que la réalisation de traits biologiques et écologiques identifiés réponse et effet au niveau des communautés (régime alimentaire, cycle de reproduction, distribution de taille, stratégie d'occupation de l'espace). La réponse des traits des espèces indicatrices pourra être confrontée aux réponses observées aux niveaux supérieurs afin : (i) d'examiner si la variation dans l'expression des traits modifie les interactions interspécifiques (ex. compétition, facilitation, complémentarité) et la vulnérabilité des communautés aux toxiques et (ii) de sélectionner des traits (traits fonctionnels) dont la réponse modifie la contribution des populations à la réalisation des processus écosystémiques. L'étude des profils de traits biologiques et écologiques des communautés, quant à elle permet de définir un seuil de variation (réponse létale et sublétale) qui peut être compensé par la redondance fonctionnelle et servir de base à la prédiction des impacts sur les processus fonctionnels. Enfin la mesure de processus écosystémiques est indispensable pour identifier les traits fonctionnels et d'effet à intégrer dans les méthodologies d'évaluation des risques écologiques.

En conclusion, l'évaluation des risques écologiques induits par la présence de sédiments contaminés dans les retenues au fil de l'eau, en se basant sur la réponse des traits biologiques et écologiques, permettrait de définir l'état de vulnérabilité de l'écosystème à chaque niveau d'intégration biologique :

- ✓ au niveau des populations *via* la modification de l'expression des traits suite à l'interaction avec le milieu (abiotique et biotique),
- ✓ au niveau des communautés *via* la perte de redondance et de diversité fonctionnelle et,
- ✓ au niveau des écosystèmes *via* la perte (i) des mécanismes de complémentarité promu par la richesse et la diversité fonctionnelle des communauté et (ii) des performances des espèces dans la réalisation des processus écosystémiques.



Vulnérabilité des populations < Vulnérabilité des communautés < Vulnérabilité des écosystèmes

Fig.14 : Démarche méthodologique proposée dans l'évaluation des risques écologiques associée à la présence de sédiments contaminés dans les retenues au fil de l'eau, intégrative de la vulnérabilité de chaque niveau d'organisation biologique

Chapitre VI

Conclusion générale et perspectives

1. Le « bon fonctionnement » d'un écosystème : vision politique et concept théorique

Le bon fonctionnement d'un écosystème peut se référer aux rôles des espèces qu'il abrite, à la réalisation des processus et des services écologiques qui en résultent. Traditionnellement, le fonctionnement d'un écosystème est défini par l'**ensemble des activités, processus ou propriétés écosystémiques influencé par son biota** (Meyer, 1997; Naeem, 2002).

Si scientifiquement, l'importance du lien diversité-processus dans la définition et la compréhension du fonctionnement des écosystèmes est mondialement admise, les **cadres réglementaires** nationaux et européens de la gestion de la ressource en eau limitent son évaluation à des **aspects structuraux**. En effet, la Directive Cadre européenne sur l'Eau stipule que la qualité écologique des eaux de surface doit être quantifiée comme « une expression de la qualité, de la structure et du fonctionnement des écosystèmes aquatiques » où la structure se réfère aux paramètres physiques et chimiques et à la structure biologique des écosystèmes. Bien que le terme « fonctionnement » soit intégré dans la formulation, il n'est question d'aucune définition dans les textes réglementaires. La DCE suppose ainsi que la structure biologique (ex. composition spécifique, diversité, indicateurs basés sur les espèces sensibles) est directement liée au fonctionnement de l'écosystème (Sandin et Solimini, 2009). Cette absence de définition précise du fonctionnement d'un écosystème par la DCE entrave son évaluation et de ce fait la mise en place d'un suivi opérationnel de l'intégrité des écosystèmes aquatiques.

La mesure directe des paramètres structuraux comme attributs des aspects fonctionnels est un parti pris par la DCE relativement imprudent, dans la mesure où les relations biodiversité-fonction sont relativement méconnues, bien que de nombreuses hypothèses existent (cf. Chapitre I §2.3.5). Même si de nombreux travaux nous permettent aujourd'hui de mieux appréhender le fonctionnement d'un écosystème, **établir un lien entre structure des communautés et processus écosystémiques** reste un **défi majeur en écologie**. L'extrapolation des informations issues de l'évaluation de la diversité des communautés au niveau écosystémique, comme le conjecture la DCE, suppose que **chaque espèce contribue de manière unique** au fonctionnement de l'écosystème (hypothèse linéaire). Cette théorie

n'est pas toujours vérifiée et justifie la considération d'autres hypothèses qui soutiennent l'existence (i) de **redondance fonctionnelle** supposant une plus grande **sensibilité de la structure** que de la mesure des processus ou (ii) d'un lien diversité-fonction **dépendant du contexte** environnemental et imprévisible, justifiant l'**évaluation combinée** de la structure et des processus (Naeem, 2002).

Classiquement, les recherches sur les **relations diversité-fonction** se sont focalisées sur l'**identité des espèces** et de ce fait sur la richesse des communautés. Pourtant, utiliser la richesse comme une simple mesure de la diversité biologique manque de pouvoir explicatif (Hooper *et al.*, 2002) dans la mesure où les processus écosystémiques sont affectés par les caractéristiques fonctionnelles des organismes impliqués plutôt que par leur identité taxonomique. L'effet positif de la richesse spécifique sur la réalisation de processus fonctionnels peut être expliqué par la diversification des niches (mécanismes de complémentarité, ex. Tilman *et al.*, 2001; Kahmen *et al.*, 2006), les interactions facilitatrices entre les espèces (Cardinale *et al.*, 2002) ou encore par la contribution remarquable de quelques espèces dans la communauté (Loreau, 1998; Symstad *et al.*, 1998), mécanismes qui **dépendent finalement de l'expression des traits** des espèces (Naeem et Wright, 2003; Spooner *et al.*, 2011). En d'autres termes, il est primordial d'intégrer l'étude de la distribution des traits dans la recherche des mécanismes reliant la biodiversité et le fonctionnement des écosystèmes (Peterson *et al.*, 1998; Diaz et Cabido, 2001; Naeem et Wright, 2003; Suding *et al.*, 2008; Gessner *et al.*, 2010).

Tout au long de ce travail de thèse, nous avons pu constater que les effets des perturbations sur la structure taxonomique et fonctionnelle des communautés ne se répercutaient pas nécessairement sur le fonctionnement de l'écosystème, en concordance avec l'hypothèse de la présence de mécanismes de compensation (redondance fonctionnelle). Même si l'écosystème dégradé peut fonctionner de manière similaire à un écosystème intact, la perte de redondance diminue la capacité du système à résister aux perturbations et à de nouvelles pertes d'espèces. Les conséquences de la perte d'espèce peuvent ne pas être immédiatement visibles mais pour autant, la diminution de la richesse **affecte la résilience écologique** aux perturbations, produit **des écosystèmes plus vulnérables** aux effondrements écologiques et réduit la variété de réorganisations écologiques possibles (Peterson *et al.*, 1998). Sur cette hypothèse de l'existence d'une assurance biologique (Johnson *et al.*, 1996) contre les perturbations environnementales, il apparaît crucial d'**identifier les seuils au-dessous desquels les**

mécanismes compensatoires n'opèrent plus et conduisent à des modifications disproportionnées et parfois irréversibles des écosystèmes (Burkett *et al.*, 2005; Clements et Rohr, 2009). Une plus grande considération des seuils de réponses et des facteurs écologiques qui déterminent la résistance et la résilience des communautés est un enjeu majeur en écologie et en écotoxicologie et devrait améliorer notre capacité à prédire comment et quand les écosystèmes répondront et récupéreront de la présence de perturbations.

Un certain niveau de modifications biologiques et écologiques des communautés (RT : seuil de réponses) doit pouvoir être compensé, permettant le maintien des processus écosystémiques grâce à la redondance fonctionnelle des espèces dans la communauté ou encore grâce à la plasticité des niches au sein d'une population. Au-delà de ce seuil il est probable que les conséquences fonctionnelles soient disproportionnées et irrémédiables (ET : seuil d'effets). La recherche et la **définition de ces seuils** nécessitent la **considération des réponses <u>structurelles et fonctionnelles</u>** et devrait favoriser le développement de méthodologies d'évaluation des risques écologiques **prédictives des effets** sur le fonctionnement des écosystèmes.

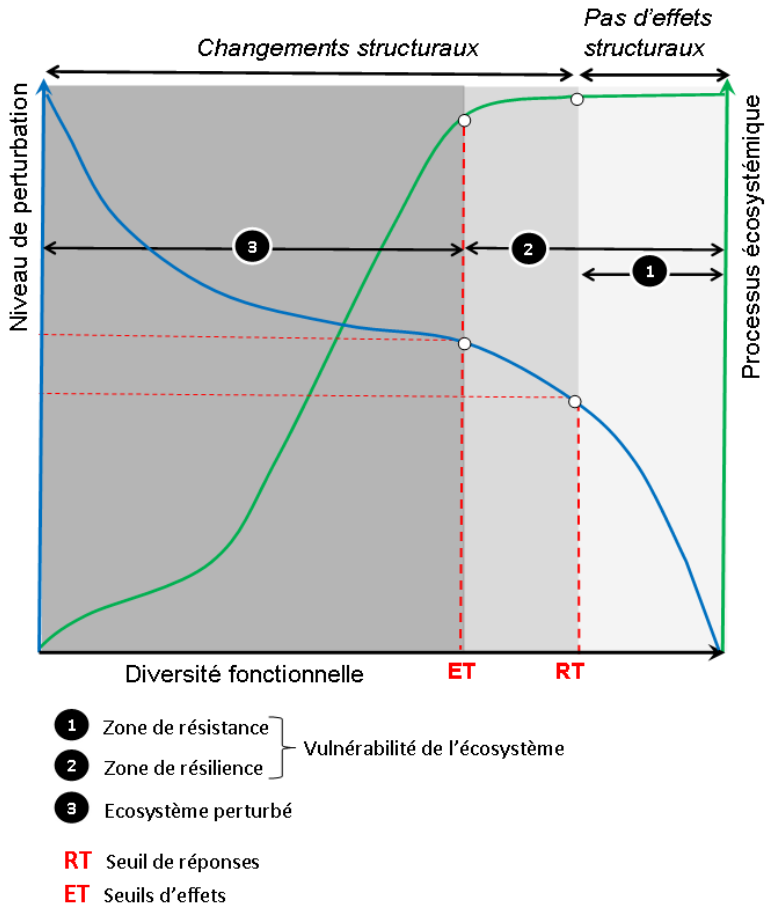


Fig.15 : Schéma conceptuel de la définition de seuils de résistance et résilience des communautés

L'identification de seuils de réponses basés sur les capacités de résistance et de résilience des communautés et consécutivement sur la vulnérabilité des écosystèmes est primordiale dans la **définition de la qualité des masses d'eau** et dans la **planification des mesures de gestion et de restauration** des écosystèmes aquatiques. Les seuils peuvent aider à **fixer des objectifs** appropriés de restauration et **sélectionner des indicateurs écologiques** permettant de suivre l'efficacité de cette restauration (Ryder et Miller, 2005). Si les mesures de restauration sont prioritairement préconisées pour les écosystèmes perturbés, davantage d'effort devrait être conduit dès le seuil de réponse et avant que le seuil de résilience soit dépassé (Fig.15, zone 2) puisqu'au-delà (zone 3), l'existence d'états alternatifs pourrait retarder la récupération de l'écosystème. Pour les écosystèmes perturbés (zone 3), le **premier objectif** de qualité à atteindre dans le cas d'une restauration est la **récupération des processus fonctionnels**, pré requis d'une récupération structurelle totale. La mesure du processus de décomposition des litières pourrait être un processus facile à utiliser en routine afin d'évaluer le succès de la restauration fonctionnelle (Gessner et Chauvet, 2002). Le **deuxième objectif**, sans doute le plus difficile à atteindre, est la **récupération** (structurelle) des **capacités de résilience** des communautés (Clements *et al.*, 2010), essentielle afin de **garantir la durabilité des effets de la restauration**.

En conclusion, suivant la logique établit par la DCE qui détermine l'état fonctionnel d'un écosystème via l'évaluation des aspects structuraux, le **bon fonctionnement d'un écosystème** pourrait être défini par **sa capacité à subir une perturbation tout en maintenant les processus écosystémiques** (soit par ses capacités de résilience). Par conséquent, un écosystème fonctionnellement perturbé devrait être définit **sur son état de vulnérabilité** et pas seulement sur la perturbation effective du processus (Fig.16). Cette vulnérabilité telle que défini par Williams et Kapustka (2000) est le potentiel d'un écosystème à moduler sa réponse aux facteurs de stress dans le temps et l'espace, où ce potentiel est déterminé par les caractéristiques d'un écosystème qui inclut **plusieurs niveaux d'organisation biologique**.

Il nous paraît essentiel de définir le bon fonctionnement d'un écosystème à de plus bas niveaux d'intégration afin d'anticiper les mesures de préservation, gestion et restauration de la ressource en eau et d'appliquer **le principe de précaution** : «*en cas de risque de dommages graves et irréversibles, l'absence de certitudes scientifiques absolue ne doit pas servir de prétexte pour remettre à plus tard l'adaptation de mesures effectives visant à prévenir la*

dégradation de l'environnement » (principe 15,Organisation des Nations Unies, convention de Rio, 1992).

L'utilisation des traits des macroinvertébrés aux différents niveaux d'organisation est d'un grand intérêt pour évaluer la vulnérabilité écologique et présente également l'avantage d'être intégré dans les programmes actuels d'évaluation sans effort d'échantillonnage additionnel (Baird *et al.*, 2008; Culp *et al.*, 2010; De Lange *et al.*, 2010). Outre le compartiment macrobenthique, la diminution de la diversité des réseaux trophiques (diversité verticale) peut profondément altérer les relations diversité-fonctions (Duffy *et al.*, 2007). Par exemple, nous avons évoqué à de nombreuses reprises l'importance du compartiment microbien dans la réalisation des processus écosystémiques et dans la réponse des communautés de macroinvertébrés. Il est peu probable que la réponse d'un seul compartiment puisse permettre d'évaluer efficacement la vulnérabilité des écosystèmes tout comme il l'est également d'observer les réponses à un seul niveau d'intégration biologique. Nous préconisons que les futures recherches se concentrent sur la compréhension des facteurs qui influencent la sensibilité et l'exposition des populations et des communautés de plusieurs compartiments aux perturbations environnementales et leur influence sur les processus fonctionnels et la vulnérabilité des écosystèmes. A cette condition, nous pourrons **anticiper les effets des perturbations et mettre en place une politique de gestion et restauration environnementale préventive et durable de la ressource en eau**.

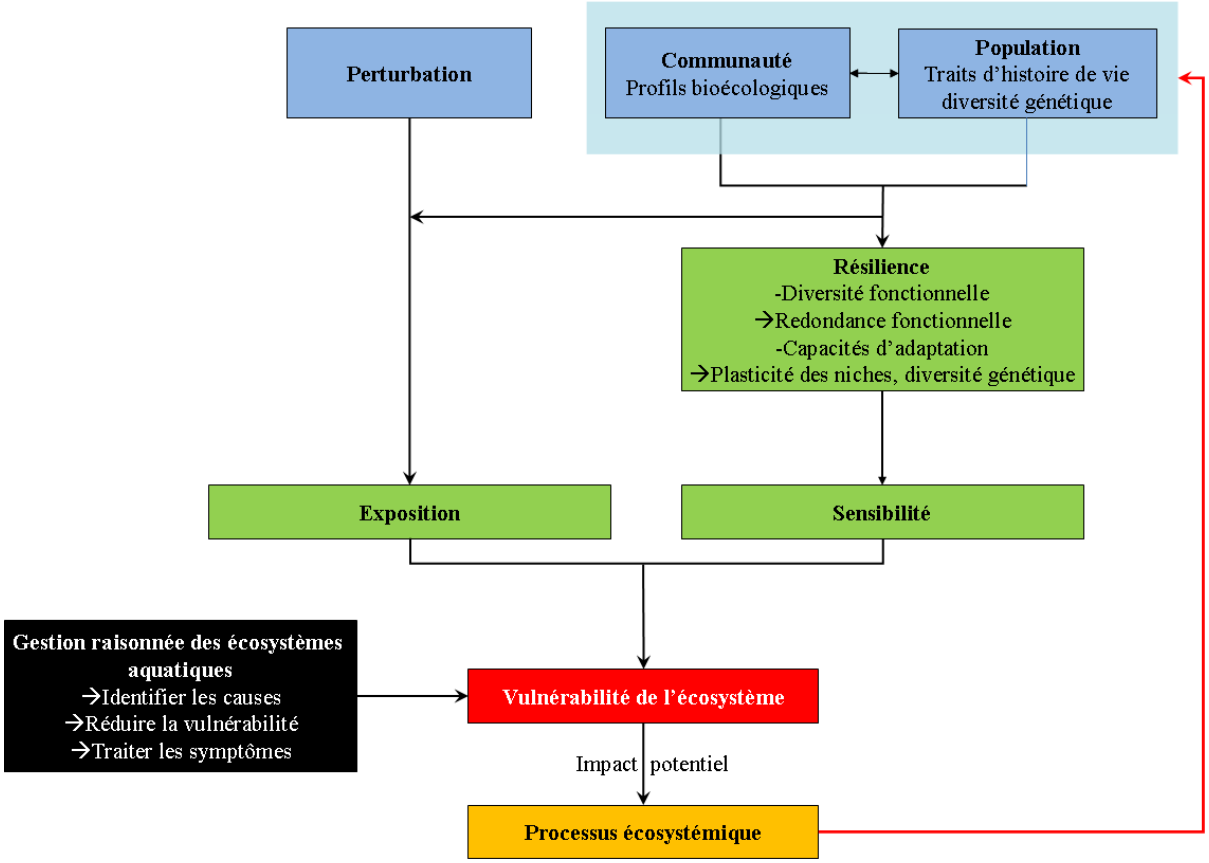


Fig.16 : Procédure générale pour évaluer la vulnérabilité d'un écosystème soumis à une perturbation. Cette vulnérabilité est fonction de la sensibilité et de l'exposition des communautés et des populations qui sont gouvernés par l'expression des traits biologiques et écologiques des organismes (adapté de Williams *et al.*, 2008).

2. Bilan et perspectives

L'ensemble de ces travaux de thèse a permis de mettre en évidence les risques écologiques associés à la présence de sédiments contaminés dans les retenues au fil de l'eau. Les résultats obtenus soulignent l'importance de considérer l'existence de multiples facteurs de stress, en étudiant et en intégrant leurs effets sur plusieurs échelles d'observations spatiales (habitat, berges/chenal, retenue, écosystèmes en aval) et biologiques (compartiment microbien et macrobenthique, de la population à l'écosystème), afin de mieux appréhender les différentes composantes de la vulnérabilité d'un écosystème à la contamination historique des sédiments de retenues au fil de l'eau.

Bien que nos travaux aient apporté des éléments de réponse quant aux mécanismes qui influencent la diversité et le fonctionnement des retenues au fil de l'eau, ils n'ont concerné qu'un nombre limité de sites d'étude. De plus amples recherches devraient être entreprises afin d'évaluer les impacts de la contamination des sédiments dans un plus grand nombre de retenues aux contextes géographiques différents. D'une manière générale, il semble nécessaire d'examiner plus finement les effets de la qualité de ces systèmes sur les écosystèmes en aval. D'autres perturbations peuvent se combiner à la contamination métallique des sédiments dans les retenues telles que la présence d'autres contaminants, l'augmentation de la température, l'eutrophisation et la variation des niveaux d'eau (marnage). Leur intégration dans la définition et l'évaluation du bon potentiel écologique de ces systèmes devrait être considérée et promouvoir de futurs travaux de recherche.

Afin de mieux discriminer les effets des contaminants stockés dans les sédiments, il apparaît essentiel de mieux caractériser les impacts physiques associés à la présence de barrage. Une évaluation plus précise de l'évolution de la qualité hydromorphologique et l'intégration de variables physiques dans des modèles d'habitat-hydraulique pour les macroinvertébrés, à l'instar de ceux développés pour les poissons (Lamouroux *et al.*, 1999; Lamouroux *et al.*, 2002), pourraient permettre de mieux identifier les effets des perturbations physiques. Bien que nous ayons clarifié l'importance de la contamination des sédiments sur la structuration des réponses biologiques, les réponses à la présence de barrière physique sont moins évidentes. Toutefois, il serait intéressant d'éprouver ces résultats en examinant les mêmes réponses biologiques le long d'un gradient de perturbation physique, allant de la présence de petits seuils à des barrages excédant 5 mètres de haut.

Il a été difficile dans la réalisation de ces travaux de thèse, de dissocier les effets de la contamination des sédiments de l'impact de l'accumulation de sédiments fins eux-mêmes. Une approche en mésocosmes pourrait résoudre la difficulté de dissocier les effets *in situ*, en permettant de contrôler les apports en sédiments fins d'une part et les niveaux de contamination d'autre part. Cela permettrait de discriminer l'importance relative des deux perturbations sur les réponses des populations, des communautés et des processus fonctionnels associés. Enfin l'importance et le lien entre les différentes échelles spatiales devraient être examinés avec plus d'attention. La contribution des apports d'espèces des rivières en amont à la diversité des retenues ainsi que les transferts d'espèces et d'énergie entre les berges et le chenal pourraient être étudiés et permettre de mieux appréhender la

structuration des écosystèmes retenues et leur vulnérabilité. Par ailleurs, il serait intéressant d'étudier plus finement dans quelle mesure la diversité et le fonctionnement des retenues influencent la résilience des écosystèmes en aval des barrages.

Nous avons montré à plusieurs reprises l'avantage d'utiliser les traits biologiques et écologiques au niveau des populations et des communautés à la fois dans la discrimination des impacts toxiques et physiques et comme variables prédictives des processus écosystémiques (Kremen, 2005). Il apparaît essentiel de développer les recherches sur l'identification des corrélations entre traits de réponse et efficacité fonctionnelle (trait d'effet) afin de prédire les capacités de résistance et de résilience des communautés et des populations aux perturbations (Walker *et al.*, 1999; Elmqvist *et al.*, 2003; Culp *et al.*, 2010). Il est maintenant admis que les traits fonctionnels et leur diversité sont un déterminant important des processus de l'écosystème ainsi les changements dans la diversité fonctionnelle seraient indicateurs de changements dans le fonctionnement des écosystèmes (Tilman *et al.*, 1997; Hulot *et al.*, 2000; Hooper *et al.*, 2002; Diaz *et al.*, 2003; Petchey et Gaston, 2009). Il reste nécessaire d'explorer le rôle des différentes composantes dans les relations diversité-fonction, afin d'aider à l'identification de seuils au-delà desquels le système évolue vers un état alternatif pouvant être irréversible, et ainsi de mettre en place une gestion préventive des écosystèmes aquatiques.

L'étude de la diversité fonctionnelle au sein des groupes fonctionnels ou des communautés devrait nous permettre de mieux appréhender les mécanismes de complémentarité et de compensations (Tilman *et al.*, 1997; Elmqvist *et al.*, 2003). De même, afin d'identifier et de caractériser de manière pertinente ces mécanismes, l'intégration du suivi de plusieurs compartiments dans les recherches sur les relations diversité-fonction et dans la définition de la vulnérabilité des écosystèmes est nécessaire (Hillebrand et Cardinale, 2004; Duffy *et al.*, 2007), ainsi que la prise en compte des « effets cascades » (effets top-down et bottom-up). Enfin, l'examen des facteurs intrinsèques à la diversité des communautés (dissimilarités fonctionnelles, compétition, diversité verticale…) et extrinsèques (perturbations, qualité de la ressource alimentaire…) qui influencent ces mécanismes nous semble primordial pour la compréhension de la vulnérabilité d'un écosystème.

Concernant l'étude des processus fonctionnels, il apparaît essentiel d'explorer les réponses aux perturbations de plusieurs processus simultanément. Associés à l'étude des processus de

décomposition des litières, de bioturbation et des flux benthiques, d'autres processus tels que le transport de particules organiques fines (Wallace *et al.*, 1996), les taux d'absorption des nutriments (Sabater *et al.*, 2000; Hall et Tank, 2003) et le métabolisme des écosystèmes (Houser *et al.*, 2005; Tank *et al.*, 2010) pourraient être examinés. Outre l'importance de caractériser la multifonctionnalité des écosystèmes (Hector et Bagchi, 2007), le suivi des réponses aux perturbations de plusieurs processus pourrait permettre d'identifier les effets compensatoires et/ou indirects pouvant probablement se produire aussi à cette échelle d'intégration biologique. Nous proposons d'explorer l'utilisation des chambres benthiques et des activités de bioturbation *in situ* afin de caractériser le fonctionnement des retenues au fil de l'eau et d'une manière générale les systèmes lentiques, et d'identifier les enjeux de la gestion de la qualité des sédiments. Le déploiement des chambres benthiques devrait être réalisé par un suivi saisonnier afin d'intégrer les effets de la température et de l'oxygène sur l'activité biologique et les comportements d'adsorption et désorption des sédiments, cela, conjointement au suivi de la qualité de l'eau dans les retenues (eau interstitielle et colonne d'eau) et en aval des barrages. Par ailleurs, il serait intéressant d'étudier les effets des vidanges et du marnage sur la structuration des communautés microbiennes et macrobenthiques et sur le potentiel redox des sédiments, celui-ci pouvant fortement influencer la nature et l'intensité des flux benthiques. L'exondation des sédiments, pendant les vidanges et lors du retrait de barrage, induit une réoxygénation pouvant favoriser la remobilisation des contaminants (Saeki *et al.*, 1993; de Carvalho *et al.*, 1998; Ahearn et Dahlgren, 2005). Cette considération des risques associés au devenir des sédiments contaminés dans le cas de retrait de barrage devrait être intégrée dans la mise en place des mesures de gestion et de restauration, et pourrait conduire au curage des sédiments ou à des projets de phytoremédiation dans l'emplacement du réservoir (Riggsbee *et al.*, 2011).

Il est probable que la disponibilité et la distribution des nutriments, associées à la présence de barrage et au fonctionnement biogéochimique des sédiments, influencent fortement les processus de décomposition des litières. De tels liens devraient être examinés en mésocosmes et *in situ*. Par ailleurs, certaines études ont évalué l'importance de la structure du sédiment (porosité) sur le devenir des litières enfouies (Cornut *et al.*, 2010; Navel *et al.*, 2010). Il pourrait être intéressant d'étudier les effets du devenir de cette matière organique sur le fonctionnement biogéochimique des sédiments (flux benthiques et bioturbation). L'étude de la qualité de la ressource alimentaire et des habitats devrait être intégrée dans la compréhension de la vulnérabilité des écosystèmes aux perturbations. Par exemple, au niveau

des sédiments, il serait intéressant d'évaluer dans quelle mesure les sédiments riches en nutriments peuvent contrebalancer les effets de la contamination sur les organismes associés au fonctionnement biogéochimique des sédiments. Concernant les litières, nous avons évalué la qualité de la ressource en étudiant le compartiment fongique et les ratios élémentaires des feuilles. Le suivi de l'accumulation des contaminants sur les surfaces foliaires et le biofilm (D'Souza *et al.*, 2006; Watanabe *et al.*, 2008; Purchase *et al.*, 2009; Schaller *et al.*, 2011) pourrait également être réalisé et permettre une meilleur caractérisation de l'exposition des consommateurs aux contaminants. Enfin, dans la mesure où la qualité de la ressource ainsi que la compétition peuvent fortement influencer la vulnérabilité des individus et des populations à la présence de toxiques, des études complémentaires en laboratoire et en mésocosmes pourraient être développées.

D'une manière générale, les méthodologies d'évaluation des risques associés à la présence de sédiments contaminés devraient intégrer une identification précise de l'exposition des organismes aux contaminants (caractérisation chimique, biodisponibilité, formes des contaminants dans les sédiments et sur l'ensemble des habitats et des ressources alimentaires). Elles devraient également utiliser des approches en laboratoires ou en mésocosmes sur des espèces modèles choisies via la concordance de leurs traits biologiques et écologiques avec les profils identifiés comme intégrateurs de la vulnérabilité des populations et des communautés. Enfin, des approches *in situ* devraient être développées pour confronter les résultats obtenus en laboratoire avec les réponses des populations, des communautés et des processus qu'elles assurent.

Tout au long de ce travail, nous avons été confrontés à une parfaite méconnaissance des retenues au fil de l'eau parce que déconsidérées par les scientifiques, comme la plupart des écosystèmes aquatiques d'origine anthropique, et par les politiques environnementales nationales et européennes du fait de leur complexité et sans doute des pressions sociétales omniprésentes sur ce type de système (production d'hydroélectricité, agriculture…). Pourtant, la présence de sédiments contaminés dans les retenues menace profondément l'intégrité des écosystèmes aquatiques et nécessiterait d'être identifiée prioritairement dans les enjeux de préservation et de gestion de la ressource en eau. Plus de soixante mille obstacles similaires à ceux que nous avons étudiés ont été identifiés en France, et sont autant de sources potentielles de contamination et de « bombes à retardement » dans le cas de remise en suspension des sédiments et de retrait de barrage sans contrôle préalable. Aux retenues déjà existantes,

viendront peut-être s'en ajouter de nouvelles promues par le projet d'un décret (modification de l'article R.214-1 du code de l'environnement) visant à faciliter leur création pour l'irrigation (actuellement proposé à la consultation du public). La création de ces retenues ne sera plus soumise, comme prévue par le code de l'environnement, à autorisation mais à une simple déclaration qui n'engage pas à la réalisation d'étude d'impact ni à une enquête publique. Ce décret concernera l'ensemble des retenues jusqu'à 3 hectares ; les retenues que nous avons étudiées dans ces travaux de thèse ont une superficie comprise entre 2 et 7 hectares. Depuis la loi grenelle, l'inquiétude était principalement posée sur la nécessité de restaurer la continuité écologique des rivières fragmentées par une multitude d'obstacles et sur les modalités de cette restauration notamment dans le cas de contamination des sédiments stockés dans les retenues. Ce projet de décret avorte les engagements du grenelle et souligne un besoin urgent d'étudier et de comprendre le fonctionnement de ces systèmes afin de mieux appréhender et évaluer leur potentiel écologique et atténuer les effets sur les écosystèmes en aval ; à défaut de réussir à dissuader les acteurs de les construire.

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Résumé. A la fois témoins et acteurs de contamination, les sédiments constituent un élément essentiel des écosystèmes aquatiques qu'il convient de surveiller, évaluer et protéger. Les méthodes actuelles d'évaluation de leurs risques écotoxiques restent peu transférables aux écosystèmes, et ne rendent pas compte de la présence de multiples facteurs de stress abiotiques et biotiques. Les sédiments stockés par les seuils et barrages offrent l'opportunité de développer des méthodes originales de diagnose des réponses biologiques *in situ*. Six retenues au fil de l'eau dont les sédiments présentent un gradient de contamination métallique et organique ont été étudiées. Les effets de la contamination ont été explorés à différentes échelles spatiales et biologiques *via* des approches structurelles et fonctionnelles. Dans les retenues, en réponse à l'augmentation de la perturbation chimique, nos résultats montrent une sélection de cortèges faunistiques associée à une réduction de la diversité taxonomique et fonctionnelle. Des réponses sublétales des macroinvertébrés ont été identifiées, notamment sur les niches spatiales, les régimes alimentaires ou la compétition interspécifique. La contamination des sédiments impacte aussi le potentiel métabolique bactérien et la richesse et la biomasse fongique. L'ensemble de ces altérations biocénotiques se traduisent au niveau écosystémique par la rupture du processus de décomposition des litières et la modification des flux benthiques à l'interface eau-sédiment. Les écosystèmes en aval sont également perturbés *via* la remise en suspension des sédiments contaminés, l'altération de la qualité de l'eau et les effets en cascades des réponses structurelles et fonctionnelles des communautés des retenues. L'ensemble de nos résultats soulignent les enjeux de préservation de la qualité des sédiments et la nécessité de développer des méthodologies intégratives de la vulnérabilité à chaque niveau d'organisation biologique pour mieux appréhender l'état et les trajectoires écologiques des écosystèmes aquatiques.
Mots-clés: Sediment - Retenues au fil de l'eau – Perturbations multiples - Ecologie fonctionnelle

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Abstract. Sediment evaluation and monitoring is an essential part of ecosystem monitoring since sediments represent an important component of aquatic habitats and are also a potential source of contamination. Current methodologies of their ecotoxic risk assessment do not encompass ecosystemic responses and do not take into account multiple abiotic and biotic stressors. Run-of-river reservoirs entrap a large amount of sediments and constitute an opportunity to develop original risk assessment methodologies that integrate biological responses *in situ* and their potential effects for river ecosystem functioning. Six run-of-river reservoirs were selected to study the effects of sediment contamination at several spatial and biological scales, thanks to structural and functional approaches. Our results evidenced a selection in faunistic assemblages in response to contamination, associated with low taxonomic and functional diversity. Our results also evidenced sublethal responses, with niches shifts of invertebrate population and modification of biotic interactions. Sediment contamination has also impacted metabolic functional diversity of bacterial communities and fungal richness and biomass. These biocenotic alterations have resulted in disturbances in ecosystemic processes such as leaf breakdown and benthic flux at the water-sediment interface. Ecosystems downstream dams were also impacted, through resuspension of contaminated sediments, alteration of water quality and cascading effects related to structural and functional responses of reservoirs communities. Our findings evidenced challenges of the sediment quality preservation and the need to develop risk assessment methodologies based on the vulnerability at each biological scale in order to understand and elucidate ecological status and trajectories of aquatic ecosystems.
Keywords: Sediment – Run-of-river reservoirs – Multiple stressors – Functional ecology