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Sébastien GAYRAUD

Les sédiments du lit des cours d'eau : quantification de leur influence sur les peuplements de macro-invertébrés par une approche multi-sites

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Travaux réalisés dans le Laboratoire d'Hydroécologie Quantitative
Cemagref – Unité de Recherche en Biologie des Ecosystèmes Aquatiques.

SOMMAIRE

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RESUME

Le fond du lit des cours d'eau est depuis longtemps reconnu comme un élément fondamental des systèmes aquatiques en raison des nombreuses fonctions de production et de transformation d'énergie qui s'y produisent et par la faune diversifiée qu'il abrite. Il est caractérisé par des gradients longitudinal, latéral et vertical qui affectent sa composition, sa structure et ses propriétés physico-chimiques. Les variables qui définissent l'habitat interstitiel sont contrôlées par des facteurs à large échelle - géologie, climat, occupation du sol - et des facteurs locaux - géomorphologie, échanges hydriques -. Par ailleurs, cet habitat varie dans le temps en réponse à la mobilisation par les crues. Les peuplements d'invertébrés s'ajustent dans l'espace et dans le temps en réponse à ces variations d'habitat. Dans ce contexte, la problématique centrale réside dans la détermination des variables clés qui contrôlent l'ajustement des peuplements à cet habitat.

Une première partie est consacrée à explorer les relations entre les caractéristiques physiques des sédiments et le peuplement de macroinvertébrés. Les relations entre la composition granulométrique, le tassement vertical, la nature géologique des sédiments et la disponibilité de l'habitat interstitiel - porosité efficace - ont été testées sur près de 100 carottes de sédiments prélevés dans 17 sites d'étude. La disponibilité locale de l'habitat influence l'abondance et la diversité du peuplement, ainsi que l'assemblage des espèces par l'intermédiaire de leur morphologie qui détermine leur capacité à pénétrer dans les sédiments. Les invertébrés de petite taille et de forme cylindrique sont proportionnellement plus abondants dans les sédiments à faible porosité – c'est à dire les sédiments colmatés -. Ces préférences d'habitat basées sur la morphologie permettent d'expliquer des différences dans la structure des peuplements au niveau de sites d'étude se distinguant par leur degré de colmatage.

Une deuxième partie est consacrée à explorer l'influence sur les invertébrés des crues d'intensité suffisante pour mobiliser les sédiments du lit. L'hypothèse de la migration verticale des invertébrés en réponse à ces crues a été testée dans deux cours d'eau à l'aide d'un simulateur de crue. L'hypothèse a été rejetée mais une réduction de l'abondance en surface et une augmentation de la dérive ont été observées avec des différences entre les taxons. Les crues sont des événements fréquents qui peuvent être quantifiés par leur fréquence, leur intensité et leur durée. Nous avons testé leur influence sur les structures faunistique et fonctionnelle de 9 cours d'eau au régime hydrologique contrasté. La durée des crues est un facteur important qui structure les peuplements par le biais de traits biologiques décrivant les exigences trophiques, physiologiques ainsi que le comportement des invertébrés. Les invertébrés qui ont au moins un stade à l'extérieur du milieu aquatique, qui peuvent pondre hors du milieu aquatique, qui ont une valence trophique large – c'est à dire ceux qui sont peu exigents sur la nature de la ressource trophique - ou qui se nourissent par capture de matière organique dérivante - les organismes filtreurs -, sont proportionellement plus abondants dans les cours d'eau les plus perturbés – ceux pour lesquels le nombre de jours en crue et la durée des crues est maximale -. Au contraire, les invertébrés qui ont un fort attachement au substrat et qui se nourissent de matière organique déposée sont proportionellement moins abondants dans ces cours d'eau.

ABSTRACT

For a long time, bed-sediments are recognised as a major component of streams because they support a diversified fauna and primary production and transformation processes. Composition, structure and physic-chemical properties define the habitat for invertebrates. These characteristics are affected by longitudinal, lateral and vertical gradients acting at large scale - geology, climate, watershed characteristics - and local scale - geomorphology, hydraulic vertical gradients -. The habitat also exhibit temporal variations in response to scouring. These spatial and temporal variations create a template to which invertebrates communities are adapted to. The central questions is to determine the true variables governing communities structure.

The first part of this work deals with the relations between bed-sediment characteristics and invertebrate assemblages. We tested the influence of grain-size distribution, bed-packing and geology on the availability of the interstitial habitat for invertebrates, using about 100 frozen cores collected in 17 sites. The effective porosity influences abundance, richness and morphological traits of the invertebrates. Invertebrates that are small or with a cylindrical body shape exhibit are more abundant in habitats having low porosity. These preferences were found to explain variations in invertebrate abundance and invertebrate morphology among 17 sites.

The second part deals with the role of floods scouring bed-sediments on communities. The downward migration of invertebrates in response to floods was tested in 2 streams using a new technique that simulates the increase in velocity like in a flood. We rejected the hypothesis and we observed an increase in drifting animals with some differences between taxa. Floods are relative discrete events, frequent in time that are quantified in terms of frequency and duration. We tested their influence on community and functional structures of 9 streams differing by disturbance regime. Flood frequency and flood duration can also influence communities through biological traits describing functional feeding groups, invertebrate physiology or behaviour. We found that invertebrates having at least one stage outside the stream, ovipositing outside the water, being trophic generalist or being filter-feeders were more abundant in streams frequently disturbed - characterized by highest number of floods and highest flood duration -. In constrast, invertebrates strongly attached to the substrate and being detritivores were less abundant in these streams.

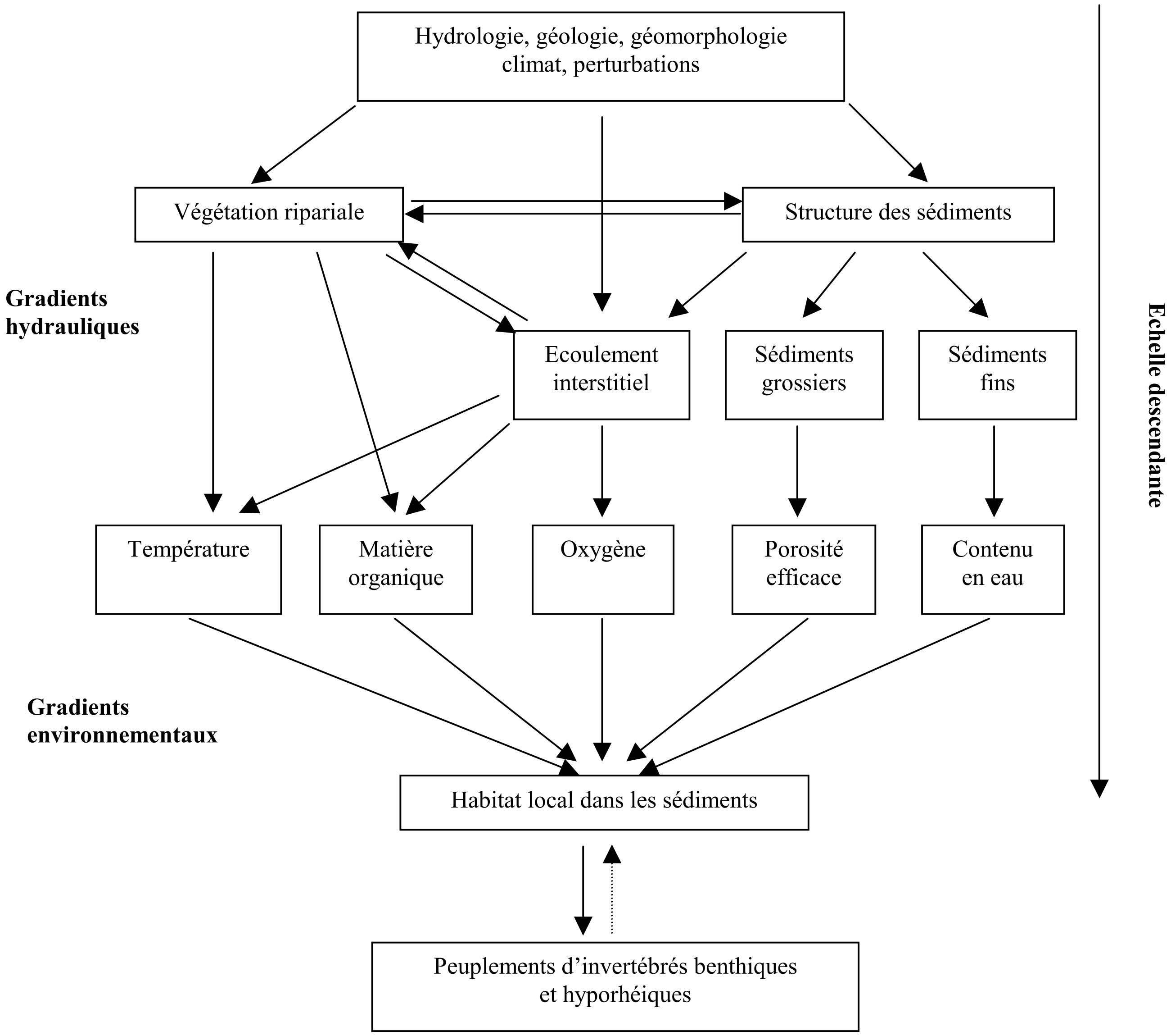


Figure 1. Hiérarchie des facteurs qui contrôlent l'habitat local dans les sédiments. (d'après Ward *et al.* 1998, modifié).

I – SYNTHESE : LES SEDIMENTS DU LIT DES COURS D'EAU : QUANTIFICATION DE LEUR INFLUENCE SUR LES PEUPLEMENTS DE MACRO-INVERTEBRES PAR UNE APPROCHE MULTI-SITES

INTRODUCTION

Le fond du lit des cours d'eau est depuis longtemps reconnu comme un élément fondamental des systèmes aquatiques en raison des nombreuses fonctions de production et de transformation d'énergie qui s'y produisent et par la faune diversifiée qu'il abrite. Toutefois, sa vision par les biologistes a considérablement évolué durant les cinquante dernières années, notamment par la prise en compte de sa dimension verticale et de sa position d'interface avec les eaux souterraines (Gibert *et al.*, 1997). Il est caractérisé par des gradients longitudinal, latéral et vertical qui affectent sa composition minérale et organique, sa structure et ses propriétés physico-chimiques (Brunke & Gonser, 1997 ; Brunke *et al.*, 1998 ; Ward *et al.*, 1998). En particulier, la granulométrie et la taille des interstices diminue avec la profondeur dans **les sédiments du lit**. De la même manière, la taille, l'abondance et la nature des ressources trophiques constituées par la matière organique évoluent également avec la profondeur (Leichtfreid, 1985 ; Rulik, 1994 ; Lenting *et al.* 1997). Enfin, le degré d'oxygénation, partiellement contrôlé par la diffusion à partir de la surface peut également fluctuer au sein des sédiments. Ces variables qui caractérisent partiellement l'habitat interstitiel sont contrôlées par des facteurs à large échelle – la géologie, le climat, l'occupation du sol - et des facteurs locaux (au sens de Frissell *et al.*, 1986) – la géomorphologie, les échanges hydriques - (Fig. 1). Cet ensemble de facteurs affecte fortement la distribution des invertébrés épigés et hypogés ce qui conduit à un assemblage d'espèces complexe (Brunke & Gonser, 1999 ; Strayer *et al.*, 1997), qui peut varier dans le temps en réponse aux variations d'habitat consécutives aux changements de débit (Dole-Olivier & Marmonier, 1992b).

Dans ce contexte, l'identification des variables clés qui contrôlent l'occupation de cet habitat constitue un challenge important à la fois du point de vue théorique et appliqué. Du point de vue théorique car elle est nécessaire à une meilleure compréhension du fonctionnement des cours d'eau. Du point de vue appliqué car elle est fondamentale pour créer des outils fiables de gestion et de prévision d'impact – par exemple en cas de colmatage - basés sur les mécanismes réels qui structurent les peuplements. L'identification de ces variables clés est particulièrement difficile en raison de la structure hiérarchique des systèmes aquatiques et de la multiplicité des facteurs qui influencent la distribution des espèces. Face à cette complexité, deux types de démarches permettent d'accéder aux mécanismes qui contrôlent la structure des peuplements. Tout d'abord, l'expérimentation en conditions contrôlées qui permet d'isoler différents facteurs et de quantifier leur rôle respectif sur des espèces cibles. Un des inconvénients de cette démarche réside dans la difficulté d'extrapolation des résultats à l'échelle du peuplement et à l'échelle du cours d'eau. La seconde démarche est basée sur la recherche de relations entre l'habitat et les invertébrés dans des conditions naturelles. Les nombreux

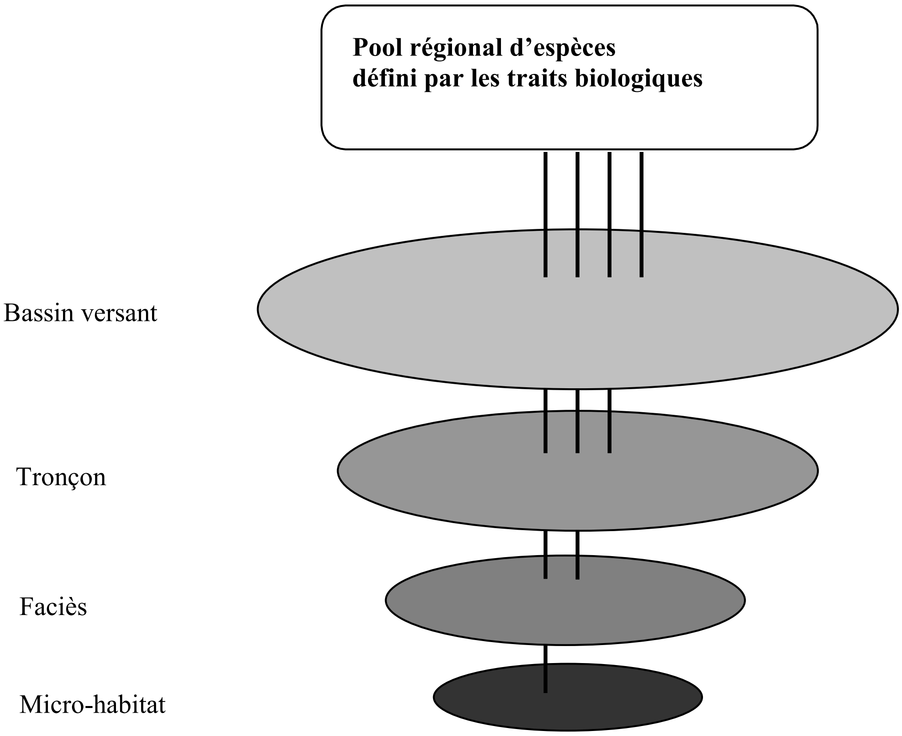


Figure 2. Schéma conceptuel du filtre multi-échelle. La distribution et l'abondance des espèces sont la conséquence de leur aptitude à passer les différents filtres. Par exemple, la présence d'une espèce dans un micro-habitat signifie qu'elle possède tous les traits lui permettant de survivre aux contraintes d'habitat cumulées par les différents niveaux (d'après Poff, 1997 modifié).

facteurs qui interagissent rendent la compréhension des mécanismes plus complexe, mais assure des fondements solides à ces relations lorsqu'elles sont communes à un large ensemble de sites d'études (Lamouroux, 1999). C'est la démarche qui a été suivie dans cette thèse et qui justifie l'utilisation du terme « **multi-sites** » dans le titre de la thèse.

Notre démarche s'inscrit dans le contexte théorique de l'« habitat template » (Southwood, 1977 ; Townsend, 1989 ; Townsend & Hildrew, 1994) dans lequel l'habitat constitue un cadre dont les caractéristiques varient dans l'espace et dans le temps. Le maintien ou l'élimination des espèces dans ce cadre est dictée par l'adéquation entre leurs traits morphologiques, physiologiques et comportementaux, et les caractéristiques de l'habitat. Cette approche des liens entre l'habitat et les organismes peut être appréhendée à plusieurs échelles spatiales afin d'intégrer la structure hiérarchique des cours d'eau. On peut ainsi définir un ensemble de variables d'habitat qui sont structurantes à ces différentes échelles (Poff, 1997) et qui constituent une série de filtres sélectionnant les espèces en fonction de l'adéquation de leurs traits aux contraintes imposées par les différents filtres (Fig. 2).

Dans ce schéma, les filtres qui agissent à large échelle ne permettent pas d'expliquer les variations locales de l'assemblage mais ils conditionnent la réponse moyenne des espèces aux conditions locales d'habitat. Sous l'hypothèse que les relations entre l'habitat local et les espèces sont fortes – par exemple les préférences des espèces pour la vitesse du courant ou la granulométrie -, l'intégration de ces relations au niveau des sites permettrait d'expliquer les différences de peuplement entre différents sites d'étude. Toutefois, l'expression de ces relations locales habitat-espèces au niveau des sites peut être modulée par l'action d'autres filtres agissant à plus large échelle tels que le régime de perturbations, la géologie ou la température. Dans ce contexte, l'étude des relations habitat-espèce à plusieurs échelles permet de comprendre comment les processus structurant localement les assemblages se traduisent au niveau des peuplements à plus large échelle (Levin, 1992 ; Peckarsky *et al.*, 1997). C'est cette approche qui a été utilisée pour déterminer l'influence des caractéristiques des sédiments sur les assemblages d'invertébrés décrits soit par leur structure faunistique soit par leur structure de traits biologiques.

Parmi les facteurs qui contrôlent la dispersion des invertébrés dans cet habitat interstitiel, **la porosité efficace** des sédiments – c'est à dire le volume d'interstices potentiellement colonisable par les invertébrés - à jusqu'à présent été peu étudiée malgré le rôle qu'elle pourrait exercer sur la colonisation des sédiments (Maridet *et al.*, 1992 ; Maridet *et al.* 1996). Maridet & Philippe (1995) montrent que la distribution verticale des invertébrés covarie de manière étroite avec l'évolution verticale de la porosité. Plus précisémment, ces auteurs ont observé une réduction de l'abondance en relation avec la diminution de la porosité efficace en profondeur. Ces résultats préliminaires ont suscité les recherches plus approfondies qui ont été effectuées au cours de cette thèse, d'une part afin de tester l'influence de cette variable indépendamment de la profondeur dans les sédiments et ce sur plusieurs sites d'études, et d'autre part afin d'étudier les facteurs qui contrôlent la porosité des sédiments.

Dans une première partie nous présenterons les relations entre la composition granulométrique des sédiments, la disponibilité de l'habitat interstitiel –la porosité efficace- et les peuplements d'invertébrés. Nous présenterons tout d'abord les facteurs qui contrôlent la porosité dans un cadre théorique et montrerons en quoi ces facteurs diffèrent dans le cas particulier des sédiments aquatiques. Ensuite, nous nous efforcerons de hiérarchiser l'influence des facteurs de contrôle que sont le degré de tassement des sédiments, la composition granulométrique et la nature des géologique des sédiments. La disponibilité de l'habitat interstitiel peut influencer l'assemblage des invertébrés par l'intermédiaire de leurs exigences trophiques et physiologiques (Hynes, 1970). Nous avons également supposé que des critères morphologiques tels que la taille, la forme et la flexibilité du corps pouvaient influencer la distribution des invertébrés (Williams & Hynes, 1974) les assemblages. Ces préférences d'habitat basées sur la morphologie ont été testées au niveau de l'habitat local et pour différentes profondeurs dans la zone hyporhéique. Afin de tester l'importance de ces liens, nous avons regardé comment ces préférences d'habitat pouvaient expliquer des différences de morphologie au niveau des peuplements de sites d'étude se distinguant par la porosité efficace de leurs sédiments.

Une seconde partie de la thèse traite d'un aspect plus dynamique des relations sédiments-invertébrés. Nous avons regardé l'influence des crues décapantes d'abord à une échelle locale sur l'assemblage et le comportement des invertébrés, puis à une échelle plus large sur les structures faunistique et fonctionnelle des peuplements. Dans un premier temps, nous avons regardé comment les invertébrés utilisaient les sédiments interstitiels lors de ces événements, en quantifiant leur comportement de migration verticale et leur comportement de dérive dans deux cours d'eau de la Drôme. Compte tenu des difficultés d'observation et de mesure liées au caractère aléatoire des crues, nous avons développé un simulateur expérimental de crue permettant de recréer localement les conditions hydrauliques proches de celles observées pendant les crues. Dans un deuxième temps, nous nous sommes intéressés au rôle de ces événements, non plus en temps qu'événements ponctuels mais du point de vue statistique. Nous avons regardé comment la répétition des crues dans le temps constituait un facteur de structuration des peuplements, en fonction de leur fréquence, de leur durée moyenne et de leur durée totale sur une année. Ceci a été testé en comparant le peuplement de neuf cours d'eau se distinguant par leur régime hydrologique, décrit à la fois du point de vue faunistique et fonctionnel.

Quelques pas le long d'un cours d'eau suffisent à montrer que la distribution des sédiments dans le lit n'est pas quelconque et en tout cas pas homogène. Fondamentalement, la dynamique des sédiments conduit à deux grands types d'arrangements autour desquels s'organisent les communautés d'invertébrés ; les sédiments fins et les sédiments grossiers. Les **sédiments fins** sont constitués d'un mélange d'argiles, de limons et de sables et contiennent une forte teneur en eau (> 60 %) qui rend leur structure relativement fluide ce qui permet aux invertébrés une aisance de mouvement et de pénétration. Par opposition, les **sédiments grossiers** ont une teneur en eau plus faible (< 30 %) et une structure plus résistante. La pénétration des invertébrés y est contrainte par la taille et la quantité d'interstices résultant de l'arrangement des particules.

Comment la taille, la forme et la texture des particules, ou bien leur degré de compaction influencent-ils la quantité d'interstices résultant de l'arrangement des particules ? Ces questions qui ont suscité d'importantes recherches en géologie et en ingénierie ont produit une littérature riche (Westman & Hugill, 1930 ; Furnas, 1931 ; Fraser, 1935 ; Graton & Fraser, 1935 ; Pryor, 1973 ; Atkins & McBride, 1990). Dans la majorité des cas, cette littérature fait référence à l'arrangement de matériaux lisses et sphériques répartis dans un faible nombre de classes de tailles. Or pour des particules sphériques de taille homogène, le volume des interstices est indépendant de la taille des particules mais dépend uniquement de leur arrangement. Pour les sédiments hétérogènes, la quantité d'interstices est inférieure à celle observée pour un sédiment homogène et dépend tout d'abord des proportions des différents éléments, puis de leur arrangement. Les vides créés par les éléments les plus gros sont comblés par les éléments plus petits qui créent à leur tour des vides comblés par des éléments de taille encore inférieure. Le non respect de la sphéricité complique sérieusement le problème, puisque l'empilement de formes géométriques plus complexes conduit à des arrangements plus ou moins compacts selon la forme des particules (Tickell & Hiatt, 1938). Enfin, il faut noter que la présence de micro ou de macro-cavités à la surface des particules ne peut qu'augmenter la quantité d'interstices des sédiments.

Dans les cours d'eau, ces modèles théoriques (*e.g.* Ouchlyama & Tanaka, 1984 ; Ouchlyama & Tanaka, 1986) **sont peu réalistes en raison de la forte hétérogénéité de la taille et de la forme des particules**. Les sédiments sont naturellement constitués d'une large gamme de taille de particules, des argiles-limons jusqu'aux galets de plusieurs décimètres de longueur. En ce qui concerne leur forme, Bretschko (1994) montre d'après l'étude des sédiments de cinq cours d'eau que le rapport des longueurs caractéristiques des particules - a/b et b/c, a étant la plus grande longueur et c la plus petite - varie entre 1 et 5. Le rapport a/b moyen observé au niveau des sites d'étude varie entre 1.37 et 1.47, tandis que le rapport b/c moyen varie entre 1.47 et 2.09. Ceci nous a conduit à évaluer directement l'importance relative de la granulométrie, de la forme et de la texture des particules ainsi que de leur profondeur dans la zone hyporhéique sur la porosité efficace dans les sédiments aquatiques.

Définition de la porosité efficace

La porosité efficace des sédiments est définie comme la quantité d'interstices accessibles aux macro-invertébrés. Dans les cours d'eau, ces interstices sont généralement remplis d'eau dont la majeure partie est libre - eau libre - tandis qu'une part reste fortement liée aux particules - eau liée - par un phénomène d'adsorption (Kemper *et al.*, 1964). L'eau adsorbée constitue une fine pellicule – d'une épaisseur maximale = 0.06 mm - à la surface des particules les plus larges ainsi qu'entre les petites particules (Briggs, 1977). Elle représente donc des volumes qui ont certainement un rôle important dans le fonctionnement des cours d'eau - *e.g.* pour la production du biofilm bactérien -, mais qui ne sont pas utilisables par les macro-invertébrés. De ce point de vue, l'eau liée peut être considérée comme faisant partie de la structure. Dans notre étude, la porosité efficace des sédiments a été évaluée par un calcul de porosité basé sur la prise en compte de l'eau libre (Maridet, 1990 ; Maridet, 1994 ; A1 p. 6), tandis que l'eau liée a été considérée comme faisant partie des sédiments. La prise en compte ou non de l'eau adsorbée par les particules peut induire des différences d'autant plus importantes dans l'évaluation de la porosité que la proportion de sédiments fins est importante dans l'échantillon (Fig. 3). En effet, le volume d'eau adsorbée est d'autant plus important que le sédiment est fin en raison de l'accroissement de la surface particulaire totale (Leichtfried, 1985).

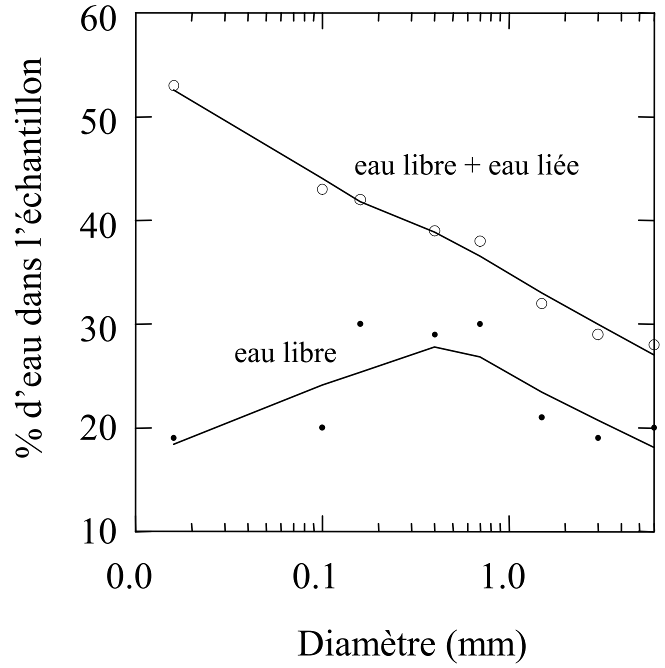


Figure 3. Proportion d'eau et proportion d'eau libre en fonction du diamètre des sédiments. (d'après Cohen, 1965 modifié).

Tableau 1. Caractéristiques générales, date d'échantillonnage, et nombre d'échantillons pour les différents sites d'étude présentés dans la thèse. Les lettres suivant le nom du cours d'eau (D, L, R) indiquent leur appartenance aux bassins versants de la Dordogne, de la Loire, et du Rhône. La géologie décrit la roche principalement rencontrée sur le bassin versant. La localisation (Loc.) est indiquée en coordonnées Lambert II et l'altitude (Alt.) en mètres au dessus du niveau de la mer. L'ordre indiqué est l'ordre de Stralher. La largeur moyenne (Larg.), et la pente du secteur ont été relevées sur le terrain lors de campagnes d'échantillonnage. N'ayant été mesurées qu'à une seule reprise, les mesures du pH et de la conductivité (Cd) ne doivent être considérées qu'à titre indicatif. (-) indique l'absence de mesures.

Cours d'eau	Année / saison	Géologie	Loc. / Alt.	Ordre	Larg. (m)	Pente (m/km)	pH	Cd (µS/cm)	Carottages	Surbers
Le Bez1^R	02-96	Sédimentaire	844.09, 1969.20,	3	12	9.8	7.8	290	4	6 × 0.1m^2
Le Bez2^R	05-99	Sédimentaire	844.12, 1969.21,	3	12	9.8	7.8	290	4	10 × 0.03m^2
La Bourne1^R	12-97, 02-99, 06-99	Sédimentaire	847.50, 2014.45,	3	15	10.0	8.4	380	3 × 3	6 × 0.1m^2
La Bourne2^R	12-97	Sédimentaire	841.57, 2011.47,	3	20	6.4	8.4	370	3	6 × 0.1m^2
La Bourne3^R	12-97, 02-99, 06-99	Sédimentaire	839.20, 2011.98,650	3	14	5.6	8.2	380	3 × 3	6 × 0.1m^2
Le Drac^R	03-89	Sédimentaire	910.74, 1977.14,	3	11	10.3	-	-	4	6 × 0.1m^2
La Drôme	05-99	Sédimentaire	844.09, 1970.21,	3	10	9.8	7.8	480	4	10 × 0.03m^2
L'Eygues^R	03-98	Sédimentaire	846.77, 1935.20 ,	3	8	8.7	8.3	380	4	10 × 0.03m^2
La Galaure1^R	03-89	Alluvial	818.68, 2032.62,	3	8	8.6	8.2	280	4	6 × 0.1m^2
La Galaure2^R	03-97, 03-98	Alluvial	818.69, 2032.63,	3	8	8.6	8.2	280	6 + 4	10 × 0.03m^2
La Gère^R	03-98	Alluvial	810.17, 2056.12,	3	5	8.6	8.6	305	4	10 × 0.03m^2
L'Herbasse^R	03-97, 03-98	Alluvial	807.20, 2016.12,	3	9	8.0	8.1	480	6 + 4	10 × 0.03m^2
La Loire^L	03-89	Alluvial	730.00, 2142.10,	5	50	1.0	-	-	4	6 × 0.1m^2
L'Ouvèze^R	03-98	Sédimentaire	839.73, 1926.71,	3	10	10.1	8.3	330	4	10 × 0.03m^2
L'Ozange^D	10-91, 01-92, 04-92, 07-9	Granitique	593.20, 2054.43,	3	5	2.7	6.6	45	4 × 4	4 × 6 × 0.1m^2
La Sanne^R	1999	Alluvial	798.25, 2045.25,	3	4	8.0	8.1	525	4	10 × 0.03m^2
La	10-91, 01-92, 04-92, 07-9	Granitique	592.70, 2053.93,	3	9	2.9	6.7	30	4 × 4	4 × 6 × 0.1m^2
La Varèze^R	03-99	Alluvial	809.68, 2052.80,	3	8	8.2	8.2	295	4	10 × 0.03m^2
Le Vianon^D	10-91, 01-92, 04-92, 07-9	Granitique	587.30, 2035.53,	4	5	18.5	6.9	35	4 × 4	4 × 6 × 0.1m^2

Méthode de prélèvement et nature des données

Nous avons exploré les liens qui existent entre les caractéristiques des sédiments et leur porosité efficace à partir de l'analyse de 99 carottes de sédiment prélevées par congélation à l'azote liquide (Bretschko & Klemens, 1986 ; Annexe 1) dans 17 sites d'études répartis sur 15 cours d'eau du Rhône, de la Loire et de la Dordogne (Tableau 1). Cette technique est la seule qui permette le prélèvement de la faune et des sédiments grossiers tout en préservant la structure des sédiments. Après leur extraction, les carottes sont découpées en 3 strates (0-15 cm, 15-30 cm, 30-45 cm) et transportées congelées au laboratoire où elles sont analysées (293 échantillons). Une fois l'extraction des invertébrés (> 0.5 mm) et de la matière organique grossière (> 1 mm) effectuée, les sédiments sont tamisés, séchés puis pesés. Le volume d'eau interstitielle libre est calculé par différence entre la masse totale et la masse des sédiments humidifiés et égouttés en faisant l'hypothèse que l'eau a une densité de 1000 kg.m^{-3}. La porosité efficace est calculée comme le ratio du volume d'eau libre au volume total de l'échantillon.

Modèles descriptifs

Pour quantifier l'influence relative des différents facteurs contrôlant la porosité efficace des sédiments, deux modèles intégrant la granulométrie et la profondeur de l'échantillon dans les sédiments ont été construits ; l'un à partir d'une description adimensionelle de la distribution granulométrique - hétérogénéité (ΦSo) et symétrie de la distribution -, l'autre à partir des proportions par classe de taille - Si : argiles et limons, Sa : sables, G : graviers, P : petits galets, C : gros galets -. Le premier modèle a permis de relier la porosité efficace à l'hétérogénéité de la distribution (ΦSo). Le second modèle qui s'est avéré plus performant pour expliquer la variabilité de la porosité a ensuite été utilisé pour tester l'influence de la texture et de la forme des particules sur des sédiments d'origine géologique différente. Ce dernier modèle appartient à la famille des modèles linéaires généralisés qui permettent de tester un ensemble de variables qualitatives et quantitatives dans une même analyse. Dans notre cas, le modèle utilisé est en plus adapté pour tester un ensemble de variables quantitatives dont la somme est égale à une constante (Marquardt & Snee, 1974). Après avoir éliminé les effets non significatifs, le modèle suivant a été obtenu :

Porosité efficace = *f* (Strate, Si, Sa, G, P, C, Sa × G, Sa × P, Sa × C, G × P, G × C).

Influence de la profondeur, de la distribution granulométrique et de la géologie

Sur l'ensemble des échantillons, les différences de profondeur expliquent 27 % de la variabilité de la porosité efficace. Celle-ci décroît avec la profondeur ce qui conduit à une porosité moyenne (±SD) de 8.7% (±4.9) pour la surface contre 3.7% (±3.1) et 3.2% (±2.5) pour les strates inférieures. Ceci s'explique par 1) une plus fréquente mobilisation par les crues des sédiments de surface (0-15 cm) ce qui conduit à leur plus faible tassement (Matthaei *et al.*, 1999) et 2) par la

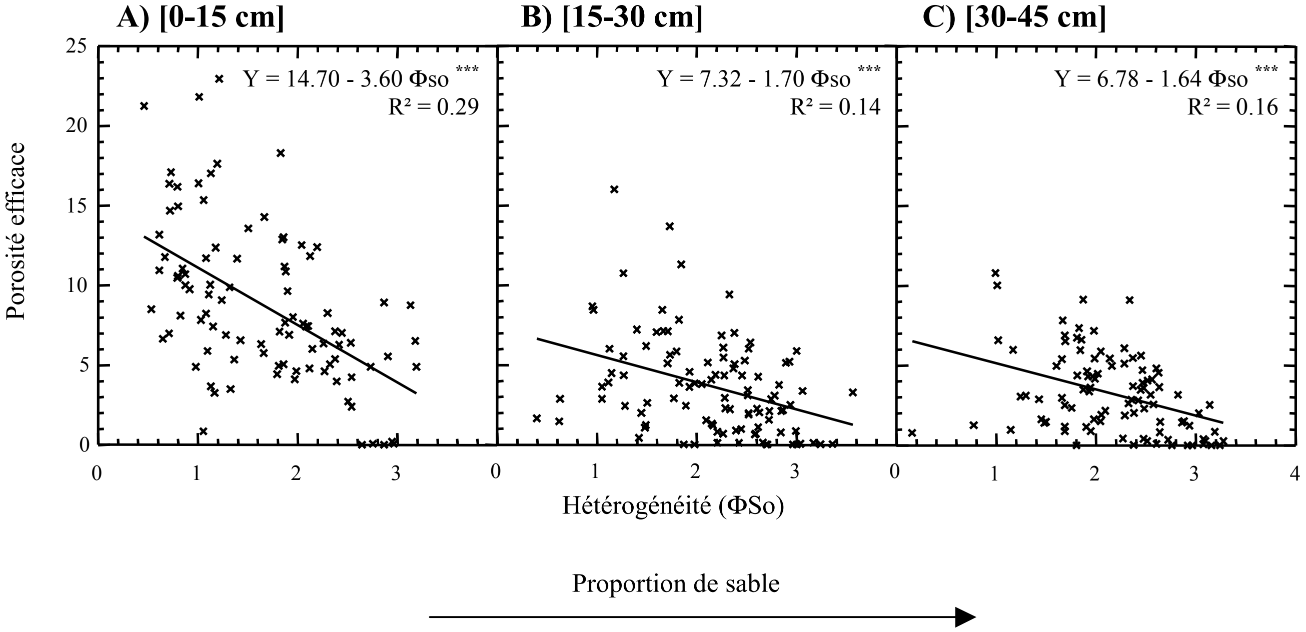


Figure 4. Influence de l'hétérogénéité des sédiments sur la porosité efficace pour les 3 strates.

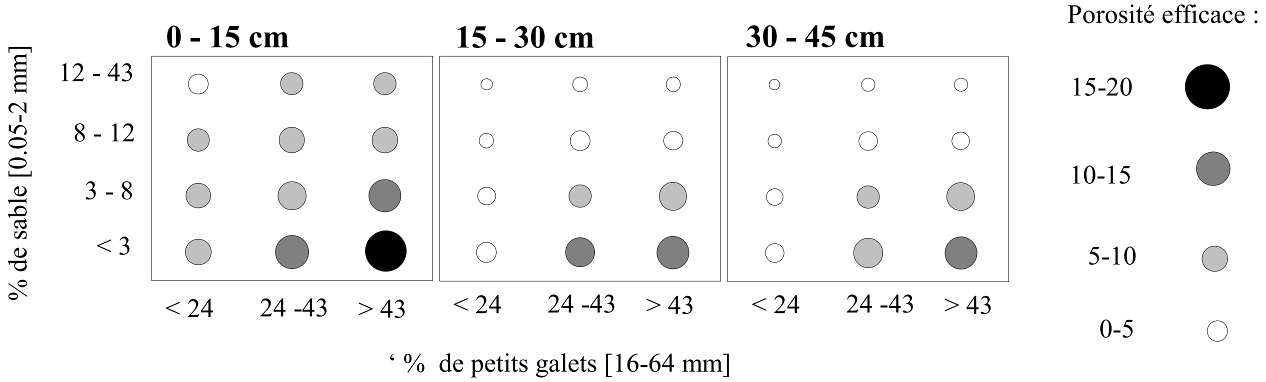


Figure 5. Influence de la profondeur, des proportions de sable et de petits galets sur la porosité moyenne des sédiments pour les 3 strates.

position d'interface de cette strate dont les interstices ne sont que partiellement remplis de sédiments fins.

Au sein de chaque strate, la distribution granulométrique influence la porosité de manière importante puisque elle explique à elle seule 45 % de sa variabilité. Cette influence se résume principalement à un effet de l'hétérogénéité ainsi qu'aux proportions relatives de sables et de petits galets. **Une forte hétérogénéité des sédiments se traduit par une faible porosité efficace quelle que soit la profondeur dans la zone hyporhéique** (Fig. 4). **La porosité efficace augmente avec une proportion croissante de petits galets et diminue lorsque la proportion de sable s'accroît** (Fig. 5).

La texture et la forme des particules n'ont pas été mesurées de manière précise mais ont été appréciées sur les plus grosses particules trouvés dans les échantillons. Nous avons distingué trois groupes de sites : les sites constitués de particules de forme anguleuse et à surface creusée de micro-cavités (têtes de bassin de roches granitiques), les sites constitués de particules anguleuses et lisses (têtes de bassin de roches sédimentaires) et les sites constitués de particules arrondies et à surface lisse ou creusée de micro-cavités (plaines alluviales). Nous avons effectué des prédictions croisées entre ces trois groupes à partir du modèle général calé pour chacun des groupes. Dans la majorité des cas, les prédictions sont non biaisées et ont une précision à peine plus faible que celle fournie par le modèle général établi sur l'ensemble des données (A1 Fig. 4.), montrant la **faible influence de la texture et/ou de la forme des particules sur la porosité efficace des sédiments.**

Les effets conjugués de la profondeur et de la distribution granulométrique expliquent environ 70 % des variations de la porosité efficace. La variance résiduelle de ce modèle représente d'une part l'aspect aléatoire de l'arrangement des particules et d'autre part l'imprécision de mesure associée aux techniques de prélèvement et de traitement des échantillons. L'aspect aléatoire dans l'arrangement peut conduire à des structures non optimales – c'est à dire qui ne minimisent pas la porosité efficace - notamment par la présence de macro-pores. On peut supposer que le temps écoulé depuis le dernier événement hydrologique ayant mobilisé le lit est important pour expliquer les écarts entre la structure observée et la structure optimale. Comme toute technique de prélèvement, le carottage cryogénique présente des limites. En particulier, la faible taille de l'échantillon a parfois été critiqué en raison de sa faible représentativité des sédiments en place (Carling, 1981). Ceci pourrait induire un biais important sur les calculs dérivés (proportions des classes de taille et porosité efficace), toutefois il reste difficile à quantifier en l'absence d'études plus précises sur le sujet.

Le modèle construit est restreint au cas des substrats grossiers et est adapté pour prévoir la réduction de porosité efficace en cas de colmatage par un apport de sédiments fins. Son utilisation doit être limitée aux cas où la proportion maximale de sable reste inférieure à 42 %

de la masse totale, valeur maximale utilisée pour caler le modèle. Au delà de cette valeur, des mécanismes de structuration propres aux sédiments fins apparaissent, ce qui pourrait rendre les prédictions du modèle moins fiables.

INFLUENCE DE L'HABITAT INTERSTITIEL SUR L'ASSEMBLAGE LOCAL DES INVERTEBRES

Certains invertébrés benthiques (*Leuctra sp., Elmis sp.*) accomplissent une partie de leur cycle vital dans les sédiments profonds (Williams, 1984). Comme dans tout habitat, leur survie y est subordonnée à la nécessité d'équilibrer leur balance énergétique résultant d'une part des apports trophiques et d'autres part des dépenses physiologiques. Or, la recherche de nourriture dans cet habitat nécessiterait une dépense énergétique plus importante d'une part en raison de sa moindre concentration qu'en surface (Brunke & Gonser, 1999) et d'autre part en raison de l'énergie nécessaire pour pénétrer les interstices. Dans le cas des substrats grossiers où la structure des sédiments est peu déformable, la taille et la quantité d'interstices peuvent constituer une contrainte forte et ainsi sélectionner les invertébrés sur leur capacité à pénétrer les sédiments. Dans ce contexte, en plus du comportement de fouissage, **la petite taille, les formes allongées ou sphériques et la forte flexibilité pourraient constituer un avantage pour coloniser les sédiments profonds** (Williams & Hynes, 1974). Par ailleurs, la densité en invertébrés - nombre d'individus par litre de sédiments - ainsi que la richesse taxonomique de l'assemblage pourraient également être influencées par la porosité efficace des sédiments.

Méthode de prélèvement et nature des données

L'adéquation entre la morphologie des invertébrés et la porosité des sédiments a été testée en comparant les traits morphologiques d'assemblages pris dans différentes conditions de porosité efficace sur 243 des 293 échantillons utilisés dans l'étude précédente. Les échantillons où la densité en invertébrés était nulle ont été éliminés car ne permettant pas de calculer une proportion de traits. L'habitat interstitiel a été décrit par sa porosité efficace, l'hétérogénéité des particules, la proportion de sable et le diamètre médian des particules. A l'exception des Oligochètes qui n'ont pas été décomptés en raison de leur destruction lors de la congélation des sédiments, les invertébrés benthiques ayant une taille supérieure à 0.5 mm ont été dénombrés et la richesse taxonomique a été calculée sur la base d'une détermination au niveau de la famille - minimum commun à tous les échantillons -. La morphologie des invertébrés - qui tient compte d'éventuels fourreaux ou logettes - a été décrite par la taille maximale potentielle des individus, la capacité du corps à se déformer - la flexibilité - et la forme du corps. Les traits de l'assemblage ont été calculés en pondérant la densité de chaque famille par son affinité pour les différentes modalités de taille - < 5 mm, 5-10 mm, > 10 mm -, de flexibilité - < 10°, 10-300°, > 300° - et de forme du corps - hydrodynamique, aplatie, cylindrique, sphérique -, (voir A2, p.7, Annexe). Les modalités ont ensuite été exprimées en terme de proportion. De tels traits ont été utilisés auparavant dans des études plus générales car ils permettent la description d'un ensemble de taxons de niveau taxonomique très varié sur la base de critères communs (voir Statzner *et al.*, 1994).

Modèle descriptif

Afin d'éliminer l'effet de variables agissant à une échelle globale - *e.g.* géologie, régime de perturbation - qui pourraient induire des différences moyennes de morphologie de l'assemblage entre les sites, les données ont été centrées par site. Nous avons utilisé le modèle de covariance pour tester l'influence de l'habitat au sein de chaque strate de sédiments :

$$\% \text{ d'un trait} = a_{(\text{strate } i)} + b \times \text{habitat},$$

où $a_{(\text{strate } i)}$ varie en fonction de la strate et où b est fixé pour l'ensemble des données. Ce modèle permet de mettre en évidence des relations qui sont communes à un ensemble d'objets - ici les strates de sédiment - tout en tenant compte d'éventuelles différences de moyenne entre les objets.

Effet de la profondeur et de la porosité efficace

Les résultats révèlent tout d'abord une **forte réduction de la densité en macro-invertébrés ainsi que de la diversité de l'assemblage avec la profondeur dans la zone hyporhéique** (Tableau 2). L'effet de la profondeur explique respectivement 51.9 %, 45.7 % et 41.1 % de la variance intra-sites de la densité, de la richesse taxonomique totale et de la richesse EPT - Ephémérotpères, Plécoptères et Trichoptères -. Du point de vue des traits, **les invertébrés de grande taille (> 1 cm), de forme hydrodynamique ou aplatie sont proportionnellement plus abondants en surface qu'en profondeur, contrairement aux invertébrés de petite taille (< 5 mm)**. La profondeur explique entre 6.7 % et 10.4 % de la variabilité de ces traits dans les sites.

Au sein des strates, la densité, la richesse totale et la richesse des EPT augmente avec la porosité efficace, mais cette dernière explique une part de variance plus faible (4.3 à 8 % de la variance intra-sites) que la profondeur. En ce qui concerne les traits, à l'exception des modalités 'forte flexibilité' et 'forme sphérique', les modalités sont significativement liées à au moins l'une des variables décrivant les sédiments. **La proportion des invertébrés de petite taille ou ayant une forme cylindrique diminue lorsque la porosité efficace augmente tandis que la proportion des individus de taille intermédiaire (5-10 mm) et de forme hydrodynamique augmente**. Curieusement, le trait de flexibilité présente une réponse inverse à celle attendue ; la faible flexibilité (< 10°) diminue avec la porosité tandis que la flexibilité intermédiaire (10-300°) augmente. En réalité, il semble que la réponse de ce trait soit principalement liée à la composition granulométrique. La plus

Tableau 2. Résultat des analyses de covariance (% de trait = $a_{(\text{strate } i)} + b \times \text{habitat}$) entre la profondeur dans la zone hyporhéique (Facteur), les variables d'habitat (la porosité efficace, la proportion de sable, l'hétérogénéité du sédiment, le diamètre médian des particules), et la densité en invertébrés (Nb / litre de sédiment), la richesse taxonomique (Nb de familles) et la proportion de traits morphologiques de l'assemblage. La valeur moyenne des variables est calculée pour l'ensemble de l'échantillon (N =243). Les analyses ont été conduites sur les échantillons dont la densité en invertébrés est différente de 0 afin de pouvoir calculer les proportions de traits. Le signe indique la pente de la relation (coefficient b) et la variance expliquée est indiquée entre parenthèses. *** P<0.001 ; ** P<0.01, * P< 0.05. Le signe × indique un effet de l'habitat qui diffère selon la profondeur.

		Facteur	Covariable			
Variable biologique / catégorie	Moyenne	Strate	Porosité efficace	Sable	Hétérogénéité	D50
Densité des invertébrés	23.3	- *** (51.9)	+ *** (8.0)			
Richesse taxonomique	7.5	- *** (45.7)	+ *** (4.7) ×	- *** (4.8)	- ** (1.9)	+ *** (3.2)
Richesse EPT	3.4	- *** (41.1)	+ *** (4.3) ×	- *** (5.2)	- *** (4.4)	+ ** (2.6)
Taille maximale						
< 5 mm	35.5 %	+ ** (8.1)	- ** (2.6)			
5-10 mm	36.5 %		+ ** (2.7)			
> 10 mm	28.3 %	- ** (10.4)				
Forme du corps						
Hydrodynamique	6.5 %	- *** (14.4)	+ *** (3.9)	- * (1.5)	- *** (4.4)	
Aplatie	10.2 %	- ** (6.7)			- ** (2.1)	
Cylindrique	76.9 %		- *** (4.7)	+ ** (3.6)	+ *** (4.1)	
Sphérique	5.8 %					
Flexibilité du corps						
< 10°	50.2 %		- *** (6.8)	+ ** (3.8)	+ *** (5.8)	
10-300°	45.4 %		+ *** (7.8)	- *** (5.6)	- *** (6.9)	
> 300°	3.5 %					

forte proportion de sédiments fins qui caractérise les sédiments colmatés, rendent ces derniers plus facilement accessibles aux invertébrés peu flexibles qui pourront s'y déplacer en modifiant l'arrangement des grains. Au contraire, dans les sédiments les plus poreux, qui sont aussi les plus « rigides », les formes plus flexibles seront favorisés dans leur déplacement.

D'un point de vue purement quantitatif, la proportion de variance expliquée par la porosité efficace est faible puisqu'elle varie entre 2.6 et 7.8 %. Ceci est normal si l'on considère qu'à l'échelle du microhabitat, la présence d'une espèce dans un habitat est la résultante d'un ensemble de variables de description de l'habitat et non d'une seule variable. De plus, compte tenu de la forte mobilité des invertébrés dans leur milieu, la présence des individus d'une espèce dans un habitat revêt également un caractère aléatoire et transitoire (Fonseca & Hart, 2001). Les individus peuvent en effet être échantillonnés dans des conditions d'habitat non-optimales, par exemple à la faveur d'un déplacement d'un d'habitat vers un habitat plus favorable. Malgré la faible variance expliquée par ces relations, il faut toutefois bien considérer que **ces relations reflètent des préférences d'habitat qui sont communes à différentes strates de sédiments ainsi qu'à un ensemble de sites relativement important (n = 17)**. Du fait de leur caractère multi-sites et –strates, ces relations sont particulièrement intéressantes pour la constructions de modèles prédictifs.

Les résultats précédents montrent clairement qu'à la fois la profondeur et la porosité au sein de chaque strate influencent les caractéristiques morphologiques de l'assemblage. Toutefois, plusieurs points méritent d'être discutés. Tout d'abord, la nécessité d'utiliser des données antérieures nous a contraint à utiliser des traits morphologiques élaborés au niveau de détermination de la famille et non au niveau du genre, ce qui pourrait constituer une perte d'information substantielle. Par exemple pour un ensemble de traits biologiques plus large, Dolédec *et al.* (2000) évaluent à environ 7% la perte d'information entre l'espèce et le genre et à environ 12% la perte entre l'espèce et la famille. Pour nuancer ce point, il faut considérer que les traits morphologiques sont parmi les traits biologiques les moins variables au sein des familles et qu'une meilleure description de ces traits devrait normalement produire des relations plus précises. Par ailleurs, les résultats ne sont basés que sur des estimations de traits et non sur leur expression au niveau des sites. Ceci est particulièrement important pour la taille dans la mesure où certains insectes (*e.g.* Chironomidae et Elmidae) accomplissent une migration verticale durant leur cycle vital conduisant à un enfouissement des jeunes larves tandis que les individus plus âgés remontent à la surface pour accomplir le passage au stade adulte. La mesure de la taille pourrait donc révéler un effet encore plus important de la profondeur dans les sédiments. Enfin nos conclusions ne portent que sur une partie du benthos puisque les Oligochètes, les Hydracariens et la meiofaune n'ont pas été analysés dans cette étude.

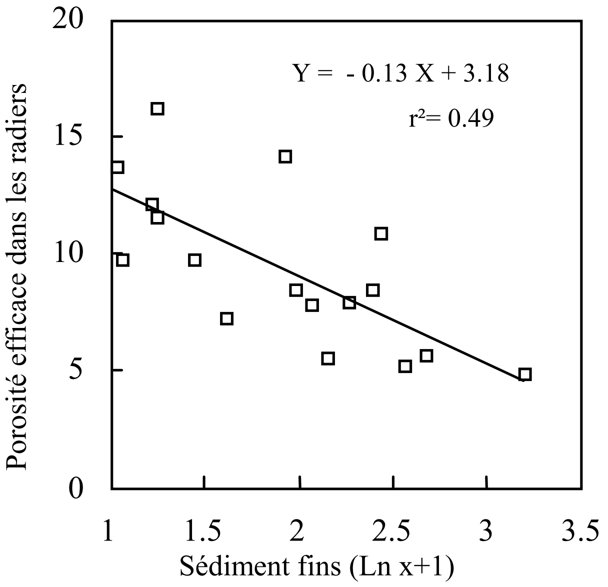


Figure 6. Influence de la proportion moyenne de sédiments fins (< 2 mm) sur la porosité efficace moyenne des sédiments de sub-surface (0-15 cm) dans les radiers de 17 sites d'étude.

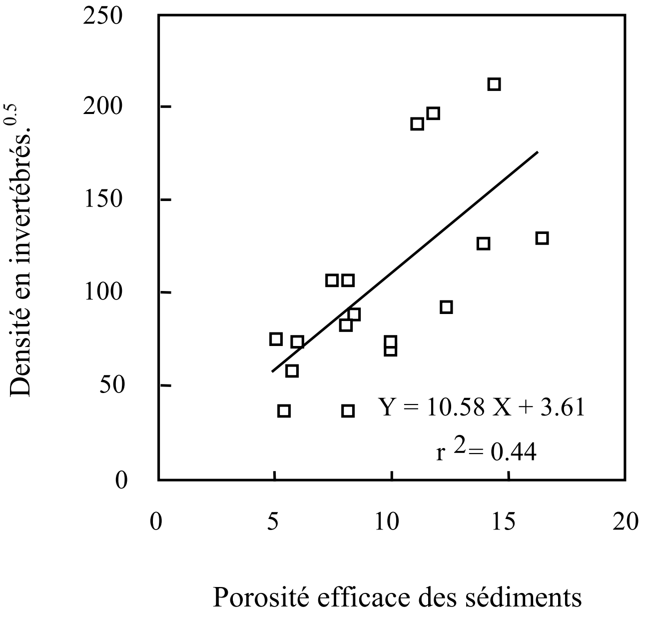


Figure 7. Influence de la porosité efficace des sédiments de sub-surface (0-15 cm) des radiers sur la densité en invertébrés benthiques dans 17 sites d'études.

Nous avons montré qu'il existait des préférences à l'échelle locale pour la porosité efficace des sédiments, basées sur la morphologie des invertébrés. Dans quelle mesure de tels mécanismes peuvent-ils expliquer des différences moyennes de morphologie de peuplements de sites caractérisés par une porosité moyenne différente ? En d'autre terme **ces préférences d'habitat locales sont elles suffisamment fortes pour structurer les peuplements ou bien sont elles masquées par d'autres facteurs agissant à l'échelle du site ?**

Méthodes de prélèvement et nature des données

Pour tester cette hypothèse, nous avons mis en relation les caractéristiques générales et les traits morphologiques de la macro-faune benthique avec la porosité des sédiments superficiels des radiers (strate 0-15 cm) mesurés en saison hivernale sur les mêmes 17 sites d'étude (voir A3 et Annexe 2). Les caractéristiques de la macro-faune et des sédiments ont été évaluées de manière indépendante ; la faune a été prélevée par filet Surber (n = 6 à 10) et les sédiments par carottage (n = 2 à 4). En utilisant les mêmes traits morphologiques qu'au chapitre précédent, les caractéristiques morphologiques des peuplements ont été évaluées et mises en relation avec la porosité, la proportion de sédiments fins (< 2 mm), l'hétérogénéité de la granulométrie de surface, le diamètre des particules. D'autres variables telles la concentration en matières organiques fines (FPOM) et grossières (CPOM) dans les sédiments et la pente du lit ont également été prises en compte pour avoir une description sommaire de la disponibilité des ressources trophiques et des conditions hydrauliques.

Influence de la porosité moyenne des sites sur les caractéristiques générales et la morphologie des peuplements

En inter-sites, on retrouve des relations entre la porosité des sédiments, la proportion de sable et l'hétérogénéité de la granulométrie qui sont similaires à celles observées au niveau local. Les sites présentant une forte porosité moyenne présentent également un sédiment homogène avec une faible proportion d'argiles, de limons et de sables (Fig. 6).

Les résultats confirment le rôle important de la porosité efficace comme facteur structurant le peuplement, puisque les différences inter-sites expliquent environ 45 % des différences de densité en invertébrés (Fig. 7). Au contraire la richesse globale du peuplement n'est pas influencée par la porosité moyenne. Les relations observées avec la morphologie à l'échelle des micro-habitats se retrouvent à l'échelle des sites. **Les sites présentant une forte porosité sont caractérisés par une plus faible proportion de petits individus (< 5 mm), et de plus fortes proportions de taille intermédiaire (5-10 mm), de forme aplatie ou hydrodynamique et de flexibilité intermédiaire** (Fig. 8).

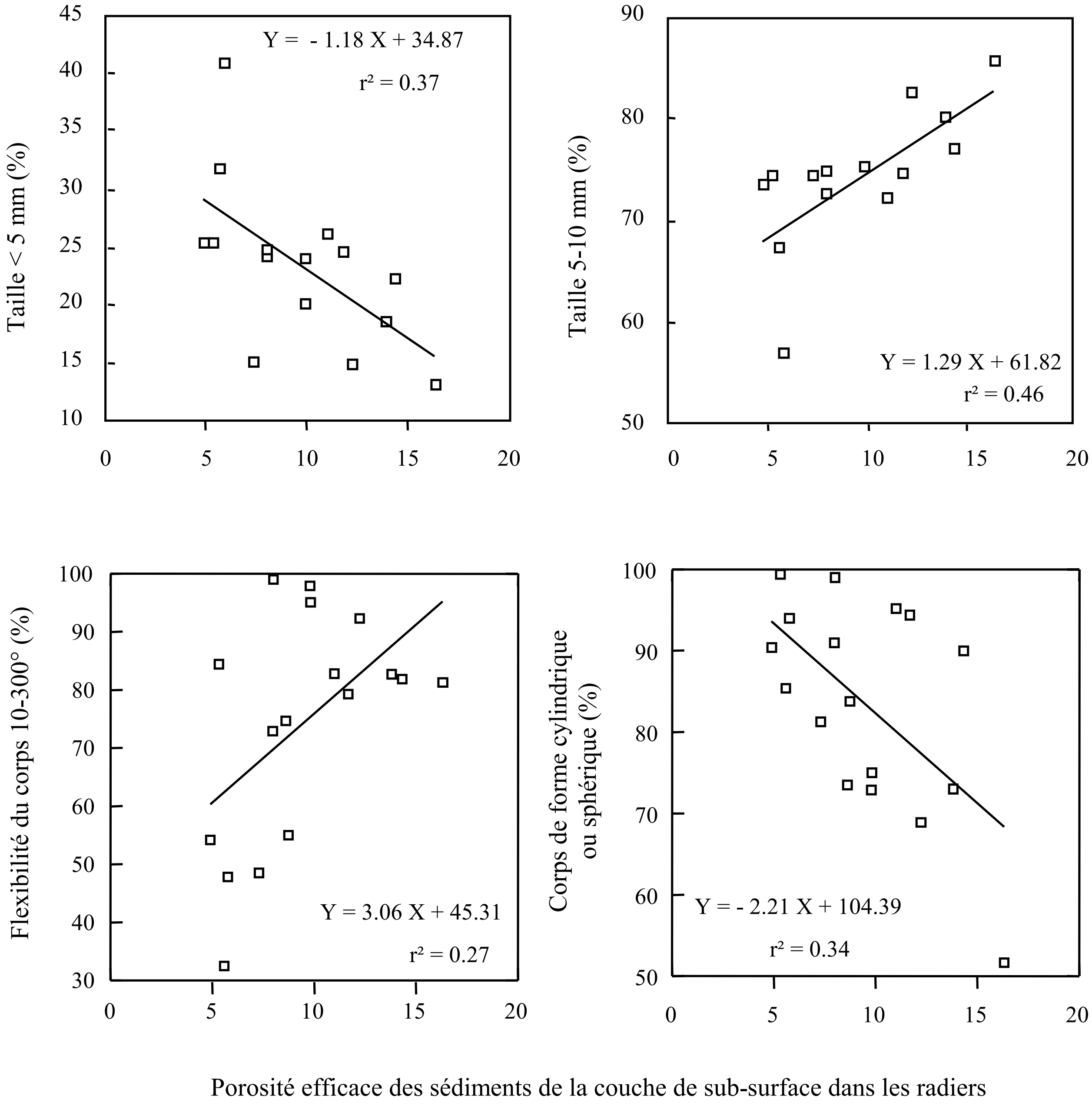


Figure 8. Influence de la porosité efficace des sédiments des radiers sur les proportions de traits morphologiques des peuplements benthiques de 17 sites d'étude.

REPONSE DES INVERTEBRES A DES CONDITIONS DE CRUE SIMULEES

En plus d'être variable dans l'espace, l'occupation des sédiments par les invertébrés varie dans le temps sous l'influence des conditions hydrologiques (Dole-Olivier & Marmonier, 1992b). Dans les cours d'eau, les crues mobilisant le lit font partie des événements les plus perturbateurs pour le peuplement d'invertébrés (Resh *et al.*, 1988 ; Townsend, 1989), car de tels événements peuvent réduire fortement l'abondance (Giller & Sangpradub, 1991 ; Marmonier & Creuzé des Châtelliers, 1991) et parfois la richesse taxonomique du peuplement. Malgré l'impact important des crues, la restauration

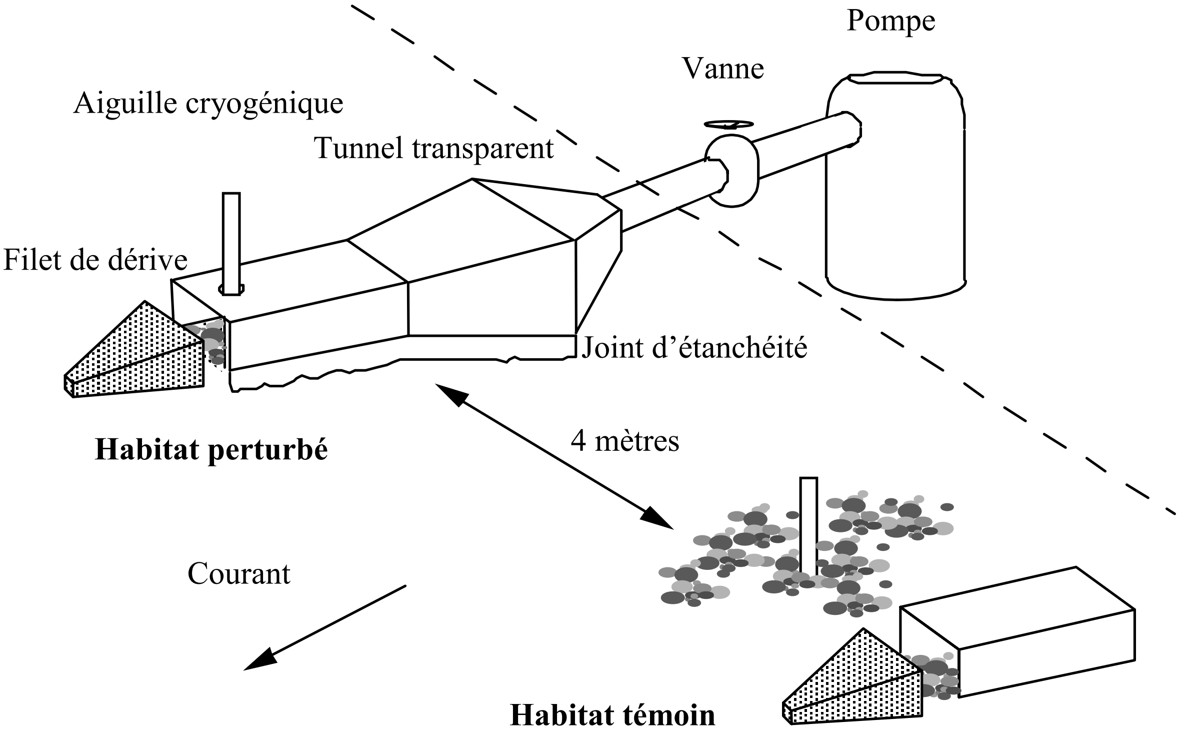


Figure 9. Schéma de principe du Décolofond. L'eau est pompée en amont du site expérimental et conduite dans le tunnel transparent. Le débit peut être régulé grâce à une vanne. Le filet de dérive permet de collecter les invertébrés qui dérivent depuis les habitats perturbés et témoins, l'aiguille cryogénique permet de collecter les invertébrés dans les sédiments.

des caractéristiques du peuplement est généralement rapide et ne dépasse pas quelques semaines à quelques mois (Wallace, 1990). Ce retour rapide ne peut s'expliquer uniquement par la croissance intrinsèque des populations, mais suggère la présence de zones refuges où les invertébrés survivraient aux conditions défavorables et à partir desquelles ils coloniseraient les aires perturbées (Townsend, 1989 ; Reice *et al.*, 1990 ; Sedell *et al.*, 1990). Au niveau du site d'étude, les zones avec des contraintes hydrauliques faibles et constantes, les accumulations de bois mort, les berges, les aires immergées lors de la crue constituent des refuges dans lesquels les invertébrés subissent moins ses effets. Au niveau du cours d'eau dans son ensemble, les aires non perturbées situées en amont permettraient la recolonisation par dérive, tandis que la proximité d'autres systèmes aquatiques dans un rayon de quelques kilomètres de la zone perturbée permettrait la recolonisation par voie aérienne pour de nombreux insectes (Townsend, 1989 ; Sedell *et al.*, 1990). Dans ce contexte, la zone hyporhéique a très tôt été revendiquée comme un refuge - 'Hyporheic refuge hypothesis' (Williams & Hynes, 1974) et a été testée plus récemment dans différents contextes (cours d'eau sableux et expérimentations : Palmer *et al.*, 1992 ; grands cours d'eau : Dole-Olivier *et al.*, 1997 ; expérimentations : Imbert & Perry, 1999).

Le caractère imprévisible des crues et les difficultés de mesure liées à ces événements ont suscité la création d'un appareil transportable (le Décolofond) permettant de simuler, en rivière et à l'échelle du micro-habitat, l'augmentation de la vitesse du courant qui se produit lors des crues. Le Décolofond a été construit en collaboration avec l'unité de recherche d'Hydrologie et d'Hydraulique du *Cemagref* (E. Hérouin & B. Pratx) sur la base de travaux antérieurs de l'équipe 'Bases théoriques pour la gestion écologique des eaux courantes' de l'Université Lyon I (B. Statzner).

La réponse des invertébrés a été évaluée en comparant leur distribution verticale dans les sédiments sur des zones témoins et des zones perturbées à l'aide du Décolofond. En cas de migration verticale, nous avons supposé que la densité des invertébrés devait diminuer dans la strate de surface (0-8 cm) et augmenter dans les strates profondes (8-60 cm). La dérive qui constitue une alternative à la migration dans les sédiments a également été mesurée sur les zones témoins et perturbées.

Matériels et méthodes

La perturbation a été créée à l'aide du Décolofond (Fig. 9) qui permet d'augmenter la vitesse du courant sur une surface de 0.20 m². Cet appareil prélève de l'eau en amont à l'aide d'une pompe et l'injecte par un tunnel transparent posé à même le lit. L'étanchéité entre l'intérieur et l'extérieur du tunnel est assuré par une jupe d'étanchéité. Le débit passant dans le tunnel peut alors être contrôlé précisément par une vanne située à la sortie de la pompe. **Lors de la perturbation, la vitesse a été augmentée par paliers de 0.1 ms^{-1} tous les ¼ d'heure à partir de la vitesse initiale trouvée sur la zone, jusqu'au seuil de mouvement des sédiments les plus fins (< 2 mm)**. La durée totale de la

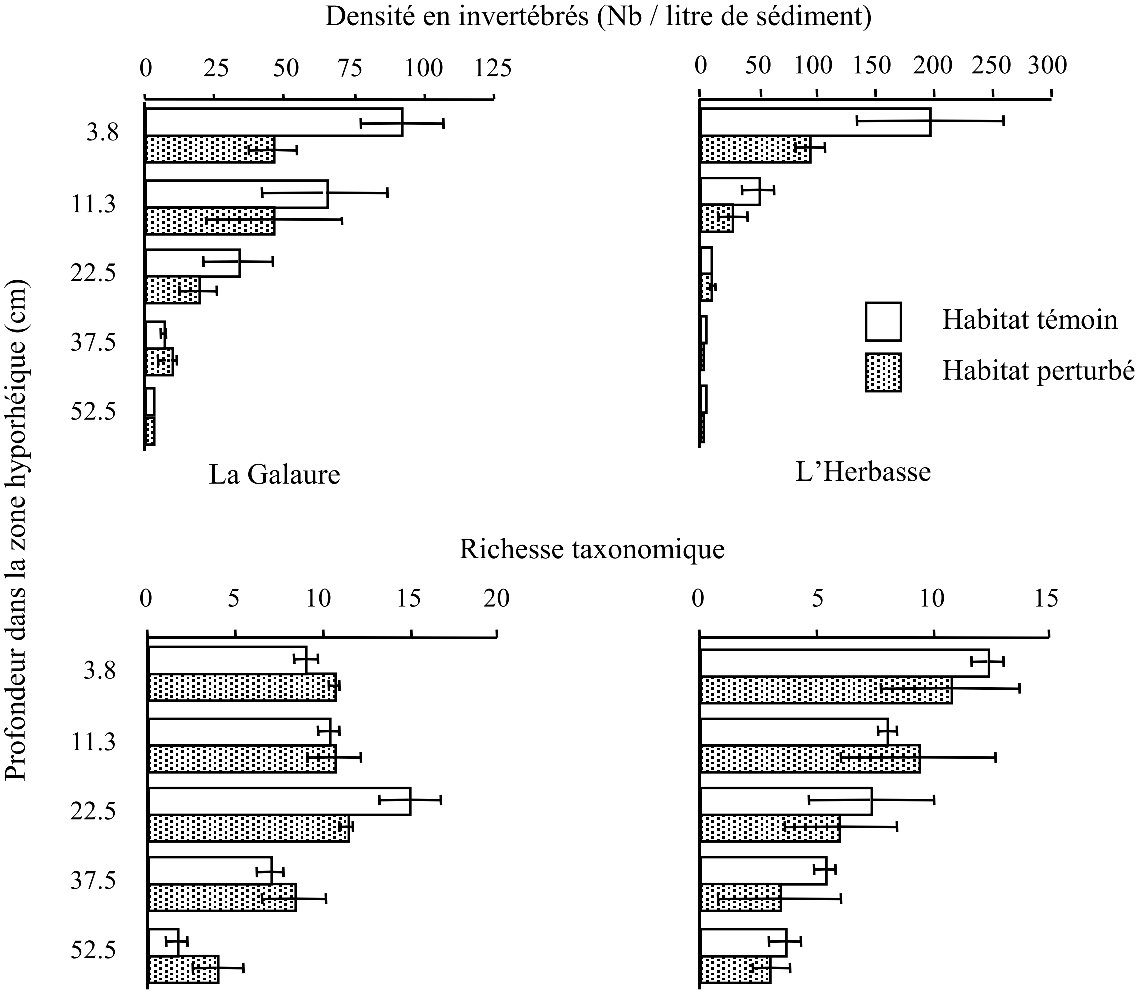


Figure 10. Evolution verticale de la densité en invertébrés et de la richesse taxonomique sur les habitats témoins et perturbés par le Décolofond.

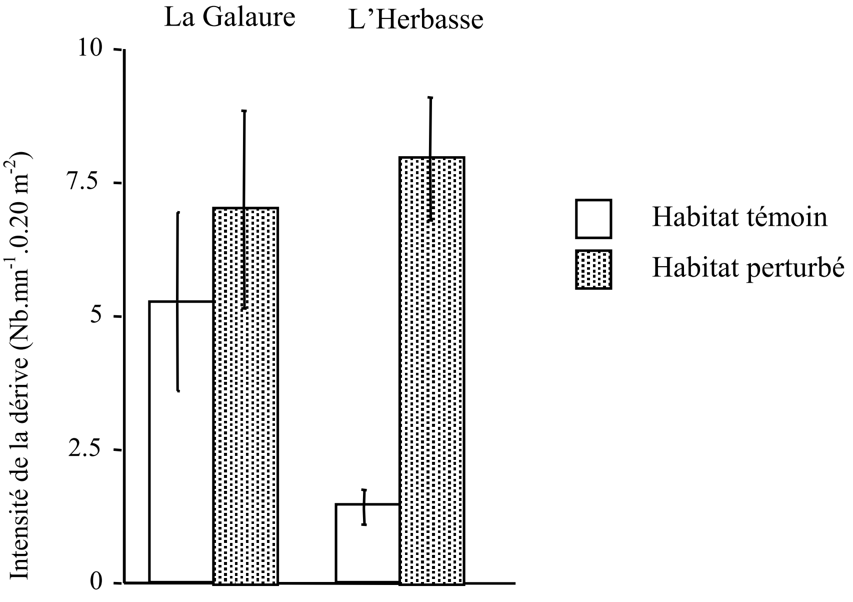


Figure 11. Intensité de la dérive sur les habitats témoins et perturbés.

perturbation a duré environ deux heures. La distribution verticale a été évaluée par carottage cryogénique, les carottes de sédiments ont été découpées en cinq strates (0-8 cm, 8-15, 15-30, 30-45, 45-60) et la densité en invertébrés calculée pour chaque strate. La dérive a été mesurée avec un filet filtrant les invertébrés dérivant de la zone d'étude et a été exprimée en nombre d'individus dérivant par minute et par m².

Nous avons procédé à six répétitions de ce protocole réparties dans deux cours d'eau Drômois (l'Herbasse et la Galaure) caractérisés par des sédiments poreux.

Migration verticale ou dérive ?

La comparaison des zones perturbées avec les zones témoins montre **une absence de migration verticale** malgré une forte réduction de la densité en surface (Fig. 10). Une **augmentation de la dérive est observée en parallèle** (Fig. 11). Les trois principaux taxons composant le peuplement, Heptageniidae, Chironomidae et Gammaridae montrent une réponse similaire à celle de l'ensemble du peuplement, avec une réduction nette de l'abondance en surface et l'absence de migration significative dans les sédiments profonds. Afin de déceler d'éventuelles différences dans le comportement de dérive chez ces invertébrés morphologiquement très différents, nous avons comparé leurs proportions dans le benthos (0-8 cm) et la dérive. Si les proportions des 3 taxons ne diffèrent pas significativement entre le benthos des zones perturbées et des zones témoins, la proportion de larves de Chironomidae est significativement plus forte dans la dérive que dans le benthos quelles que soient les conditions hydrauliques (A3, Tableau 3). Pour les Heptageniidae et les Gammaridae, en l'absence de perturbation, leur proportion est plus faible dans la dérive que dans le benthos suggérant un comportement d'évitement des contraintes. La proportion des Gammaridae et des nymphes de Chironomidae augmente significativement dans la dérive lorsque les sédiments sont perturbés.

Lors de cette étude, nous avons tenté de **simuler localement** les conditions d'écoulement qui se produisent lors d'une crue, en faisant l'hypothèse qu'en cas de migration active des invertébrés, celle-ci devait se produire avant le mouvement des particules les plus fines. Comme pour toute approche expérimentale, il est nécessaire d'évaluer dans quelle mesure les résultats représentent un **processus réel ou un biais expérimental** lié à la technique utilisée. La petite taille des zones sur lesquelles la perturbation a été appliquée est un défaut important de l'approche. En effet en cas de crue, il est probable que la migration dans les sédiments s'effectue dans les trois dimensions du lit et pas seulement dans la dimension verticale. En conséquence, la perturbation produite sur la zone a pu se traduire par une migration verticale en aval de la zone perturbée. Par ailleurs, il faut considérer que le signal produit par le Décolofond ne reproduit que partiellement le signal perceptible par les invertébrés lors de la crue. En particulier, la baisse de la luminosité et de la température de l'eau peuvent constituer des signaux importants qui n'ont pas été simulés par le Décolofond.

Les crues mobilisant les sédiments du lit peuvent être vues comme des événements indépendants générant une destruction au niveau du peuplement ou bien comme une série d'événements caractérisés par une fréquence, une durée et une intensité et qui constituent un filtre agissant au niveau du cours d'eau pour sélectionner les espèces présentant les traits biologiques les plus adaptés pour survivre et se reproduire dans ces conditions de perturbation. Par ailleurs, en réponse à la variabilité spatiale des effets des crues, certaines composantes de l'habitat peuvent constituer des refuges et apporter une protection aux invertébrés durant ces événements et ainsi sélectionner sur le long terme les invertébrés capables d'utiliser ces habitats refuges.

Afin de tester l'influence du régime de perturbation et de la disponibilité en refuges, nous avons échantillonné le peuplement d'invertébrés benthiques de 9 cours d'eau contrastés du point de vue de leur régime hydrologique.

La perturbation a été définie comme « un événement limité dans le temps qui tend à chasser les organismes de leur habitat qui sera ensuite colonisé par d'autres individus de la même espèce ou d'espèces différentes » (Townsend, 1989). En nous basant sur les résultats de l'étude précédente, nous avons considéré que le débit mobilisant les sables constituait une perturbation suffisante pour produire à l'échelle locale un phénomène de dérive capable de mofifier l'assemblage des invertébrés. Le régime de perturbation a été décrit par la fréquence de ces crues, leur durée moyenne et leur durée annuelle cumulée. D'un autre côté, la disponibilité en refuge a été définie comme un ensemble d'habitats dont la pertinence en temps que refuge a été démontrée dans la littérature.

Evaluation du régime de perturbation et de la disponibilité des refuges

Les sites d'études choisis pour cette étude diffèrent peu de par leur taille (4-12 m), leur pente (8.0-10.1 m.km^{-1}), la proportion d'habitats rapides (57-64 %) et la taille médiane du substrat (2.3 - 4.5 cm) mais diffèrent par la stabilité latérale et longitudinale de leur lit. Les cours d'eau sont situés dans le bassin du Rhône et sont distants au maximum de 130 km (A4 p. 32). Le débit critique mobilisant les sédiments a été évalué en utilisant les équations classiques du transport solide (Milhous, 1998) et de la géomorphologie (Leopold *et al.*, 1964) (voir A4, p 6-7). Les cours d'eau présentent un régime de perturbation très différent. **La fréquence et la durée totale des crues sur l'année - calculée sur 10 ans - varient respectivement de 1.3 à 6.8 crues / an et de 1.7 à 34.2 jours / an.** La fréquence, la durée totale et la durée moyenne des crues ont été combinées pour créer un indice synthétique de perturbation. De la même manière, les variables décrivant les refuges – porosité efficace des sédiments, zone avec de faibles contraintes, proportion de particules très stables, distance à la source - ont été combinées pour créer un indice synthétique de disponibilité en refuges.

Les peuplements ont été décrits en terme d'abondance, de richesse, de structures faunistique et fonctionnelle. La structure fonctionnelle a été décrite par un ensemble de traits biologiques (Usseglio-Polatera *et al.*, 2000) décrivant la taille des individus, le nombre de stades se déroulant hors du milieu aquatique, la possibilité de ponte terrestre, la relation aux sédiments, le mode alimentaire, la valence trophique et la valence pour l'habitat (A4 p. 33). Ces traits ont été exprimés en terme de proportion d'individus et de proportion de taxons - 16 variables au total -. Les structures faunistiques et fonctionnelles ont ensuite été résumées par les 2 premiers axes d'analyses multivariées (voir A4 p. 11-12). Un test global de l'influence du régime de perturbation et de la disponibilité en refuges sur les structures faunistique et fonctionnelle a été effectué. Puis afin de quantifier l'importance relative des variables de départ, nous les avons sélectionnées par régression pas à pas pour expliquer les proportions des différents traits biologiques dans les sites.

Influence du régime de perturbation et de la disponibilité en refuges

L'indice de perturbation qui combine la fréquence, la durée moyenne et la durée annuelle totale des crues mobilisant les sédiments est significativement **relié à la structure faunistique** (Fig. 12). L'axe sépare les insectes des autres groupes - Oligochètes, Mollusques, Crustacés - tandis que les différents Ordres d'insectes sont répartis régulièrement le long de l'axe. L'indice de perturbation est **relié à la structure fonctionnelle** des peuplements décrite par les traits biologiques (Fig. 13). La disponibilité en refuge a été mise en relation avec la structure faunistique et la structure fonctionnelle mais l'analyse n'a pas détecté de relation significative avec ces variables.

Parmi les trois variables décrivant le régime de perturbation, **la durée annuelle totale et la durée moyenne des crues sont les variables les plus pertinentes pour décrire les proportions de traits.** Sur les seize variables décrivant les traits, huit d'entre elles présentent le lien le plus fort avec la durée totale des crues et deux d'entre elles avec leur durée moyenne, tandis que la fréquence des crues reste une variable explicative de second ordre. La proportion de taxons ayant au moins un stade hors du milieu aquatique, la proportion de taxons et d'individus pouvant pondre hors de l'eau, et la proportion d'individus qui s'alimentent en filtrant la matière organique particulaire sont proportionnelles au nombre de jours en crue par an (Fig. 14). Au contraire, la proportion de taxons et d'individus ayant une forte relation avec les sédiments - espèces rampantes, fouisseuses et interstitielles - ou qui se nourrissent de détritus organiques diminuent. Enfin la proportion de taxons ayant au moins un stade hors de l'eau et la proportion d'individus ayant une large valence écologique augmentent avec la durée moyenne des crues (Fig. 15). La même analyse effectuée avec les variables refuges n'a pas mis en évidence de relations significatives avec les traits.

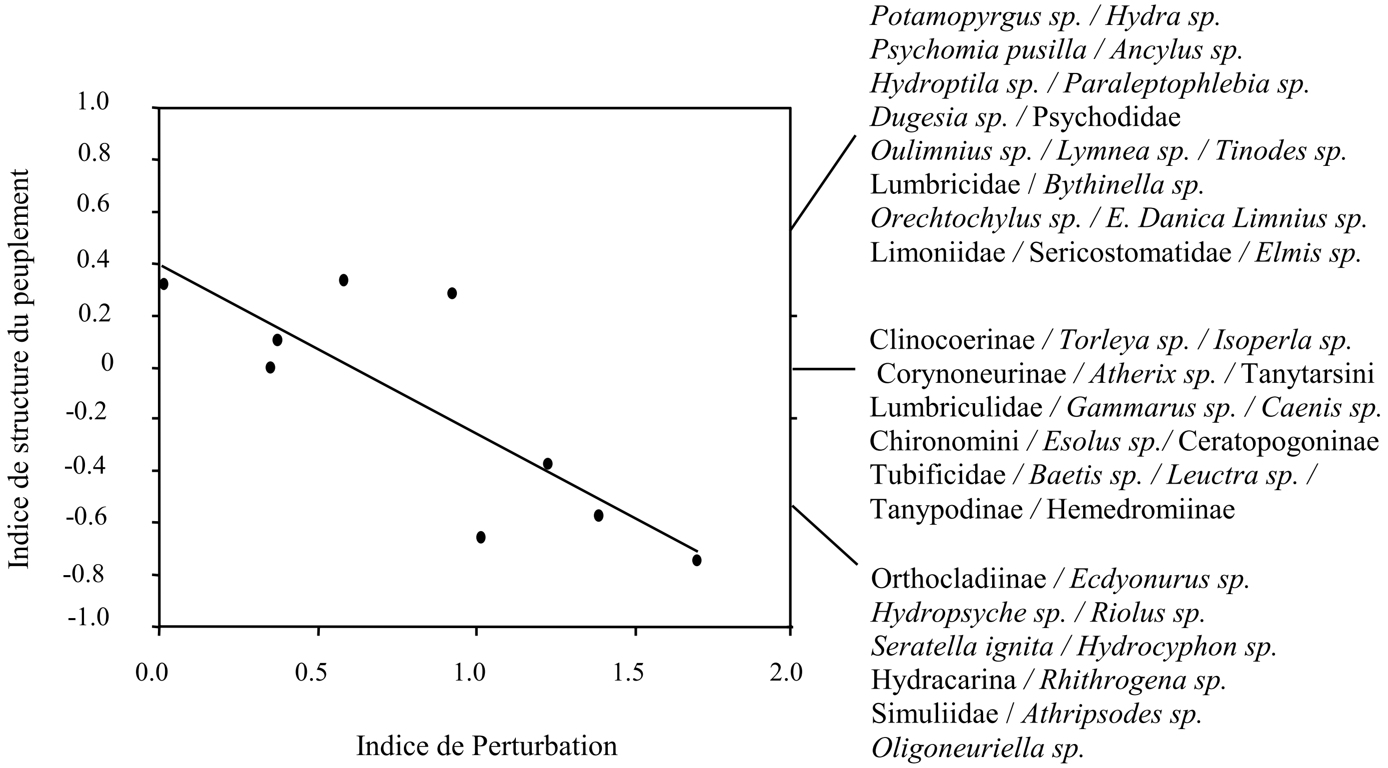


Figure 12. Relation entre l'indice de perturbation et l'indice de structure du peuplement (coordonnées d'AFC) basé sur la faune des sites. La correspondance avec les taxons est indiquée sur la droite du graphique.

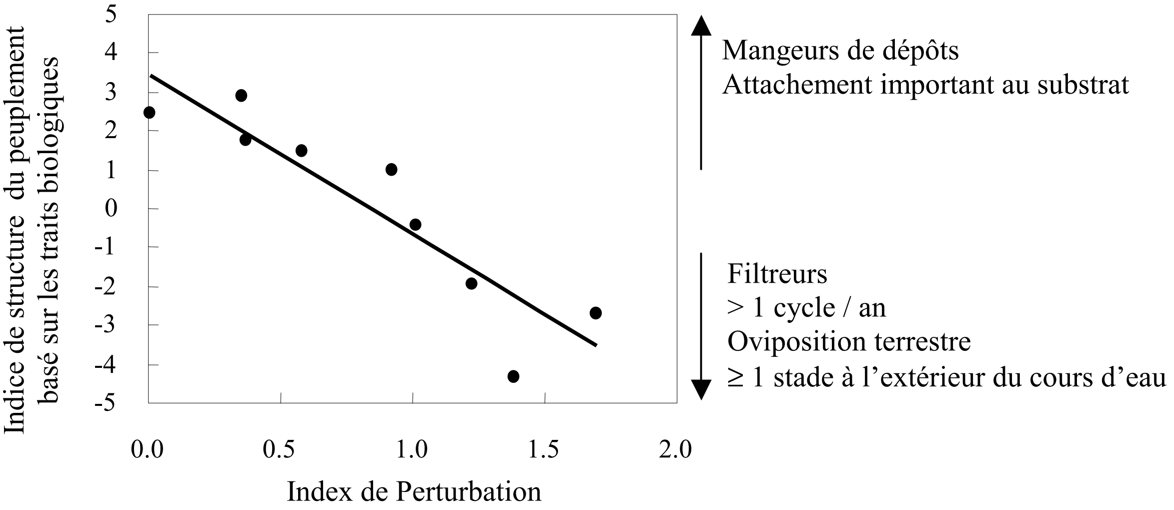


Figure 13. Relation entre l'indice de perturbation et l'indice de structure du peuplement basé sur les traits biologiques.

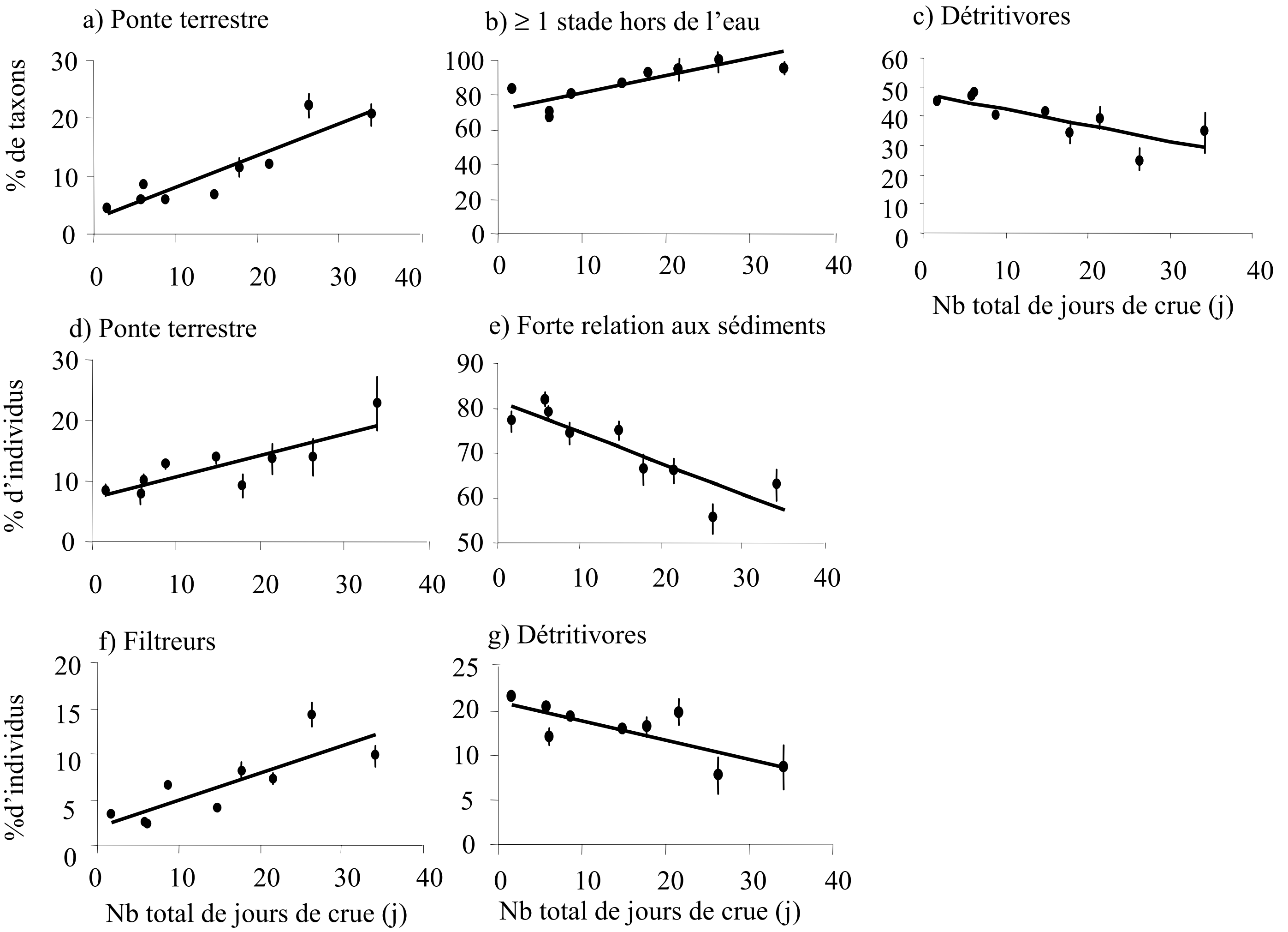
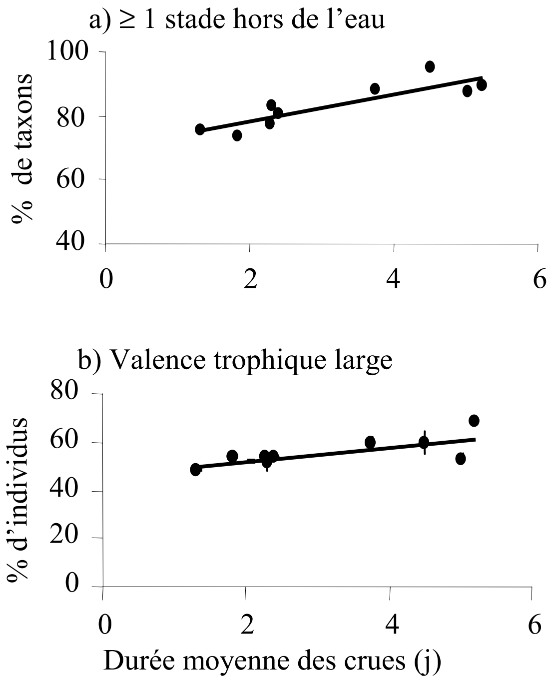


Figure 14. Relation entre le nombre de jours en crue par an avec les proportions de différents traits : a) ponte terrestre (% de taxons), b) ≥ 1 stade hors de l'eau, c) détritivores (% de taxons), d) ponte terrestre (% d'individus), e) forte relation aux sédiments, f) filtreurs, g) détritivores (% d'individus).

Figure 15. Influence de la durée moyenne des crues sur a) la proportion de taxons qui ont au moins 1 stade de développement en dehors du milieu aquatique, et b) la proportion d'individus qui ont une large valence trophique. Chaque point indique une proportion moyenne (N = 10) encadrée par son erreur standard.



L'ensemble des résultats confortent l'existence de liens forts entre la structure des sédiments et les invertébrés benthiques (Minshall, 1984). La compréhension des mécanismes qui sous tendent ces relations invertébrés-sédiments est fondamentale pour mieux comprendre l'organisation des peuplements dans les trois dimensions du lit.

Du point de vue vertical, la recherche de conditions moins contraignantes - stress hydraulique et compétition réduite - en profondeur a souvent été avancée comme une explication de la colonisation de la zone hyporhéique par les invertébrés benthiques (Creuzé des Chatelliers & Marmonier, 1990 ; Brunke & Gonser, 1999). Brunke & Gonser (1999) suggèrent que leur distribution est fortement influencée par la distribution des ressources trophiques. Les invertébrés épigés se restreindraient aux zones où les ressources sont suffisamment abondantes pour subvenir à leur besoins énergétiques, tandis que les invertébrés hypogés qui ont une physiologie adaptée pour exploiter les ressources en faible concentration (Hüppop, 1985) et les conditions d'hypoxie (Hervant & Mathieu, 1995) coloniseraient les zones inexploitables par la faune épigée. Dans ce schéma d'organisation, nos résultats indiquent que la distribution verticale de la faune épigée n'est pas indépendante de leur taille et de leur forme. Les invertébrés de plus d'un cm et de forme aplatie et hydrodynamique préfèrent la surface tandis que ceux de moins de cinq mm préfèrent la profondeur.

Par ailleurs, nos résultats montrent qu'indépendamment de la profondeur, la porosité efficace des sédiments influence leur abondance, leur distribution et leur diversité. La porosité explique 8% de la densité intra-sites, et environ 25% des différences de densité intra-strates. Quelle que soit la strate, le doublement de la porosité se traduit par un doublement de la densité. Ce processus local est transposé à l'échelle des sites et permet d'expliquer 45% des différences de densité inter-sites. Les effets combinés de la porosité sur la densité et la taille des invertébrés suggère qu'elle pourrait également influencer la biomasse et ainsi influencer la biomasse piscicole dans la mesure où les invertébrés constituent l'essentiel des ressources trophiques des poissons. Par ailleurs, elle pourrait également influencer la dynamique du peuplement en contrôlant le nombre d'organismes vivant dans les sédiments profonds qui sont susceptibles de recoloniser la surface après les crues.

D'un point de vue évolutif, de nombreux invertébrés aquatiques qui constituent la faune benthique sont d'origine terrestre et ont du adapter tout ou partie de leur cycle vital à la vie aquatique (Ward *et al.*, 1998). Dans les cours d'eau, l'écoulement constitue une contrainte forte exerçant une influence sur les invertébrés et leurs ressources, et la morphologie a été vue très tôt comme le résultat d'une adaptation au courant - aplatissement dorso-ventral, forme hydrodynamique – (Steinmann, 1907 ; Ambühl, 1959). Les recherches les plus récentes montrent qu'effectivement la morphologie influence la nature des forces subies par les invertébrés mais que des adaptations telles que, par exemple, l'aplatissement dorso-ventral ne permettent pas aux invertébrés de se soustraire aux contraintes de l'écoulement (Statzner & Holm, 1982 ; Statzner & Holm, 1989). L'aplatissement a également été vu très tôt comme une adaptation permettant l'utilisation des larges interstices de la sous-couche de l'armure (Nielsen, 1951; Hynes, 1970). Nos résultats élargissent cette hypothèse et suggèrent que la morphologie est une adaptation à l'utilisation des sédiments, où les formes cylindriques et sphériques et la petite taille permettent la pénétration dans les sédiments profonds ou peu poreux. Certains invertébrés pourraient avoir adapté peu à peu leur morphologie mais aussi leur physiologie et leur comportement à la vie dans les sédiments profonds. Ces processus ont par ailleurs été avancés pour expliquer l'origine de la faune souterraine (Rouch & Danielopold, 1987). Toutefois, en ce qui concerne la morphologie, les mécanismes d'un tel processus évolutif sont loin d'être démontrés. Si la petite taille constitue un atout évident pour pénétrer au sein des sédiments, les fondements physiques qui permettent d'affirmer que les formes cylindriques ou sphériques constituent un avantage restent plus obscurs. La prise en considération du comportement est certainement importante pour comprendre le rôle de la morphologie. A notre connaissance, il n'existe pas de quantification des dépenses énergétiques associées à la pénétration des sédiments pour des invertébrés de différentes formes. De telles études permettraient de mieux comprendre les mécanismes qui struturent la distribution des invertébrés benthiques dans les sédiments des cours d'eau.

L'occupation des sédiments du lit peut varier au cours du cycle vital des organismes (Williams, 1984) mais également à la faveur d'événements perturbateurs tels que les étiages et les crues (Boulton & Lake, 1992; Dole-Olivier & Marmonier, 1992a). Dans ce contexte également, l'occupation de l'habitat a été vue comme une manière de se protéger des contraintes liées à la vie en surface. Durant les dix dernières années, les tests sur l'utilisation de la zone hyporhéique comme refuge se sont multipliés (Palmer *et al.*, 1992 ; Dole-Olivier *et al.*, 1997 ; Imbert & Perry, 1999). Les résultats acquis suggèrent que la migration n'est pas aussi courante que cela a été envisagé (Boulton & Findlay, 1998), mais qu'elle pourrait se restreindre dans des zones d'échange entre les eaux de surface et les eaux souterraines. La zone hyporhéique constituerait donc un refuge morcelé où la migration verticale serait principalement localisée dans les zones de « downwelling ».

Malgré le nombre important de preuves d'une survie différentielle des invertébrés dans les refuges (Lancaster & Hildrew, 1993 ; Robertson *et al.*, 1995 ; Winterbottom *et al.*, 1997 ; Rempel *et al.*, 1999 ; Maier, 2001), notre étude n'a pas permis de montrer leur rôle en temps que facteur de structuration des peuplements. Ce résultat conforte ceux de Townsend *et al.* (1997) qui, en dépit d'un nombre de sites plus important - 54 sites - concluent à la faible - mais significative - influence de la disponibilité en refuges. Dans notre étude, l'absence de liens peut s'expliquer par leur définition qui est basée sur leur utilisation potentielle. Nous n'avons pas mesuré précisément comment ces refuges étaient utilisés lors des crues.

Au contraire, les résultats confirment l'importance des perturbations comme facteur de structuration des communautés aquatiques (Resh *et al.*, 1988 ; Scarsbrook & Townsend, 1993 ; Biggs, 1995 ; Muotka & Virtanen, 1995). La définition de la perturbation en relation avec le mouvement des sédiments est pertinente pour comprendre la structure des peuplements d'invertébrés (Townsend *et al.*, 1997a). Classiquement, la fréquence et l'intensité des perturbations sont avancées comme les facteurs structurant les peuplements (Ward & Stanford, 1983 ; Resh *et al.*, 1988 ; Townsend, 1989 ; Townsend *et al.*, 1997b). Nos résultats montrent que la durée des perturbations est également pertinente dans la mesure où la plupart des traits biologiques qui ont été choisis répondent à cette variable. Les invertébrés dont une partie du cycle se déroule hors du milieu aquatique ou qui ont un faible lien avec les sédiments sont favorisés dans les systèmes les plus perturbés. Ces traits pourraient réduire la probabilité de destruction par l' « érosion » due au transport des particules. Par ailleurs, la forte valence trophique pourrait également constituer un avantage dans ces systèmes (voir Mihuc & Minshall, 1995) dans la mesure où les crues influencent la dynamique temporelle des ressources trophiques (*e.g.* périphyton, Biggs, 1995). De la même manière, les invertébrés filtreurs pourraient être favorisés au détriment des invertébrés détritivores, en raison d'une disponibilité en matière organique dérivante plus forte dans les sites ayant un régime hydrologique plus perturbé (Wallace *et al.*, 1991).

CONCLUSIONS ET PERSPECTIVES

La distribution des invertébrés en surface ou au sein des sédiments est sous le contrôle de facteurs à large échelle et de facteurs locaux. Dans ce contexte, les sédiments fins ont un rôle important puisqu'ils contrôlent partiellement la porosité des sédiments. Cette dernière influence la distribution des invertébrés en fonction de critères morphologiques. Bien entendu, il est évident que l'aspect morphologique des préférences d'habitat que nous avons présenté ne constitue qu'une partie des paramètres qui entrent en ligne de compte pour le choix de l'habitat. Les besoins énergétiques et physiologiques à satisfaire, l'évitement des prédateurs sont autant de critères qui entrent en considération dans ce choix. Enfin, compte-tenu des inter-relations entre l'hydraulique, la structure des sédiments et la répartition des ressources trophiques, il est important d'élargir le choix des variables de description de l'habitat pour comprendre les raisons qui dictent les choix d'habitat.

Le couplage de variables d'habitat, avec des variables décrivant diverses fonctions des invertébrés constitue un pas important pour comprendre les préférences d'habitat (voir A6). Cette approche, conduite à plusieurs échelles spatiales - micro-habitat, site, cours d'eau, région -, est intéressante pour déterminer quelles sont les variables clés qui filtrent les espèces, et sur quels critères elles agissent. Les descripteurs sans dimensions de l'hydraulique que sont le nombre de Froude et le nombre de

Reynolds sont des variables pertinentes pour caractériser l'habitat (Lamouroux, 1997) car elles représentent des ratio énergétiques qui contrôlent le transport et la diffusion des substances - oxygène, sédiments fins, matière organique dérivante - dans le cours d'eau. En ce qui concerne les sédiments, nos résultats indiquent que la proportion de sables et de petits galets ou la taille des sédiments fins (voir A6) dans la couche superficielle du lit semblent être également des descripteurs pertinents des conditions d'habitat.

Les événements tels que les crues ont un rôle fort dans la structuration des peuplements d'invertébrés. Les fortes crues qui ont faible récurrence produisent d'importants effets sur les peuplements en réduisant l'abondance et la richesse taxonomique de manière drastique et en produisant de nouveaux assemblages qui sont rapidement remplacés par les assemblages précédant la crue. Ces événements peu fréquents sont donc importants au terme de quelques mois. Au contraire, les événements plus fréquents que les invertébrés subissent plusieurs fois durant leur cycle vital sont susceptibles de sélectionner les invertébrés. On connaît peu de choses sur le comportement et les activités des invertébrés durant les crues. Les relations entre la durée des crues et les traits trophiques que nous avons observées, suggèrent que la continuité de l'activité de nutrition peut être importante pour assurer la survie pendant ces événements.

La meilleure connaissance de l'utilisation des habitats et des activités des invertébrés lors des crues constitue une voie de recherche intéressante. Cette voie a été peu exploitée du fait des difficultés inhérentes à la prise de mesures pendant les crues. Cette contrainte suggère l'utilisation d'installations expérimentales dans lesquelles le comportement de « modèles biologiques » pourrait être testé. Par exemple, les trichoptères Limnephilidae avec leur fourreau imposant constituent un modèle intéressant pour tester l'utilisation des refuges de surface, tandis que *Leuctra major* (Plécoptères, Leuctridae) et *Elmis sp., Esolus sp.* (coléoptères Elmidae) peuvent être envisagés pour tester l'utilisation des interstices. L'utilisation de canaux artificiels permettrait également de comparer comment se traduisent les perturbations en terme de taux de croissance. La comparaison de modèles biologiques ayant des exigences trophiques différentes pourrait procurer des réponses intéressantes sur l'impact des crues et de leur durée à une échelle fine. A notre connaissance, des quantifications expérimentales sur ces questions simples font encore défaut.

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II – ARTICLES

A 1

INFLUENCE OF BED-SEDIMENT FEATURES ON THE INTERSTITIAL HABITAT AVAILABLE FOR MACROINVERTEBRATES IN 15 FRENCH STREAMS

(Gayraud S. & M. Philippe., Soumis à *International Journal of Hydrobiology*)

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Influence of Bed-Sediment Features on the Interstitial Habitat Available for Macroinvertebrates in 15 French Streams

Key words: grain-size, porosity, sediment, packing, geology

Abstract

The interstitial space of bed-sediments is a major component of the stream system as it influences both physical and biological processes and patterns, such as exchanges between surface-water and groundwater or the assemblage of invertebrates. To investigate the influence of grain-size distribution and vertical bed-packing on the interstitial habitat, we used 99 frozen cores collected from 15 French streams. On our data, overall invertebrate density, density of Chironomidae and taxonomic richness were more strongly related to effective porosity than to other physical variables describing bed-sediments. We built two models to quantify the influence of grain-size distribution and vertical bed-packing. The effective porosity decreased with increasing grain-size heterogeneity and was strongly related to grain-size distribution. These relationships differed with vertical bed-packing, but were consistent across three types of sediments varying in particle shape and particle texture. These general relationships suggest that effective porosity could be helpful to better understand the distribution patterns of invertebrates in bed-sediments.

1. Introduction

For lotic ecologists, the knowledge of the interstitial space created by the arrangement of particles in bed-sediments (*sensu* BRETSCHKO, 1992) is of major importance to better understand the physical, chemical and biological processes that take place in the streambed (GIBERT et al., 1990; VERVIER et al., 1992). For example, hydraulic exchanges between surface-water and groundwater result in spatial and temporal variations of flow pattern within bed-sediments (VAUX, 1968; DOLE-OLIVIER, 1998). These exchanges are strongly influenced by hydraulic gradients at the surface, depth in the hyporheic zone and characteristics of the sediments such as bed porosity and hydraulic conductivity (HARVEY and BENCALA, 1993; WHITE, 1993). The water flowing in the pore system carries dissolved chemical substances (TRISKA et al., 1993; VALETT et al., 1994), particulate and dissolved organic matter (LENTING et al., 1997), and constitutes a habitat for many benthic macroinvertebrates (WILLIAMS and HYNES, 1974). Invertebrates use bed-sediments for deposition and incubation of eggs, for feeding (MINSHALL, 1984), as well as shelter from predation (BRUSVEN and ROSE, 1981) and refuge from disturbances (PALMER et al., 1992; DOLE-OLIVIER et al., 1997; GAYRAUD et al., 2000).

The relationship between the interstitial space and invertebrates has received substantial attention during the two past decades, in response to increasing problems of clogging by fine sediments (reviewed by WATERS, 1995). The deposition and the downward migration of fines within the bed affect physicochemical patterns, for example by reducing the hydraulic conductivity (SCHÄLCHLI, 1992), the penetration of water and solutes within the bed-sediments (SCHÄLCHLI, 1995) and the interstitial-habitat volume used by the invertebrates (RICHARDS and BACON, 1994; MARIDET et al., 1996; BOULTON et al., 1997; BRUNKE and GONSER, 1999). The consequences of habitat reduction may range from slight changes in invertebrate abundance, taxonomic richness and assemblage structure to the replacement of pebble/cobble-adapted invertebrate assemblage by one adapted to fine sediments (LENAT et al., 1981). These changes in assemblage composition are the result of functional responses by organisms to the reduction in the interstitial habitat (ERIKSEN, 1963; ANGRADI, 1999). For example, GAYRAUD and PHILIPPE (2001) provided direct evidence that the amount of interstitial space exerts a selective effect on invertebrates through their morphological traits (*i.e.* body size, body flexibility and shape). Invertebrates characterised as being small, cylindrical or spherical and having a highly flexible body are selected in streams with a clogged interstitial space.

A large number of methods and equations have been used to quantify the interstitial space (DAVIS, 1969), but porosity is the most widely used parameter for its assessment both in sediments (POLLARD, 1955; STOCKER and WILLIAMS, 1972) and in soils (BRIGGS, 1977a). The total porosity is normally defined as the ratio of the pore volume to the total volume of a given sample. In streams, bed-sediments are saturated by water and the pore volume is estimated from the volume of water. As in soils, a fraction of the water is physically attached to sediments and creates thin films around particles (KEMPER et al., 1964). This water, which accounts for interstices that invertebrates cannot use, is particularly important in small pores that are created by small particles (< 0.062 mm) because all the water is sufficiently close to the particles to be affected by the adsorption forces. In the macropores created by the arrangement of large particles, only the water lining the pore sides is retained in this way. To investigate relationships with invertebrates, MARIDET et al. (1996) proposed to use the effective porosity of bed-sediments, since this method considers the water attached to particles as a part of the sediments.

Because effective porosity is a key factor controlling both invertebrate vertical distribution (MARIDET et al., 1992) and assemblage structure (GAYRAUD and PHILIPPE, 2001), it is important to identify the factors that control their variations. Among these factors, grain-size distribution, particle shape (TICKELL and HIATT, 1938), and particle packing (FURNAS, 1931; GRATON and FRASER, 1935) have been indicted to explain variations in porosity in other fields of research such as chemistry and engineering. Engineers have developed models (WESTMAN and HUGILL, 1930; OUCHLYAMA and TANAKA, 1984; 1986) to predict porosity from the grain-size distribution of substrates constituted by a finite grain-size number of spherical and smooth particles. Unfortunately, such models cannot be applied to bed-sediments because of the large diversity of particle shapes, particle sizes (BRETSCHKO, 1994), and spatial heterogeneity of particle packing (CARLING and READER, 1982). This reinforces the need for the study of relationships between bed-sediment characteristics and porosity.

2. Study sites

To quantify the relationships between bed-sediment characteristics, effective porosity and invertebrates, we used data previously collected in different studies and partly published by MARIDET et al. (1992; 1996), GAYRAUD et al. (2000), and GAYRAUD and PHILIPPE (2001). A total of 99 frozen cores was collected in 17 study sites located in 15 French streams (Table 1).

These streams are 3rd to 5th order tributaries of the Rhône River (13 reaches), the Dordogne River (3 reaches) and the Loire River (1 reach). The streams differed greatly in their geology (ANONYMOUS, 1996). We separated study sites into 3 groups according to the major rock type encountered in their catchments: granitic reaches, limestone reaches, and mixed-rock reaches which referred to catchments dominated by granitic or sandstone rocks, by limestone or dolomite, and by a mixture of different rock types, respectively.

In granitic reaches, bed-sediments are made up of large poorly-rounded particles (*i.e.* pebbles and cobbles) of variable shape and rough texture, that are deeply embedded in a large amount of sand. Limestone and dolomite rocks encountered in limestone reaches are fine-grained rocks that mainly consist of calcium and magnesium carbonates. The erosion of these rocks produces bed-sediments made up of a high proportion of large poorly-rounded particles (BORNAND, 1972), but with less sand and more silt and clay than in granitic reaches. In mixed-rock reaches, the heterogeneity of rocks is explained by the transport and the deposition of alluvium in the Rhône basin during the Quaternary period. In these streams, sedimentary dynamics produce bed-sediments made up of rounded pebbles that are slightly embedded in sand and gravels.

3. Materials and methods

3.1. Sampling of bed-sediments and invertebrates

Sampling was conducted at different seasons over a decade (1989-1999). The season of sampling and the number of sampling occasions varied, leading to a variable number of samples among the three groups of sites and among study sites (Table 1). To collect bed-sediments and invertebrates, we used freeze-coring preceded by electro-positioning (BRETSCHKO and KLEMENS, 1986) which immobilised the invertebrates with an electric current (650 V, 50 Hz, 15 minutes). The corer and the electrodes were placed in the substratum and a 45 cm deep core was extracted 2 days later. Before sampling, the corer was protected with a flow deflector to prevent erosion and warming by the water. The freezing operation required the injection of about 25 litres of liquid nitrogen for 15 minutes. The 99 frozen cores we collected were separated into three sediment layers (surface layer: [0–15 cm], intermediate layer: [15-30 cm] and deep layer: [30-45 cm]), transported frozen to the laboratory and stored in a freezer (-20 °C). Finally, 99, 98, and 96 samples (total = 293) were collected in the surface layer, the intermediate layer and the deep layer, respectively. The presence of bedrock sometimes limited the hyporheic zone to a depth of 15 or 30 cm, explaining why the number of samples differed among layers.

In the laboratory, we measured the total weight (W_t) and volume (V_t) of each sample. Weight was measured with an electronic balance (OHAUS IP15KS; precision 0.1 g). The sample volume was estimated from the volume of water displaced by the frozen sample in a cylinder. After thawing, invertebrates (> 500 µm) and coarse particulate organic matter (> 1 mm) were separated from the sediment by elutriation. During these operations, Oligochaeta were destroyed because of the fragility of their body. Invertebrates (except Oligochaeta) were counted, identified to family level, and described in terms of taxonomic richness (number of families) and density (number of invertebrates per litre of sediment). The largest particles (> 23 mm) were removed from the sample and sorted manually into size classes (128, 90, 64, 45, 32, 23 mm), while finer sediments were sieved in water (12, 8, 5, 2, 1, 0.50, 0.25, 0.05 mm) with an electronic sieving machine (AS 200 CONTROL RETSCH CO, HAAN, GERMANY). The finest fraction (< 0.05 mm) was obtained by continuous-flow centrifugation. The sorted sediments were dried at 105°C for 48 hours, weighed (W_d) and their weight expressed as proportions (0-1) of the total dry weight of the sediment. Then, the sorted sediments were weighed again after moistening and draining (W_w), in order to quantify the water captured by adsorption which creates thin films around particles. Moistening and draining consisted of the addition of small quantities of water to sediments until the water seeped from wet sediments.

From these characteristics, we calculated total porosity and effective porosity of sediments. The total porosity was calculated from the ratio of the volume of interstitial water to the total volume of the sample (1), whereas the effective porosity was calculated from the volume of free interstitial water (2). The volume of interstitial water was calculated from the difference between the total sample weight (W_t) and the sum of wet weight (ΣW_w) or dried weight (ΣW_d), assuming the water density (ρ) was 1000 Kg/m^3.

$$Total\,porosity = \frac{(W_t - \sum W_d) \times \rho}{V_t} \times 100 \tag{1}$$

$$Effective\,porosity = \frac{(W_t - \sum W_w) \times \rho}{V_t} \times 100 \tag{2}$$

To relate the grain-size distribution to effective porosity, we used two types of variables (grain-size proportions and dimensionless variables). We calculated the proportion of particle sizes according to the classical WENTWORTH description. Sieved sediments were grouped into 5 classes 0-0.05 (Si, silt & clay), 0.05-2 (Sa, sand), 2-16 (G, gravel), 16-64 (P, pebbles) and 64-256 mm (C, cobbles), and were expressed as proportions (0-1) of the sum of dried weights (ΣW_d). We also calculated variables classically used to describe the shape of the distribution curve, *i.e.* sorting index (3), skewness index (4) and kurtosis index (5). These were calculated from quartiles of the Φ–size distribution ($\Phi = -\mathrm{Log}_2\ \mathrm{Size}$) and were defined as follows:

$$\Phi\, So = \left(\frac{\Phi 84 - \Phi 16}{2} \right) \tag{3}$$

$$\Phi Sk = \left(\frac{\Phi 84 - \Phi 50}{\Phi 84 - \Phi 16} \right) - \left(\frac{\Phi 50 - \Phi 10}{\Phi 90 - \Phi 10} \right) \tag{4}$$

$$\Phi Ks = \left(\frac{\Phi 90 - \Phi 10}{1.9 \times (\Phi 75 - \Phi 25)} \right) \tag{5}$$

The sorting index measures the grain-size heterogeneity, and varies from ΦSo < 0.35 for very well sorted sediments to ΦSo > 4.00 for very poorly sorted sediments (BRIGGS, 1977b). The skewness index measures the degree of asymmetry of the distribution curve and varies from -1 to 1. A negatively skewed distribution indicates that large grains are more abundant than predicted with a normal distribution, whereas a positively skewed curve indicates that small grains are more abundant. The kurtosis index describes the flatness of the distribution and varies from ΦKs < 0.67 for a very flat curve, to ΦKs > 3.00 for a very peaked curve.

3.2. Quantifying the influence of effective porosity on the invertebrates

Our first objective was to quantify the relation between effective porosity and invertebrates (overall density and richness, Chironomidae density), and to compare this with the relations with other bed-sediment characteristics (total porosity, grain-size proportions, D50, ΦSo, ΦSk, ΦKs). These relationships were investigated by Pearson’s correlation and tested for significance using Bonferroni’s method that provides protection for multiple testing (SOKAL and ROHLF, 1998). Because of the large differences among study site characteristics, differences in invertebrate density and richness among study sites could result from factors other than porosity, such as sampling season, geology, trophic resources or other factors that were not quantified in the study. In addition, density and taxonomic richness of the macrobenthos are also known to decrease with depth in bed-sediments. Thus, to present relationships that were common to all study sites, years, seasons and sediment layers, data were standardised by sampling campaign (defined as a sampling occasion in a study site) and sediment layers. Before calculating correlations, we used the Kolmogorov-Smirnov test to assess the normality of data distribution. When the distribution deviated from normal distribution, we calculated leverage statistic (VELLEMAN and WELSCH, 1981), that detect data having a strong influence on the correlation. Data having a large leverage (> 0.2) were not used to calculate the correlation.

To test the consistency of the relationships between effective porosity and invertebrates, we quantified how the relationship varied among campaigns and sediment layers using General Linear Models (GLM). These models test the effects of continuous and discrete variables as well as the effect of their interactions in the same analysis. For example, we tested both the effect of porosity on the invertebrate density, and how this effect differed among the campaigns and sediment layers using the following model:

$$\textit{Invertebrate density} = a \times \textit{porosity} + b_i \times \textit{porosity} + c_j \times \textit{porosity} \qquad (6)$$

where a is a coefficient fitted to the entire data set, b_i is a coefficient fitted to each campaign, and c_j is a coefficient fitted to each sediment layer. The statistical significance of the coefficient a, and the sets of coefficients b_i and c_j, tested respectively for the overall effect of porosity and how the effect of porosity varied among the campaigns and among the sediment layers.

3.3. Relating effective porosity to bed-sediment characteristics

Our second objective was to quantify the influence of the grain-size distribution on porosity. As a first step, the relationships of effective porosity with total porosity, grain-size proportions, and dimensionless variables were quantified by Pearson correlations and tested for significance using Bonferroni’s method. As for invertebrates, the analyses were conducted on standardised data to present relationships common to all campaigns and all sediment layers. Normality of the data distribution was also tested and leverage statistic used to detect influent data (see above).

As a second step, we quantified the amount of effective porosity variance that could be explained by the two sets of variables (dimensionless variables, grain-size proportions) describing the grain-size distribution. We related effective porosity to dimensionless variables (ΦSo, ΦKs, ΦSk) using a GLM procedure. As the differences in vertical bed-packing may modulate the relationship between dimensionless variables and porosity, the coefficients of the model were allowed to vary among the sediment layers. Non-significant variables ($P > 0.01$) were removed, and the following model derived from the analysis:

$$\textit{Effective porosity} = a_i + b_1 \times \Phi\mathrm{So} + c_i \times \Phi\mathrm{So} \qquad (7)$$

where b_1 is a coefficient fitted for the entire data set, a_i and c_i are coefficients fitted separately for each sediment layer. The significance of the coefficient b_1, and the sets of coefficients a_i and c_i, tested respectively for the global effect of the effective porosity and how this effect varied among the sediment layers.

To relate effective porosity to the grain-size proportions, we used a mixture model (MARQUARDT and SNEE, 1974) that is suitable for analysing the effect of variables summing to a constant value (this is the case for grain-size proportions). This model provides a test of interaction terms and produces appropriate overall R^2 and individual P-values to test the influence of each variable (SPSS INC, 1999). The effect of sediment layer, grain-size proportions and first-order interaction terms of grain-size proportions were entered into the analysis. As in the previous model, no significant ($P > 0.01$) effects were removed and the following model was derived from the analysis:

$$\textit{Effective porosity} = a_\mathrm{i} + b_1 \times \mathrm{Si} + b_2 \times \mathrm{Sa} + b_3 \times \mathrm{G} + b_4 \times \mathrm{P} + b_5 \times \mathrm{C} + c_1 \times \mathrm{Sa} \times \mathrm{G} + c_2 \times \mathrm{Sa} \times \mathrm{P} + c_3 \times \mathrm{Sa} \times \mathrm{C} + c_4 \times \mathrm{G} \times \mathrm{P} + c_5 \times \mathrm{G} \times \mathrm{C} \qquad (8)$$

where a_i are coefficients fitted separately for each sediment layer, b_1- b_5 are coefficients fitted for each grain-size proportion and c_1- c_5 are coefficients fitted for each first order term. To limit the complexity of this last model, coefficients related to grain-size-proportions were not fitted separately for each sediment layer.

In the absence of data standardisation, most variables were not normally distributed (Kolmogorov-Smirnov test), so we calculated leverage statistic and studentized residuals (VELLEMAN and WELSCH, 1981) to detect influent data in the independent variable space and in the dependent variable space, respectively. Data having a large leverage (> 0.2) and large studentized value (> 5) were not used to build the model.

We evaluated the quality of these two models through the precision and the accuracy of the predictions. Since the variance in observed porosity could vary among groups of study sites and sediment layers, the precision of the models was evaluated by the 95% confidence interval of the model residuals. The accuracy was evaluated by fitting observed versus predicted values using linear regression, and we considered the predictions as accurate if the regression line did not differ significantly from the line of perfect agreement ($X = Y$). The comparison of the precision of the two models (7) and (8) showed that the model built from dimensionless variables gave less precise porosity predictions than the model built from the proportions of grain-sizes (*i.e.* limits of the 95% confidence interval of the residuals). We therefore tested the influence of particle shape and texture using the latter model. We tested the transferability of the model by crosswise predictions among the three groups of study sites that differed in the shape and the texture of bed-sediment particles. The coefficients of equation (8) were fitted for each rock type to predict the porosity in the remaining data set. The relevance of the model was evaluated by quantifying the accuracy and the precision of predicted values.

4. Results

4.1. Influence of effective porosity on the invertebrates

To compare the relative importance of effective porosity and the other variables that described bed-sediments, we investigated their relationships with biological variables (Table 2). Among the physical variables involved in the analysis, effective porosity best explained the invertebrate density, the Chironomidae density and the taxonomic richness. We focused on these relationships, and tested the consistency of the biological response using GLM. The invertebrate density was positively related to effective porosity (GLM, $P < 0.001$), and the slope of the regression did not differ significantly between sediment layers and sampling campaigns. Although the response of the invertebrate density was consistent, the proportion of explained variance varied between layers; 23% of the variance was explained by porosity in the surface layer (Fig. 1.A), 41% in the intermediate layer (Fig. 1.B) and 34% in the deep layer (Fig. 1.C). The density of the most frequently encountered taxon (Chironomidae) was also positively related to porosity (GLM, $P < 0.001$), and exhibited the same relationship among sediment layers and sampling campaigns. As for the overall invertebrate density, the proportion of variance explained by the relationship was lower in the surface layer ($R^2 = 0.09$; Fig. 1.D) than in the intermediate layer ($R^2 = 0.21$; Fig. 1.E) and in the deep layer ($R^2 = 0.18$; Fig. 1.F). Taxonomic richness increased with porosity (GLM, $P < 0.001$), but the slope of the regression line differed significantly among sediment layers (GLM, $P = 0.010$). The taxonomic richness was not significantly related to the porosity in the surface layer ($P > 0.10$, Fig. 4.G), whereas this latter variable explained 24% of the variability in the intermediate layer (Fig. 1.H) and 17% in the deep layer (Fig. 1.I). The regression line did not differ significantly between the sampling campaigns.

4.2. Relation between effective porosity and bed-sediment characteristics

To define the limits of the models relating porosity to grain-size distribution, we focussed on the range of variation of the sediment characteristics. The grain-size proportions showed large variations among size categories (Table 3). The proportion of silt & clay varied from 0.0 to 9.1% and the proportion of sand varied from 0.1 to 41.9%, suggesting that the relations we will present in the following section are applicable to coarse substrates embedded in fine sediments. The dimensionless variables used to describe bed-sediments show variations as large as variations normally observed in natural bed-sediments (see methods).

Effective porosity was positively related to total porosity (Table 4) and this correlation explained 29% of the effective porosity variance. Despite its significance, this correlation was not suitable to predict effective porosity from the generally used total porosity. A multiple-regression analysis was used to build a useful relationship between effective porosity selected the proportions of silt & clay and sand, in addition to total porosity (10). This relationship fitted for the full data set ($N = 290$) explained 90 % of the effective porosity variance.

$$\mathit{Effective\ porosity} = -0.93 + 0.86 \times \mathit{total\ porosity} - 59.46 \times \mathit{Si} - 86.8 \times \mathit{Sa} \qquad (9)$$

Effective porosity was negatively related to the proportion of silt & clay and to the proportion of sand, and positively related to the proportion of pebbles (Table 4). Porosity decreased with increasing heterogeneity of grain size (*i.e.* the sorting index) but was not significantly ($P > 0.05$) related to the degree of asymmetry or to the kurtosis of the distribution curve. The significant correlation between the sorting index and many grain-size proportions suggested that bed-sediments having the highest proportion of fine sediments (silt & clay, sand) were also the most heterogeneous.

The model built using the sorting index was highly significant ($P < 0.001$) and explained 47% of the overall variance in porosity. The porosity decreased with the heterogeneity of sediment but this relationship differed between the sediment layers ($P = 0.0024$). The coefficients related to the sediment layers (a_1-a_3) decreased with depth indicating that the same grain-size heterogeneity produced higher porosity in the surface than in deep sediment layers (Table 5). Because the coefficients of this model were fitted separately for each sediment layer, the accuracy of the prediction was high in all the sediment layers, (*i.e.* regression lines matched the line of perfect agreement, Fig. 2.), but the predictions precision was low (*i.e.* 95% confidence intervals of residuals were large).

The mixture model built using grain-size proportions was highly significant ($P < 0.001$) and explained 73% of the overall porosity variability. The coefficients related to the sediment layers (a_1-a_3) decreased with depth, indicating that the same grain-size composition produced a lower porosity in deep layers than in the surface layer (Table 5). We examined the accuracy and the precision of the model in all the sediment layers by fitting the linear regression observed against estimated porosity (Fig. 3.). The predictions given by the latter model were more precise than predictions by the model built from the sorting index. Accuracy and precision of predictions were similar in the three sediment layers (Fig. 3.).

The influence of shape and texture was evaluated by testing the transferability of the model built from grain-size proportions across the three groups of study sites that we defined based on catchment geology. The porosity predictions given by each partial data set model versus the porosity observed in the remaining data set were fitted by linear regression (Fig. 4.). Predictions of porosity in limestone, granitic and mixed-rock reaches were accurate, as the regression line did not differ significantly from the line of perfect agreement. These predictions were compared with predictions given by the model fitted to the full data set in terms of precision. Porosity in granitic reaches was predicted with the same precision whereas the partial data set models gave less precise porosity predictions in limestone and mixed-rock reaches.

5. Discussion

The examples of porosity-invertebrate relations we presented confirm the importance of the interstitial habitat for invertebrates, already observed or suggested in previous studies (*e.g.* RICHARDS and BACON, 1994; GAYRAUD and PHILIPPE, 2001). The relationships of invertebrates with this habitat are complex because several factors acting at different spatial scales can influence their distribution within bed-sediments. Hydrological patterns (DOLE-OLIVIER and MARMONIER, 1992; DOLE-OLIVIER et al., 1997), sediment-related features such as pore size (WILLIAMS, 1972), ratio of particulate organic matter to total fine particles (BRUNKE and GONSER, 1999), and oxygen concentration (STRAYER et al., 1997) structure the invertebrate assemblage within bed-sediments. In addition, morphological or behavioural adaptations of invertebrates to penetrate a given sediment are also important to understand these patterns (WILLIAMS and HYNES, 1974, GAYRAUD and PHILIPPE, 2001). In this context, our study shows clearly that the invertebrate assemblage is correlated with the effective porosity, since this variable explains 23-41% of within study site variations in the invertebrate density and 3-24% of variations in the taxonomic richness.

Sediment-related features controlling the distribution of invertebrates are likely to differ between “hard substrates” having a low water content, but large pores and a high permeability, and “soft substrates” having a high water content, but small pores and a low permeability (WARD et al., 1998). In soft substrates, invertebrates can move easily by disturbing the sediment structure (BREKHOVSKIKH et al., 1991), whereas in hard substrates, the structure remains more stable and invertebrates can move or swim within the interstices. In this latter case to which our study refers, the features of the interstices (*e.g.* permeability, porosity, pore size) control the dissolved oxygen concentration and the distribution of trophic resources that can create confounding patterns. Consequently, the relations we found are probably more complex than previously thought and it is not completely clear how our measure of the interstitial habitat availability is related to pore size or to other features of bed-sediments that were not measured (*e.g.* vertical hydraulic gradient). Finally, although the macrofauna probably accounts for a large part of the community in our study sites, the relations we found are partial since major components of the interstitial community such as the Oligochaeta and the micro-meiofauna were not investigated.

Our investigation revealed a strong relationship between the effective porosity and the particle-size distribution, supporting conclusions drawn from the theory of particle packing (FURNAS, 1931; OUCHLYAMA and TANAKA, 1984; 1986). The theory indicates that for sorted spherical particles, porosity is not related to particle size, but depends only on grain packing. The porosity is greatest for homogeneous material and varies from 26% for a rhomboedric packing to 48% for a cubic packing (GRATON and FRASER, 1935). The porosity is predicted to decrease with increasing heterogeneity in grain size and for mixtures made up of at least two different particle sizes (binary, ternary, or more complex mixtures); the porosity will be influenced both by the number of grain sizes and by the proportion of each grain size (FURNAS, 1931). The basic idea is that if particles of small size are introduced into a bed of large particles, the small particles will fill up the voids without changing the total volume of the sample. The volume of voids filled up with small particles is controlled by their proportion in the sample. These arguments may be extended to systems of more than two particle sizes, assuming that each size of sediment may fill up the voids of the next largest size. Therefore, the porosity will be related to the heterogeneity of particle size; the more homogeneous the bed-sediment is, higher the porosity (Fig.1.; ATKINS and MCBRIDE, 1992). This theoretical approach stresses the complexity in modelling the porosity of bed-sediments made up of a mixture of grain sizes, and explains the weakness of the univariate relationships between porosity and grain-size proportions.

In our data, the absence of any correlation between porosity and D50, the strong relationship with grain-size heterogeneity and the maximum porosity values measured in bed-sediments (Porosity < 23) were consistent with the theory. In addition, the relations we observed between porosity and the proportion of silt & clay and sand were consistent with the classical interpretation of the effect of fine sediments (clogging effect) on the interstitial habitat (CARLING, 1984; SCHÄLCHLI, 1995). Some studies reported larger ranges of variation; 36-61% in sandy-clay marine sediments (BENNETT et al., 1990), 20-60% in river sands (PRYOR, 1973; ATKINS and MCBRIDE, 1992), 7-33% in gravel-bed rivers (BRETSCHKO, 1991; ROUCH et al., 1997, BRUNKE, 1999). These high values are explained by the size of sediments that were studied. For geometric reasons, the total surface area of a given sample and therefore the amount of water attached to particles increases dramatically with decreasing grain size. As a consequence, the sediment consistency becomes increasingly fluid and the total water content is greater in fine sediments than in coarse sediments.

Our results emphasize the importance of appropriately quantifying the availability of the interstitial habitat to understand the invertebrate distribution. We found that invertebrate community characteristics were more strongly correlated with effective porosity than with total porosity. This result confirms the idea that the water captured by adsorption accounts for interstitial space that is not usable by invertebrates. Furthermore, inappropriate method can result in large differences in the estimate of interstitial habitat volume (2.1 to 34.2 for the total porosity versus 0 to 22.9 for the effective porosity). COHEN (1965) found also large differences between total porosity (30-55%) and effective porosity (19-29%) in the well sorted fine sediments of the Humboldt River (Nevada).

To test the influence of particle shape and texture, we made crosswise predictions of porosity among three groups of study sites: granitic reaches (poorly rounded, rough texture), limestone reaches (poorly rounded, smooth texture) and mixed-rock reaches (rounded, variable texture). We did not find large differences in the fit of models used to predict porosity across the 3 groups, suggesting that particle shape and texture were not crucial for explaining effective porosity variations in heterogeneous bed-sediments. These results contrast with the findings of TICKELL and HIATT (1938) who tested the influence of grain angularity of homogeneous sands on porosity. They found a bell-shaped curve in response to variations in grain roundness (defined as the cross sectional area of a grain divided by the area of its smallest circumscribing circle). The porosity was lowest (porosity = 34.7) for intermediate roundness number (Rd = 0.82) and reached 48.6 for poorly rounded grains (Rd = 0.53) and 40.4 for sphere-like grains (Rd = 1.0). In our study, it was not possible to measure the particle roundness because the material was not kept after the laboratory analysis. Although our test does not constitute a fair test compared to the experiments of TICKELL and HIATT, we think that the divergence in the conclusions may be attributed to differences in the heterogeneity of sediments. The shape (or the texture) of particles that is a major factor controlling the porosity of homogeneous sediments was masked by the strong effect of sediment heterogeneity of bed-sediments.

The influence of grain-size distribution on porosity varied between sediment layers, the same grain-size proportions producing a greater porosity in the surface layer than in the intermediate and the deep layer. This depth effect clearly reflects the increase in packing (FRASER, 1935; ATKINS and MCBRIDE, 1992), which is the result of both the compaction by weight and the action of scouring that differs with depth. During floods, when the discharge reaches the critical value of stability for the streambed, the armour layer breaks up and infiltrated fine sediments are resuspended. In an experimental gravel bed embedded by fine sediments, SCHÄLCHLI (1992) observed a large increase in hydraulic conductivity in the uppermost 15 cm after scouring, suggesting that porosity was also increased.

Despite the strong link found between the effective porosity and the grain-size distribution, the model fitted for the full data set predicted porosity with relatively low precision since the 95% confidence interval of the residuals was large (-4.2 to 5.8), in comparison to the range of variation in porosity (0 to 22.9). This relative imprecision may be explained by both the limits of the sampling methodology and the influence of biological activity. Several authors have concluded that core freezing provides a very precise bed sediment description, but the presence of large particles (cobbles) in the sample may strongly influence the grain-size proportions and derived calculations such as the porosity (CARLING, 1981).

The activity of some invertebrates could be more important in structuring “hard substrates” than previously thought since STATZNER et al. (1996) and ZANETELL and PECKARSKY (1996) demonstrated the influence of stonefly larvae of the species *Dinocras cephalotes* and *Mergacys signata*, that actively search for prey by foraging in the interstices of the stream bottom. This activity leads to a continuous removal of fine sediment that influences the packing of bed-sediments and the interstitial space at the microhabitat scale. On the other hand net-spinning larvae such as *Hydropsyche* spp. actively trap suspended sediment and incorporate the undigested particles into the sediment. DANIELOPOL (1984) suggested that within the hyporheic zone, interstitial detritivores may also modify the interstitial space by their ‘pelletization activity’ of fine materials as is the case in terrestrial soils (RUSEK, 1985; VAN VLIET et al., 1993).

6. Conclusions

The unconventional method we used to quantify the interstitial habitat provides a synthetic view of bed-sediments, summarising characteristics such as the proportion of fine sediments and the heterogeneity of particle sizes. In contrast to particule-shape and -texture that are related to differences in geology, particle-size distribution and vertical bed-packing are major factors influencing the effective porosity. The relationships we found between effective porosity and bed-sediment characteristics are general and consistent across many study sites. Furthermore, these relationships are mechanistically interpretable, that allows a better understanding of invertebrate-sediments relationships. Consequently, in addition to hydrological exchanges, trophic resources and dissolved oxygen, the effective porosity could be helpful to better understand the distribution patterns of invertebrates in bed-sediments.

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Table 1. Location, physical characteristics, year and season (S, F, W, and Su, for spring, fall, winter, and summer, respectively) of sampling, and number of samples (N) for the 17 study sites. Rock types are defined according to the major rock encountered in the catchment (see methods).

Rock type	Study reach	Location (lat., long.)	Order	Slope (m/km)	pH	Year	Season	N
Limestone								
	Bez	844.09, 1969.20	3	0.98	7.8	1996	W	10
	Bourne, site 1	847.50, 2014.45	3	1.00	8.4	1997-1999	W	9
	Bourne, site 2	841.57, 2011.47	3	0.64	8.4	1997-1999	W, W, S	27
	Bourne, site 3	839.20, 2011.98	3	0.56	8.2	1997-1999	W, W, S	25
	Drac	910.74, 1977.14	3	1.03	-	1989	W	12
	Eygues	846.77, 1935.20	3	0.87	8.3	1998	W	12
	Ouvèze	839.73, 1926.71	3	1.01	8.3	1998	W	12
Granite								
	Ozange	593.20, 2054.43	3	0.27	6.6	1992	W, S, Su, F	29
	Triouzoune	592.70, 2053.93	3	0.29	6.7	1992	W, S, Su, F	28
	Vianon	587.30, 2035.53	4	1.85	6.9	1992	W, S, Su, F	33
Mixed rocks								
	Galaure, site 1	818.68, 2032.62	3	0.86	8.2	1989-1997	W, W	19
	Galaure, site 2	818.69, 2032.63	3	0.86	8.2	1998	W	12
	Gère	810.17, 2056.12	3	0.86	8.6	1998	W	12
	Herbasse	807.20, 2016.12	3	0.80	8.1	1997-1998	W, W	19
	Loire	730.00, 2142.10	5	0.10	-	1989	S	10
	Sanne	798.25, 2045.25	3	0.80	8.1	1999	W	12
	Varèze	809.68, 2052.80	3	0.82	8.2	1999	W	12

Table 2. Pearson correlation coefficient between biological and physical variables. The Bonferroni method adapted for multiple testing indicates the significance of the correlation coefficients: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$. N = 293.

	Invertebrate density	Taxonomic richness	Chironomidae density
Effective porosity	0.56 ***	0.35 ***	0.37 ***
Total porosity	0.28 ***	-0.13	0.20
Silt & clay	-0.08	-0.04	-0.07
Sand	-0.28 ***	-0.35 ***	-0.06
Gravel	0.05	-0.22 *	0.08
Pebbles	0.14	-0.10	0.20
Cobbles	-0.04	0.25 **	-0.15
ΦSo	-0.23 *	-0.31 ***	-0.03
ΦSk	0.01	-0.20	-0.12
ΦKs	0.06	0.22 *	-0.06
D50	0.02	0.29 ***	-0.08

Table 3. Descriptive statistics on the physical variables describing bed-sediments. Effective porosity, total porosity and bed-sediment composition are expressed as percentages.

	Effective porosity	Total porosity	Bed sediment composition					ΦSo	ΦSk	ΦKs	D50 (mm)
			silt & clay	sand	gravel	pebbles	cobbles				
Mean	5.16	15.28	1.03	10.45	20.30	30.53	37.69	1.99	0.11	0.99	18.95
SD	4.38	4.51	1.09	6.45	9.76	15.95	23.87	0.71	0.28	0.31	19.98
Min	0.00	2.05	0.00	0.14	0.19	0.53	0.00	0.16	-0.84	0.62	0.22
Max	22.94	34.16	9.09	41.87	57.28	77.85	95.97	3.56	0.73	2.52	121.11

Table 4. Matrix of Pearson correlation coefficients between physical variables. The Bonferroni method for multiple testing indicates the significance of the correlation coefficients: * P < 0.01, ** P < 0.001, *** P < 0.0001. N = 293.

	Effective porosity	Total porosity	Silt & clay	Sand	Gravel	Pebbles	Cobbles	ΦSo	ΦSk	ΦKs
Total porosity	0.54 ***									
Silt & clay	-0.22 *	0.34 ***								
Sand	-0.48 ***	0.55 ***	0.15							
Gravel	0.05	0.60 ***	0.20	0.43 ***						
Pebbles	0.41 ***	0.54 ***	0.00	0.14	0.28 **					
Cobbles	-0.15	-0.72 ***	-0.17	-0.54 ***	-0.72 ***	-0.82 ***				
ΦSo	-0.53 ***	0.39 ***	0.30 ***	0.77 ***	0.46 ***	-0.08	-0.35 ***			
ΦSk	0.14	0.46 ***	-0.02	0.36 ***	0.59 ***	0.17	-0.45 ***	0.33 ***		
ΦKs	0.09	-0.13	0.05	-0.17	-0.30 ***	0.13	0.08	-0.53 ***	-0.31 ***	
D50	0.09	-0.63 ***	-0.25 *	-0.58 ***	-0.65 ***	-0.41 ***	0.71 ***	-0.68 ***	-0.55 ***	0.34 ***

Table 5. Characteristics of the models relating effective porosity to dimensionless variables (7), and to grain-size proportions (8). The models are fitted to the full data set (N = 293).

Characteristics	Model Dimensionless	Grain proportions
R^2	0.47	0.73
a_1	14.70	1.72
a_2	7.32	-0.71
a_3	6.78	-1.01
b_1	-2.32	-56.1
b_2	-	141.6
b_3	-	46.1
b_4	-	21.9
b_5	-	4.0
c_1	-1.29	-315.95
c_2	0.61	-254.87
c_3	0.68	-175.35
c_4	-	-44.94
c_5	-	-35.91

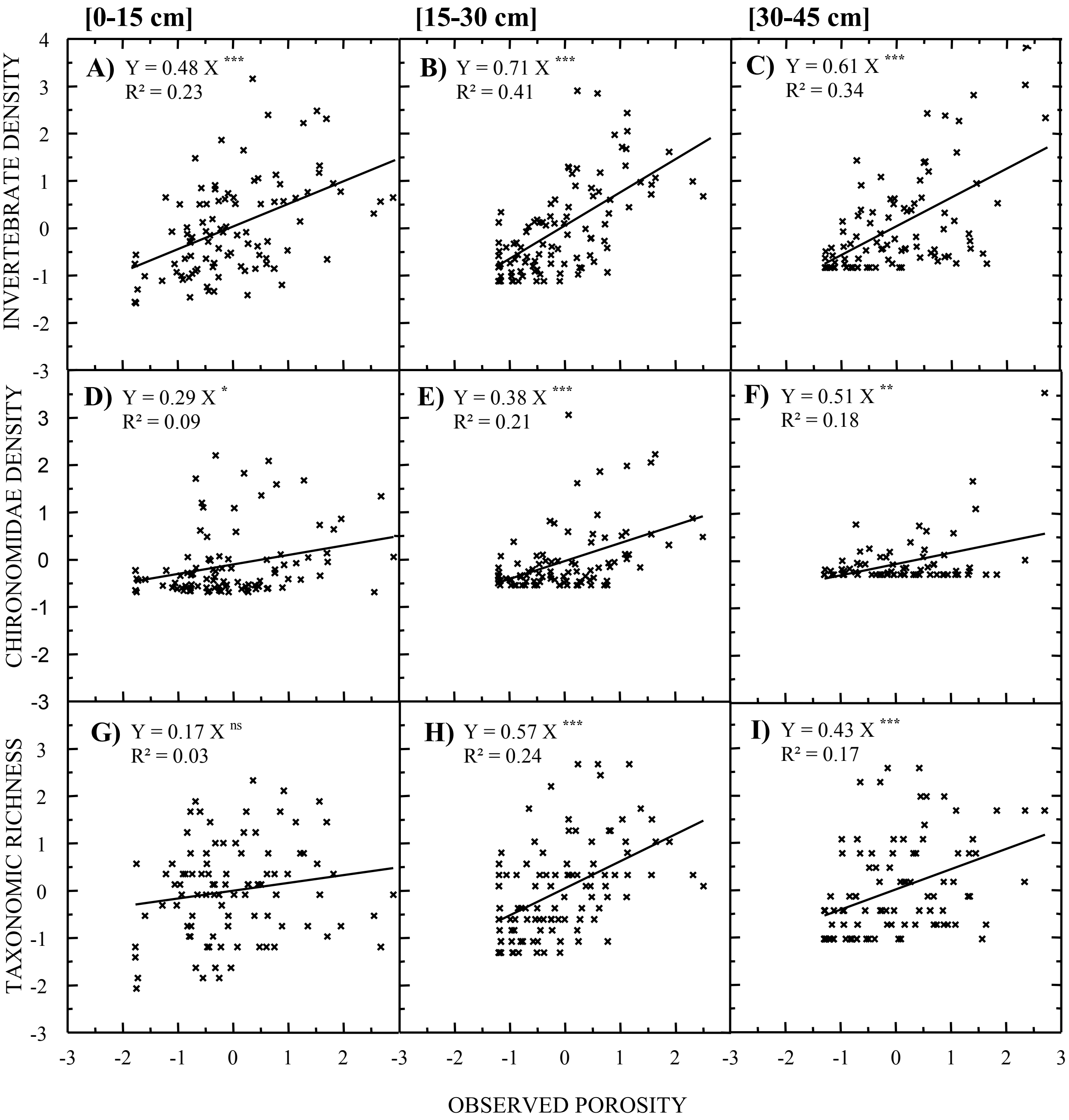

Fig. 1. Linear relationships between effective porosity and the overall invertebrate density (A, B, C), the density of Chironomidae (D, E, F), and the taxonomic richness (G, H, I), for each sediment layer. The analyses were conducted on data normalized by year and season of sampling, study site and sediment layer. Significance levels are represented as ^{ns} = not significant, * = $P < 0.01$, ** = $P < 0.001$, and *** = $P < 0.0001$.

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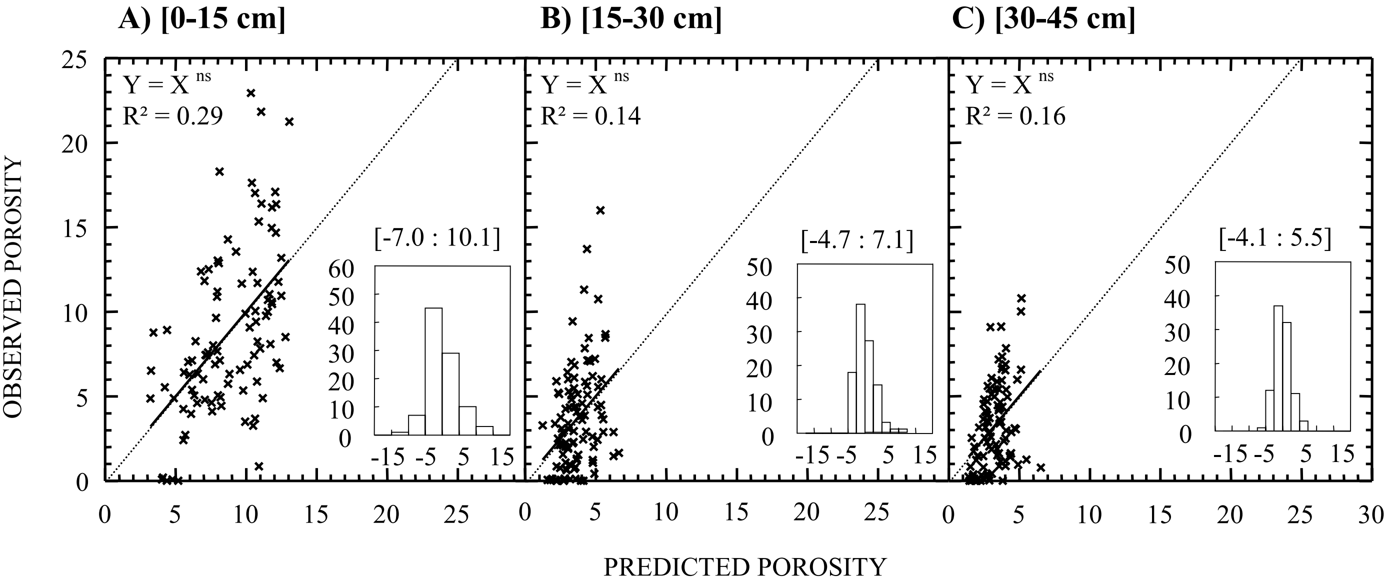

Fig. 2. Results of effective-porosity predictions by the model built using the dimensionless variables. Only the sorting index was significantly related to the porosity. Observed porosity versus effective-porosity is plotted for each sediment layer (A, B, C). To evaluate the precision of the model, the distribution of residuals (small graphs), and the 95% confidence intervals of the residuals (in brackets) are presented for each sediment layer. For each prediction, significance of the intercept against 0 and significance of the slope against 1 were tested. Significance levels are represented as: ^{ns} = not significant, * = P <0.01.

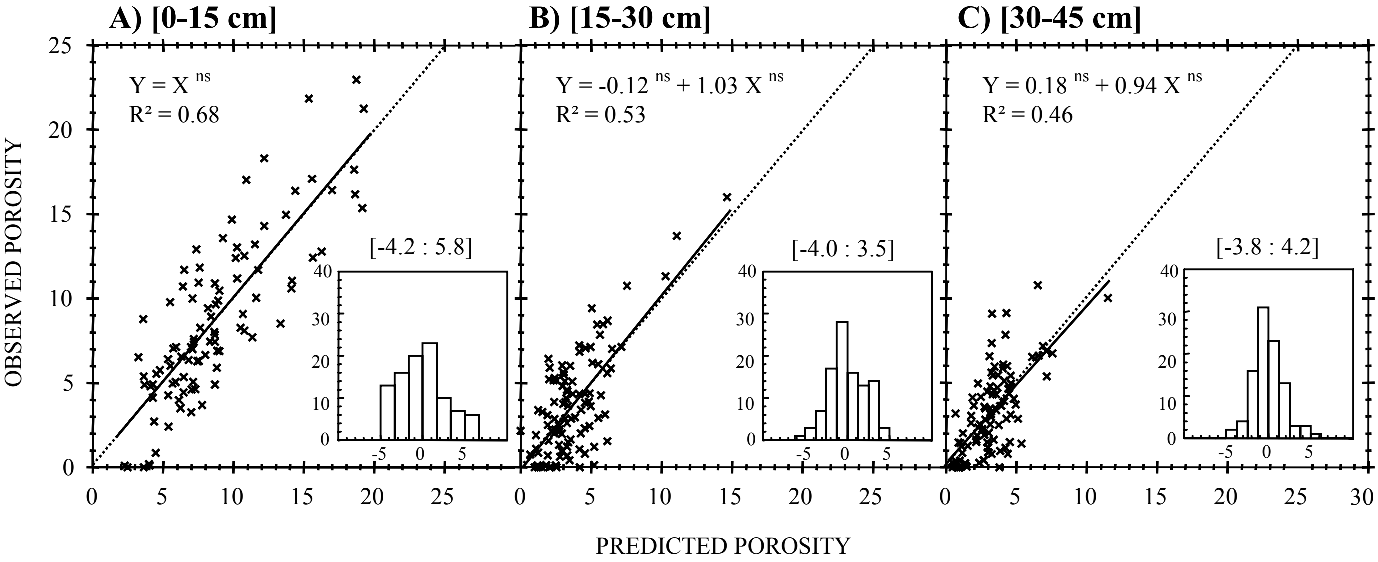

Fig. 3. Results of effective-porosity predictions by the model built using grain-size proportions. Observed porosity versus predicted porosity is plotted for each sediment layer (A, B, C). To evaluate the precision of the model, the distribution of residuals (small graphs), and the 95% confidence intervals of the residuals (in brackets) are presented for each sediment layer. For each prediction, significance of the intercept against 0 and significance of the slope against 1 were tested. Significance levels are represented as: ^{ns} = not significant, * = P <0.01.

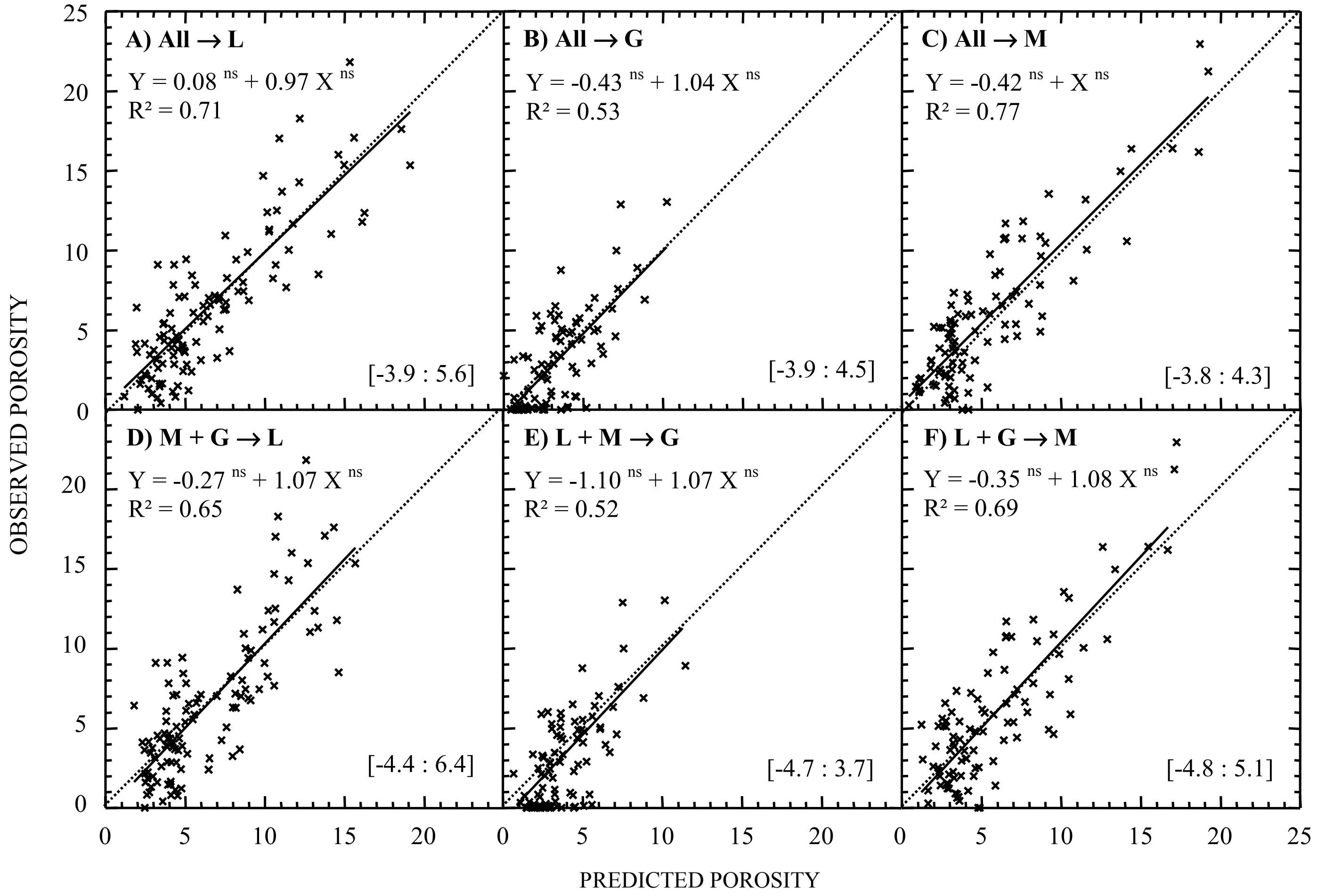

Fig. 4. Results of crosswise effective-porosity predictions among the three groups of study sites that differed in their bed-sediment characteristics. Observed porosity in mixed rock reaches (M), granitic reaches (G) and limestone reaches (L) versus porosity predicted by the grain-size proportion model fitted on full data set (A, B, C) or fitted on partial data sets (D, E, F). The 95% confidence interval of the residuals are indicated in brackets. For each prediction, the significance of the intercept against 0 and the significance of the slope against 1 were tested. Significance levels are represented as: ^{ns} = not significant, * = P <0.01.

A 2

DOES SUBSURFACE INTERSTITIAL SPACE INFLUENCE GENERAL FEATURES AND MORPHOLOGICAL TRAITS OF THE BENTHIC MACROINVERTEBRATE COMMUNITY IN STREAMS ?

(Gayraud S. & M. Philippe., *Archiv für Hydrobiologie*, 151: 667-686)

Does subsurface interstitial space influence general features and morphological traits of the benthic macroinvertebrate community in streams?

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With 4 Figures and 2 Tables

Abstract: The benthic macroinvertebrate community and substratum characteristics were assessed at 17 study sites differing in the amount of interstitial space in the subsurface interstitial zone (0-15 cm deep). The invertebrate community was described in terms of density, taxonomic richness, Shannon diversity and morphological traits (size, flexibility and body shape of the invertebrates). The amount of interstitial space in the subsurface zone that is described by porosity was significantly and negatively related to percentage of fine sediment, but not to stream slope, particle heterogeneity and particle size. Invertebrate density was significantly and positively related to the amount of interstitial space whereas taxonomic richness was slightly and negatively related to fine particulate organic matter content. Relative abundance of intermediate body size (5-10 mm), intermediate body flexibility (10-300°), and flattened or streamlined shape were significantly and positively related to the amount of interstitial space, contrasting with relative abundance of small body size (<5 mm), and cylindrical or spherical shape that were significantly and negatively related to this variable. These results highlight the importance of interstitial space, both as a factor partly controlling community structure and as an evolutionary factor acting on macroinvertebrate ability to penetrate the substratum. In addition to flow, the substratum selects the invertebrates through their different abilities to use the interstitial habitat.

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INTRODUCTION

MINSHALL (1984) summarised the role played by the substratum for invertebrates when he wrote: " the substratum is the medium upon which aquatic insects move, rest, find shelter and seek food ". Furthermore, the substratum can provide refugia during floods or severe drought and lessen the effect of disturbances (SEDELL et al. 1990). For example some invertebrates migrate deeply within the interstitial space to escape erosion by scouring (PALMER et al. 1992, DOLE-OLIVIER et al. 1997, GAYRAUD et al. 2000) or to seek protection from severe drought (WILLIAMS & HYNES 1976). Aware of this major role, for several decades biologists tried to identify important features of the substratum that may affect the structure of aquatic macroinvertebrate communities. It is already known that particle size (CUMMINS & LAUFF 1969, QUINN & HICKEY 1990), particle heterogeneity (WILLIAMS 1980, ERMAN & ERMAN 1984), embeddedness by fine sediment (BJORNN et al. 1977), and bed stability (MALMQVIST & OTTO 1987) influence the community in complex ways. Several studies (RICHARDS & BACON 1994, MARIDET et al. 1996) highlighted the effect of fine sediment on invertebrates and their habitat. They concluded that fine sediment controlled the openness of the substratum (BESCHTA & JACKSON 1979, SCHÄLCHLI 1992, MARIDET & PHILIPPE 1995) that can affect the structure (RICHARDS et al. 1993, review by WATERS 1995), the abundance (RICHARDS & BACON 1994) and the taxonomic richness of the community.

Despite its importance, the mechanism relating the interstitial space availability (*i.e.* the porosity or the percentage of fine sediment) to the invertebrate community is poorly understood, probably owing to the difficulty of measuring this substratum feature. The goal of our study was to test the influence of the characteristics of the subsurface interstitial space on the benthic invertebrate community at the reach scale (FRISSELL et al. 1986), and to compare this influence with other environmental variables that characterise the habitat (*i.e.* stream flow, trophic resources and other bed characteristics).

We hypothesised that the availability of interstitial space in the subsurface controls benthic invertebrate density, taxonomic richness and morphological traits of benthic invertebrates that inhabit the stream bottom. At one extreme, the low porosity stream reaches that provide a small amount of interstitial space were expected to exhibit the lowest invertebrate abundance, lowest taxonomic richness, and highest relative abundance of invertebrates with morphological traits that are adapted to penetrate the streambed. The relative abundance of animals with a small size, or cylindrical or spherical shape, or highly flexible body (traits needed to penetrate the substratum) would be highest in these stream reaches. At the other end of the scale, high porosity stream reaches that provide a high availability of interstitial habitat were expected to exhibit the highest invertebrate abundance, highest taxonomic richness, and lowest relative abundance of invertebrates that are adapted to penetrate the substratum.

To test these predictions, we used data from studies conducted in several streams, where the benthic invertebrate community and several characteristics of the substratum were assessed independently.

STUDY SITES

We used data previously collected in 17 French river reaches (Table 1). Of the 17 reaches, 13 were 3rd-order tributaries of the Rhône River catchment (MARIDET et al. 1992, GAYRAUD et al. 2000), two 3rd-order and one 4th-order streams were tributaries of the Dordogne River (MARIDET et al. 1996) and one was the 5th-order Loire River (MARIDET et al. 1992). Study reaches were approximately 100 metres long. The Vianon, the Drac, the Bourne, the Bez, the Ouvèze and the Eygues are located in V-shaped moderately incised valleys, the Loire, the Ozange and the Triouzoune flow through gently sloping plateaux, whereas the Galaure, the Herbasse, the Gère, the Sanne and the Varèze flow in moderately sloping alluvial plains. Catchments differ greatly by their geology, as sandstone, dolomite, limestone, granite are encountered (BORNAND 1972), which leads to differences in the substratum composition of the streambeds. Sandstone substratum is made of quartzite and feldspath, and its erosion produces particularly high amounts of sand in sandstone streams (SELLEY 1976), in comparison with limestone streams. These sedimentary dynamics lead to streambeds dominated by pebbles and cobbles strongly embedded in large amounts of sand. The limestone streambeds are also characterised by a high proportion of coarse particles (*i.e.* pebbles and cobbles) but with lower amounts of sand and higher amounts of silt and clay. Particles of sandstone and limestone reaches are poorly rounded, with a diversified shape. In contrast, the transport and deposition of alluvium in the Rhône basin during the Quaternary period has led to mixed substrata consisting of limestone, sandstone and granite. Rounded pebbles that are slightly embedded in sand dominate the streambed.

In addition, the study reaches differed greatly by their riparian and catchment vegetation. Elevation varied from 200 (the Herbasse) to 1300 (the Drac) metres a.s.l., but 95% of the sample was comprised between 320 and 595 m. Slope of the reaches ranged from 1.0 (the Loire) to 18.5 m/km (the Vianon), but 95% of the sample was comprised between 6.0 and 10.0 m/km. Sandstone streams had a pH < 7 and specific conductance < 100 µS/cm, whereas the other streams had a pH > 7.5 and specific conductance > 250 µS/cm. The French water management agency AGENCE DE L'EAU RMC (1996) indicated the absence of significant pollution at these sites. In order to acquire a coherent sample, data collections were restricted to the winter baseflow period but performed over several years (1989 to 1998).

MATERIAL AND METHODS

Physical conditions measurement

Stream bottom particle size was assessed by hand-picking of 100 particles regularly distributed (LEOPOLD 1970, HEY & THORNE 1983) along 10 transects within each 100 metres long study site. We estimated the diameter of substratum particles by the length of their B-axis (width of the particle, i.e. greatest dimension perpendicular to axis-A, the greatest length) and we classified them following the Wentworth classification. Particles with size < 2 mm were not measured but were directly assigned to the silt/clay/sand category. Median, lower and upper grain size quartiles (d50, d16, d84) were estimated from cumulative curves, and used to calculate the Sorting Index (SI) and the median particle size constituting the armour layer of the stream bottom. The SI, that measures the heterogeneity of particle size was calculated as follows: $SI = 0.5 \times (d84/d50 + d50/d16)$, (ANDREWS 1983).

The characteristics of the 15 cm deep subsurface interstitial zone (*i.e.* porosity, percentage of fine sediments and particulate organic matter content) were estimated on sediments collected by freeze-coring preceded by electro-positioning (termed electro-killing by BRETSCHKO & KLEMENS 1986) which immobilized the invertebrates with an electric current (650 V, 50 Hz, 15 minutes, MARIDET 1994). As the goal of previous studies (MARIDET et al. 1992, MARIDET et al. 1996) was to sample the hyporheic community in relation to sediment characteristics, the corer was placed in the substratum and a 45cm deep core was extracted 2 days later. Before sampling the corer was protected with a flow deflector to prevent erosion and warming by the water. The freezing operation required the injection of about 25 litres of liquid nitrogen for 15 minutes. From each core, three sediment layers (layer 1: 0–15 cm, layer 2: 15-30 cm, layer 3: 30-45 cm) were separated and transported frozen to the laboratory and stored in a freezer (-20 °C). At each site, 2 (before 1997), 3 (in 1997), or 4 (after 1997) 45 cm deep frozen cores were collected from one (before 1998) or two (in 1998 and 1999) riffles. Altogether, 44 samples were collected. As the goal of the present study was to test the influence of the subsurface features on the benthic invertebrate community, only the subsurface layer (0 to 15 cm deep) results are presented.

In the laboratory, we measured the total weight and volume of each sample in order to calculate porosity and percentage of fine sediment of the sample. Weight was measured with an electronic balance (OHAUS IP15KS; precision 0.1 g). Sample volume was estimated from the volume of water displaced by the frozen sample in a stainless steel cylinder. After thawing, invertebrates and coarse organic matter (size > 1 mm) were separated from the sediment by elutriation. As explained in the next section, invertebrates from frozen samples are not presented in the present study. The largest inorganic particles (>23 mm) were removed from the sample and sorted manually into size classes (128, 90, 64, 45, 32, 23 mm), while finer sediments were sieved in water (12, 8, 5, 2, 1, 0.500, 0.250, 0.050 mm) with an electronic sieving machine (RETSCH AS200 CONTROL). The finest fraction (size < 0.050 mm) was separated by continuous-flow centrifugation. Sorted sediments were dried at 105°C for 48 hours, weighed and the weight expressed as a percentage of the total dry weight of the sediment. Then, the sieved and dried sediments were weighed after moistening and draining, in order to quantify the water captured by capillary adsorption. Particulate organic matter was determined as the difference between dried weight and ashed-dried weight of sorted sediments. Sediments were ashed at 550°C for 30 min, wetted and dried again at 105°C for 48 hours to determine ashed-dried weight. As ashing has a drying effect stronger than drying at 105°C, sediments were wetted and dried after ashing to be sure that the difference between weight before and after ashing was due to organic matter and not to water (BUCHANAN 1984). Particulate organic matter was divided into two parts: coarse (>1mm) and fine (1-0.050 mm) particulate organic matter (CPOM, FPOM, respectively).

We calculated porosity from the ratio between the volume of free water and the volume of the total sample (STOCKER & WILLIAMS 1972, MARIDET 1994). The volume of free water was calculated from the difference between the total weight of the sample and the total weight of sieved and drained sediments, assuming that the water density was 1000 kg/m^3. The percentage of fine sediment was calculated from the ratio between the weight of sediment < 2 mm and the total sample weight.

Flow is also a major factor structuring the invertebrate community; it may select invertebrates through the adaptation of their body shape (HYNES 1970, STATZNER et al. 1988). Temporal fluctuations of the stream discharge produce variable flow patterns that may be characterised in many ways. But, as the sampling of the substratum and the invertebrates were restricted to one date in each stream reach, we decided to measure the stream slope as a rough indicator of hydraulic conditions experienced by the invertebrates.

Invertebrate sampling

As the test of our hypotheses needed independent assessment of the physical conditions and invertebrate community characteristics, we did not use the invertebrates sampled by freeze-coring, but a greater number of Surber samples. Ten 0.03 m^2 benthic samples were collected from each site in 1998 and 1999, and six 0.1 m^2 samples in the other years, using a Surber net (250 µm mesh), and preserved in 4 % formalin. Altogether, 130 Surber samples were collected. In most sampling situations, we disturbed the sediments 5 cm deep below the bottom of the armour layer, to collect the invertebrates inhabiting interstitial spaces of the stream bottom. In the laboratory, except for Oligochaeta, invertebrates were identified to family level (according to TACHET et al. 1991), and counted. Invertebrates were examined in terms of density (number/m^2), taxonomic richness (calculated on the basis of the taxonomic units described in the Appendix), Shannon diversity index (SHANNON & WEAVER 1949), and morphological traits. Three morphological traits were considered to evaluate the effect of physical variables on the invertebrate community (DOLÉDEC & STATZNER 1994, RICHOUX 1994, STATZNER et al. 1994, TACHET et al. 1994, USSEGLIO-POLATERA 1994). Maximum sizes were ranked as small (<5 mm), intermediate (5-10 mm), or large (>10 mm). Body shape referred to the streamlined, flattened, cylindrical, or spherical form of the invertebrates. Body flexibility was defined as how an animal can distort its body, and was characterised as being high (>300°), *i.e.* in animals capable of rolling up such as Oligochaeta, Achaeta, Hydridae and Triclads, intermediate (300°-10°), or low (<10°). As the number of aquatic stages differed among invertebrates, morphological traits were coded for larvae and/or adults depending on the group considered (see Appendix for details).

STATISTICAL ANALYSIS

Because of its great ability to describe the affinity of taxa for trait modalities, the fuzzy coding approach (CHEVENET et al. 1994) was used to compute morphological traits. Fuzzy coding assigns a positive score, from 0 (low affinity) to 3 (high affinity). Morphological traits were coded for all 54 taxa, according to our knowledge of the invertebrates inhabiting these stream reaches (see Appendix). Correspondence analysis was employed to analyse the fuzzy coded table in order to investigate the relationships between morphological traits and taxa. The morphological trait modalities were weighted by the average taxon density for each study site. Therefore, we calculated for each study site and each modality, the sum of the modality score times taxon abundance. This sum was standardised by dividing it by the sum of scores for the corresponding trait and expressed as the percentage of a modality in the corresponding trait for a given study site.

To determine relationships between physical variables, Pearson correlation coefficients were calculated. The Bartlett chi-square test was used to test the global hypothesis of significance of the correlation matrix and P-values were corrected with Bonferroni's method.

Backward stepwise regressions (P for enter = 0.15, P for remove = 0.05) were used to select the most significant relationships among physical variables, *i.e.* stream slope, median particle size, porosity, percentage of fine sediment, FPOM, CPOM, with invertebrate density, taxonomic richness, diversity, and the percentage of each of the morphological traits. The significance of regression coefficients (slopes) compared to 0 was tested using analysis of variance (null hypothesis rejected if $P < 0.05$). Normally distributed data and homoscedasticity are required for the use of linear models. Liliefors test and examination of the residuals showed that square root transformation was needed to meet these assumptions for invertebrate density. The examination of residuals showed that $\log (x + 1)$ transformation was sometimes needed to linearize the relationships.

We used ADE-4 software for correspondence analysis (THIOULOUSE et al. 1997) and SYSTAT 9 for the others analyses.

RESULTS

Relationships among physical variables

The analyses of the relationships among physical variables are shown in Table 2. The sorting index of the stream bottom that is classically used to describe the heterogeneity of particle size distribution was positively and strongly correlated with the percentage of fine sediments in the cores ($P < 0.001$). The percentage of fine sediment was negatively correlated with the porosity ($P = 0.082$). An ANOVA showed that porosity varied significantly ($P = 0.005$) between stream reaches. The stream slope that influences sediment transport capacity was positively but non-significantly related to the median particle size of the armour layer and negatively related to the percentage of fine sediment. Focusing on the residuals of the relationship between porosity and the percentage of fine sediment suggested that the relationship was not linear. This relationship was plotted after logarithmic transformation of the percentage of fine sediment ($P = 0.003$, Fig. 1) which gave the best fit according to the Liliefors test.

Relationships among morphological traits

The correspondence analysis of the fuzzy coded table showed that the first two eigenvalues were clearly higher than the others (Fig.2a), indicating that factors F1 and F2 explained 53.4 % of the total inertia. Body shape and body flexibility exhibited the highest correlation ratios with the two factorial axes (Fig. 2b). The first axis was highly correlated to body shape, ranking invertebrates along a spherical-cylindrical-streamlined-flattened shape gradient. The second axis was correlated to body flexibility and separated invertebrates with 'high' or 'low' flexibility (positive values) from invertebrates with 'intermediate' flexibility (negative values), (Fig. 2b). The weighted average of Molluscs was strongly associated to the modalities 'spherical shape' and 'low flexibility' (Fig. 2c). In contrast Oligochaeta, Achaeta, Triclads and Hydridae that constitute the group 'Others' were strongly associated to the modality 'high flexibility'. Crustacea were strongly associated to 'large size' and 'flattened body'. The insect group was not homogeneous, the ordination created a gradient from Coleoptera to Ephemeroptera. The weighted average of Coleoptera including aquatic larvae and adults was located between 'cylindrical shape'and 'spherical shape', and associated to 'low flexibility' and 'small size'. Trichoptera were associated to 'cylindrical shape', whereas the weighted averages of Ephemeroptera, Plecoptera and Diptera were associated to ‘streamlined shape’ and ‘cylindrical shape’, ‘intermediate flexibility’, and ‘intermediate size’ to ‘large size’.

Influence of physical variables on general and morphological features of the community

Liliefors test showed that the invertebrate density data were not normally distributed (P = 0.017). After square root transformation, invertebrate density was positively correlated (P = 0.004) with bed porosity (Fig. 3), thus conforming with the a-priori hypothesis. Taxonomic richness was slightly and negatively correlated to the amount of fine particulate organic matter ($R^2 = 0.23$, P = 0.049). However, stepwise regression involving all the physical variables failed to detect linear models that could explain variations in Shannon diversity.

Stepwise regressions showed that morphological traits were significantly related to porosity, to percentage of fine sediment and to FPOM, but not to stream slope, sorting index, and median particle size. The hypothesis that small invertebrates would be relatively more abundant in low porosity streams was supported by the data. Stepwise regression detected a negative relationship (P = 0.010) between the percentage of ‘small size’ and the amount of interstitial pore space (Fig. 4a), indicating that the percentage of small invertebrates (< 5mm) decreased with increasing porosity. In contrast, the percentage of intermediate-size invertebrates (5-10mm) increased significantly (P = 0.009, Fig. 4b) with porosity. The same approach failed to detect any relationship between the percentage of large invertebrates and the physical variables involved in the analysis. The percentage of ‘intermediate flexibility’ was positively related (P = 0.0314) to porosity (Fig. 4c) whereas the analysis did not detect any significant relationship for the other modalities of the trait ‘flexibility’. The stepwise regression detected a multiple relationship (R^2=0.51, P = 0.007) of the percentage of ‘cylindrical or spherical shape’ with porosity and FPOM ($y = -2.60 \times$ porosity (P = 0.003) $+ 27.48 \times$ FPOM (P = 0.042) + 100.245). The negative relationship between porosity and the trait ‘cylindrical or spherical’ remained significant (P = 0.015) after the removal of FPOM (Fig.4d).

DISCUSSION

Influence of physical conditions on interstitial space availability

In graded rounded sediments, porosity is constant and independent of particle size (see KHALAF & TACHET 1980). Under natural conditions, roundness and particle size homogeneity cannot be assumed, and finest sediment fills the interstices of the substratum leading to a decrease in porosity and hydraulic conductivity (BESCHTA & JACKSON 1979, SCHÄLCHLI 1992, MARIDET & PHILIPPE 1995). Our results clearly support this relationship suggesting that the amount of fine sediment is a major factor that controls the connectivity of the substratum with the water column.

As we assumed that the sediment transport capacity (*i.e.* the stream slope) influences the percentage of fine sediment in the substratum, it follows that porosity should increase with increasing slope. The data did not strongly support these assumptions despite a slight relationship showing the increase in fine sediment with decreasing stream slope (negative non-significant correlation between the slope and the percentage of fine sediment). Similarly, the classical assumption that mean particle size of the armour layer increased with slope was not significantly supported by the data ($R = 0.54$, $P > 0.10$). This weak influence of reach slope was probably masked by a stronger control by other environmental factors such as geology, catchment characteristics and geomorphologic environment (REID et al. 1997), that differed among the study reaches. In addition, the number of samples used to calculate the average porosity (2-4 samples per site) only allows a rough estimate of interstitial space conditions in the riffle reaches.

Influence of the interstitial space on the general features of the community

Despite a relatively small number of study reaches and samples, our results support the hypothesis that the openness of the substratum influences the invertebrate community. Streambeds that are characterised by a low amount of fine sediments embedding the substratum provide a higher availability of the interstitial space and thus a higher invertebrate density, as noted by BJORNN et al. (1977), RICHARDS & BACON (1994) and MARIDET et al. (1996). This result suggests that the openness of the substratum has a strong effect, when we consider the numerous other biotic and abiotic factors that are known to influence the density of invertebrates, *e.g.* abundance of trophic resources, hydraulics (STATZNER et al. 1988), discharge fluctuations (WRIGHT & SYMES 1999), predation (PECKARSKY 1984) and competition.

The physical variables we measured were not highly relevant to explain variations in taxonomic richness and Shannon-Weaver diversity. On a large data set composed of 54 stream reaches, TOWNSEND et al. (1997) found that richness was not related to particle size diversity (as it is commonly admitted), nor to the features of the interstitial space. They found that richness was significantly influenced by both the amount of dead space (*i.e.* zones with shear stress $< 0.771 \times 10\ \mu N.cm^{-2}$) at base flow and the frequency and intensity of disturbance. In contrast RICHARDS & BACON (1994) observed that the number of families in small basket samplers increased as the percentage of fine sediment decreased, suggesting that the amount of interstitial space influences the local richness but not the global richness in stream reaches.

Are invertebrates adapted to flow or to substratum?

The morphological traits we used to test the effect of interstitial space availability have been previously investigated as response variables in the 'habitat template theories' (SOUTHWOOD 1977, TOWNSEND 1989, TOWNSEND & HILDREW 1994). These theories assume that the average size of organisms increases, and that body shape and flexibility are more diversified in temporally stable and spatially diverse environments (TOWNSEND & HILDREW 1994). In this context, USSEGLIO-POLATERA (1994) did not find any clear relationship between the trait 'maximum size' and temporal variability, and observed the opposite of the predictions for 'body flexibility' and 'body shape' traits. He suggested that these traits could be more closely linked to the physical characteristics of the environment (*e.g.* flow velocity, substratum features) than to its temporal stability.

Numerous biologists have assumed that stream invertebrate body shape has progressively adapted to flow conditions, thus reducing the energetic cost of living in running water (HYNES 1970, STATZNER et al. 1988) and allowing the colonization of harsh environments. For long time, dorso-ventral flattening and streamlining in insects have been commonly considered as strong adaptations to reduce the drag force on their body (STEINMANN 1907, AMBÜHL 1959). More recent works (STATZNER & HOLM 1982, MCSHAFFREY & MCCAFFERTY 1987) showed that these adaptations could not be strong enough to minimize significantly the force of flow on invertebrates. Our results suggest that aquatic invertebrates have adapted their body to inhabit the bed sediments of streams, as proposed by other authors (NIELSEN 1951, HYNES 1970, WILLIAMS &

HYNES 1974). Invertebrates that are characterised by cylindrical or spherical shape are selected to inhabit low porosity reaches where the interstitial space is filled with fine sediments. In these reaches, invertebrates that are small (mainly Diptera, Coleoptera) or highly flexible (Oligochaeta) have a greater ability to penetrate the substratum and several authors (WILLIAMS & HYNES 1974, MCELRAVY & RESH 1991, DOLE-OLIVIER & MARMONIER 1992, MARIDET et al. 1992) reported their presence deep inside the hyporheic zone. Furthermore, WILLIAMS (1972) found that the largest marine invertebrates were excluded from small interstitial pores of the sediment. Some Ephemeroptera such as Caenidae and Ephemerellidae also have several traits, *i.e.* cylindrical shape and small size, that allow penetration within the interstices of bed sediments. In contrast, invertebrates with low-flexibility bodies (mainly Mollusca and Trichoptera) are probably more restricted to epibenthic habitat. In addition, shells and cases of such animals are unfavourable for moving in the interstitial space.

Many studies on the influence of fine sediments have stressed the importance of the interstitial space as a selective force acting on invertebrates. Several authors have reported the persistence (or the increase) of Mollusca (RIVIER & SEGUIER 1985), Diptera (LENAT et al. 1984) such as Chironomidae (BJORNN et al. 1977), Simuliidae, Athericidae (BRUSVEN & PRATHER 1974), and larvae of Coleoptera such as *Oulimnius sp.* and *Stenelmis sp.* (LENAT et al. 1984) after the addition of fine sand in experimental or natural channels. These animals are characterised by at least one of the traits we associated to low availability of interstitial space.

Instead of (or in addition to) morphology, behaviour can also be adapted to life in the sediments. For example, invertebrates such as Gammaridae and Ephemeridae, which are not characterised by the traits we associated to life in streams with a low porosity, have adopted a burrowing behaviour to penetrate sediments and animals such as *Seratella sp.* (BRUSVEN & PRATHER 1974), *Baetis sp.*, and *Caenis sp.* (CLAVEL et al. 1977) are also resistant to the addition of fine sediments.

The influence of the substratum on invertebrates is complex and can also proceed in a more subtle fashion, for example through the trophic resources the invertebrates need. The deposition of fine sediments decreases periphytic algal density, and the clogging of the interstitial space decreases the transport of fine organic matter, which can affect the density of collectors and scrapers (NUTTALL 1972). Furthermore, the finest sediments such as silt and clay may be mixed with trophic resources and then reduce growing rates and fecundity of the invertebrates (ANDERSON & CUMMINS 1979).

Last, we must consider that the relationship between substratum and freshwater invertebrates is more complicated than a unidirectional influence of the environment, since several authors demonstrated that some invertebrates may modify their habitat (STATZNER et al. 1999, STATZNER et al. 2000). For example, the change in interstitial space availability in the subsurface zone as a result of the patrolling activity of the large predaceous Plecoptera larvae of *Dinocras cephalotes* (STATZNER et al. 1996, ZANETELL & PECKARSKY 1996) might be important for the establishing and maintenance of other species. Such interactions show the complexity of substratum-invertebrate relationships and the importance of the interstitial space features as structuring factors of the community.

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Table 1. Year of sampling, location and general characteristics of study sites. Superscript letters (D, L, R) indicate the catchment to which the stream reaches belong, *i.e.* Dordogne, Loire, and Rhône, respectively. The major geological composition of the catchment is indicated with S (Sandstone), L (Limestone) or M (Mixed rock). Location is indicated in Lambert II coordinates. (-) indicates the absence of measurement.

Stream	Year	Geology	Location (x,y)	Elevation a.s.l. (m)	Stream order	Width (m)	Slope (m/km)	pH	Specific conductance (µS/cm)
Bez^R	1996	L	844.09, 1969.20	520	3	12	9.8	7.8	290
Bourne1^R	1997	L	847.50, 2014.45	280	3	15	10.0	8.4	380
Bourne2^R	1997	L	841.57, 2011.47	235	3	20	6.4	8.4	370
Bourne3^R	1997	L	839.20, 2011.98	650	3	14	5.6	8.2	380
Drac^R	1989	L	910.74, 1977.14	1300	3	11	10.3	-	-
Eygues^R	1998	L	846.77, 1935.20	610	3	8	8.7	8.3	380
Galaure1^R	1989	M	818.68, 2032.62	380	3	8	8.6	8.2	280
Galaure2^R	1998	M	818.69, 2032.63	375	3	8	8.6	8.2	280
Gère^R	1998	M	810.17, 2060.12	280	3	5	8.6	8.6	305
Herbasse^R	1998	M	807.20, 2016.12	200	3	9	8.0	8.1	480
Loire^L	1989	M	730.00, 2142.10	245	5	50	1.0	-	-
Ouvèze^R	1998	L	839.73, 1926.71	535	3	10	10.1	8.3	330
Ozange^D	1992	S	593.20, 2054.43	590	3	5	2.7	6.6	45
Sanne^R	1999	M	798.25, 2045.25	235	3	4	8.0	8.1	525
Triouzoune^D	1992	S	592.70, 2053.93	630	3	9	2.9	6.7	30
Varèze^R	1999	M	809.68, 2052.80	340	3	8	8.2	8.2	295
Vianon^D	1992	S	587.30, 2035.53	370	4	5	18.5	6.9	35

Table 2. Matrix of Pearson correlation coefficients between physical variables. The Bartlett chi-square test indicates whether one or more correlations are significant in the matrix (P<0.0001). The Bonferroni method for multiple testing indicates the significance of the correlation coefficient: * P<0.10, ** P<0.05, *** P<0.001. Sample size = 17.

	Slope	Particle size	Sorting Index	% of fine sediment	Porosity	FPOM
Particle size	0.543					
Sorting Index	-0.357	-0.030				
% of fine sediment	-0.491	-0.314	0.889***			
Porosity	0.177	0.306	-0.641	-0.661*		
FPOM	-0.145	-0.400	-0.397	-0.161	0.238	
CPOM	-0.156	-0.065	0.619	0.620	-0.244	-0.252

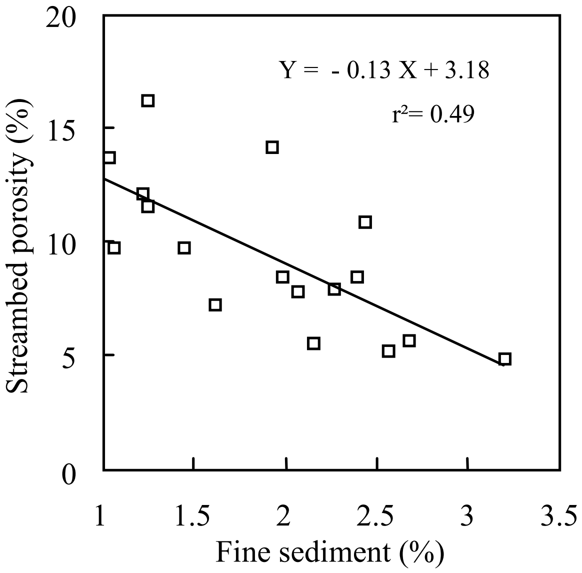

Fig. 1. Linear relationship of the mean streambed porosity with the mean percentage of fine sediment (diameter < 2 mm); fine sediment is ln (x + 1) transformed. The 17 study sites are shown as square symbols.

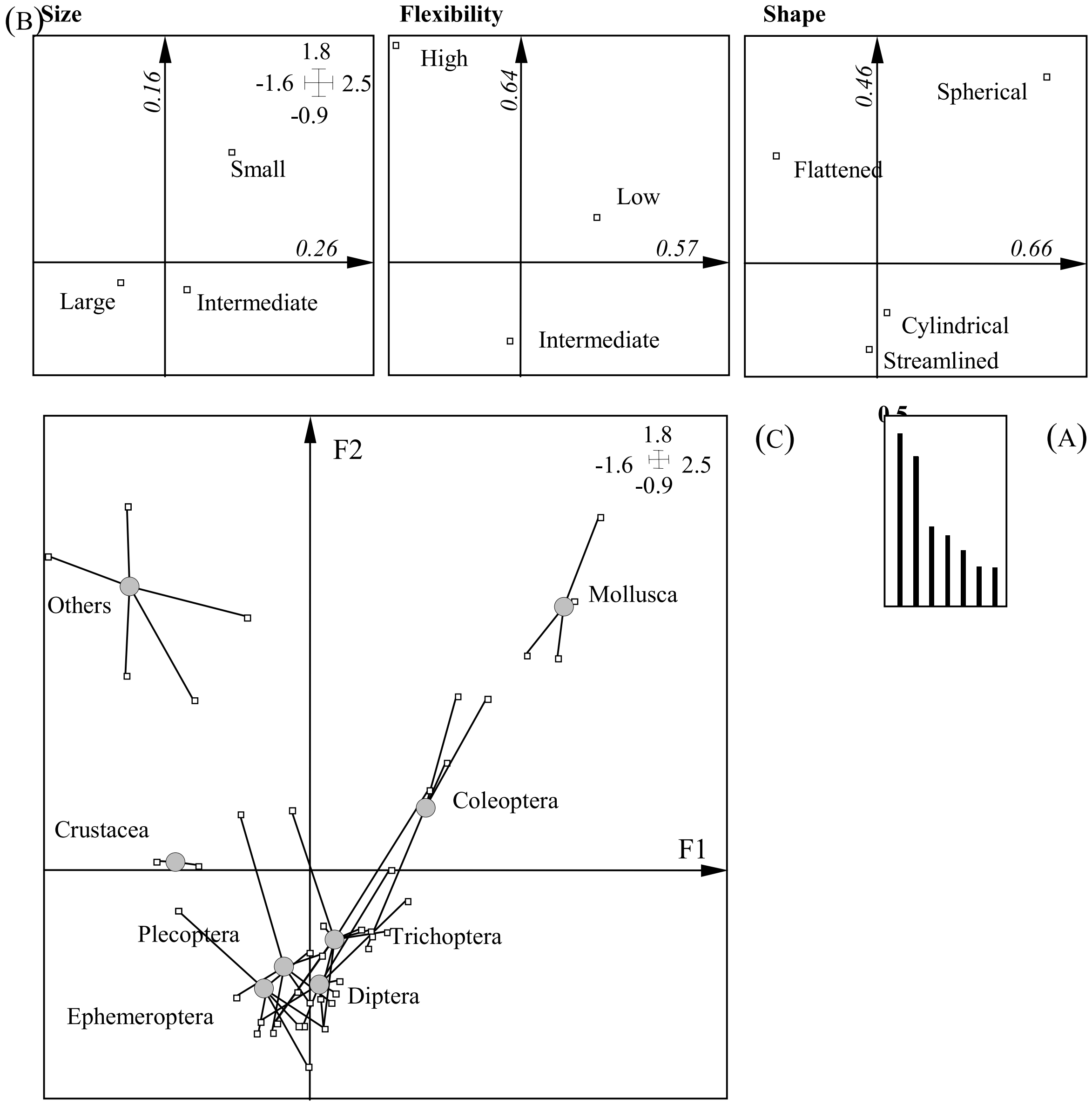

Fig. 2. Ordination of morphological traits by correspondence analysis. (a) Histogram of eigenvalues. (b) Distribution of modalities of ten morphological traits on the F1 × F2 factorial plane. Correlation ratio for each morphological trait is indicated on the axes. (c) Distribution of the different groups of invertebrates (circles) *i.e.* Insect orders, Mollusca, Crustacea and the other invertebrates (Triclads, Acheta, Hydridae, Oligochaeta) that are placed on the weighted average of their families on the factorial plane (see the Appendix for full details of the composition of invertebrate groups).

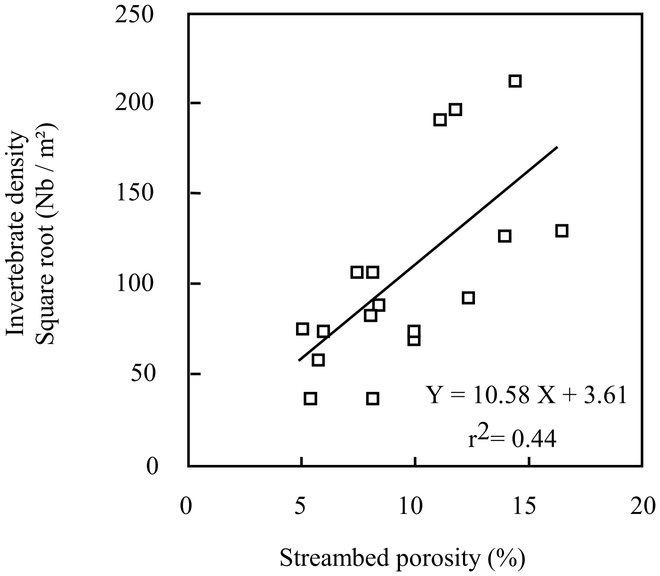

Fig. 3. Linear relationship of invertebrate density and streambed porosity; invertebrate density is square root transformed. Density was estimated by Surber sampling and porosity was estimated by freeze coring. The 17 study sites are shown as square symbols.

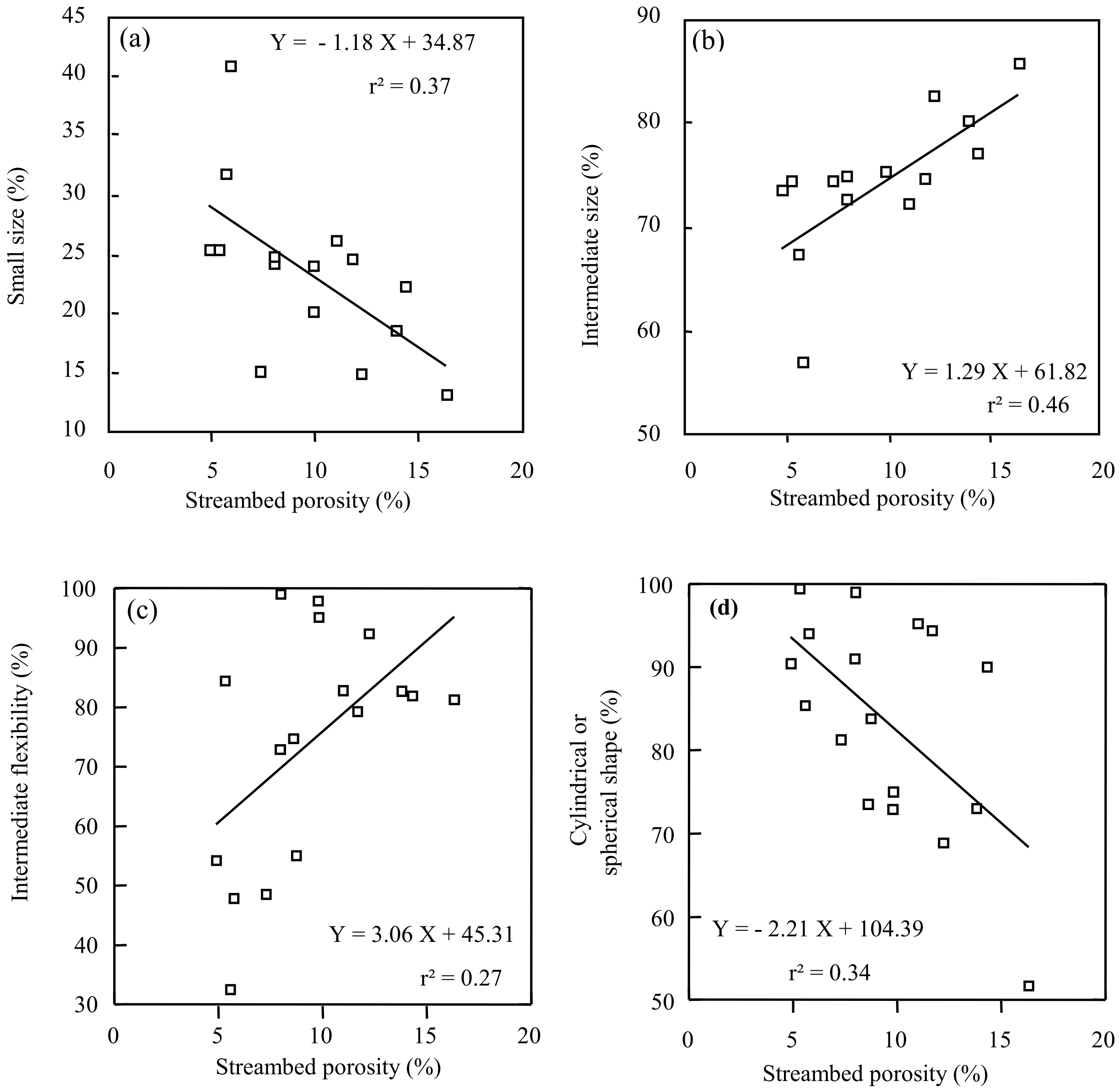

Fig. 4. Linear relationships of mean streambed porosity with (a) percentage of small invertebrates (< 5 mm), (b) percentage of intermediate invertebrates (5-10 mm), (c) percentage of invertebrates with intermediate flexibility (10-300°) and with (d) percentage of cylindrical or spherical invertebrates. The 17 study sites are shown as square symbols.

Appendix: Fuzzy coding for morphological traits of the taxa identified in the study sites. l = larvae, a = adults.

	Maximum size			Flexibility			Body shape			
	< 5 mm	5-10 mm	> 10 mm	Low	Intermediate	High	Streamlined	Flattened	Cylindrical	Spherical
Coleoptera										
Dystiscidae (l+a)	1	2	0	3	3	0	3	0	3	0
Elmidae (l+a)	3	0	0	3	3	0	0	0	3	1
Gyrinidae (l+a)	1	3	0	3	3	0	3	0	3	0
Helodidae (l)	3	0	0	3	0	0	0	0	3	1
Hydraenidae (a)	3	0	0	3	3	0	0	1	3	3
Diptera (l)										
Athericidae	0	0	3	0	3	0	0	0	3	0
Ceratopogonidae	1	2	2	3	0	0	0	0	3	0
Chironomidae	1	3	0	0	3	0	0	0	3	0
Empididae	0	3	0	0	3	0	0	0	3	0
Limoniidae	0	2	1	0	3	0	0	0	3	0
Psychodidae	0	3	0	3	0	0	0	0	3	0
Simuliidae	1	2	0	0	3	0	0	0	3	0
Tabanidae	0	0	3	0	3	0	0	0	3	0
Tipulidae	0	0	3	0	3	0	0	0	3	0
Ephemeroptera (l)										
Baetidae	0	3	0	0	3	0	3	0	0	0
Caenidae	1	3	0	0	3	0	0	1	3	0
Ephemerellidae	0	3	0	0	3	0	0	1	3	0
Ephemeridae	0	0	3	0	3	0	1	0	3	0
Heptageniidae	0	0	3	0	3	0	1	3	0	0
Leptophlebiidae	0	3	2	0	2	0	0	0	3	0
Oligoneuriidae	0	0	3	0	3	0	1	3	0	0
Plecoptera (l)										
Chloroperlidae	0	3	0	1	2	0	1	1	3	0
Leuctridae	0	2	2	1	3	0	1	0	3	0
Nemouridae	1	3	0	0	3	0	1	0	3	0
Perlidae	0	0	3	3	1	0	1	3	0	0
Perlodidae	0	0	3	0	3	0	1	1	3	0
Taeniopterygidae	0	1	3	0	3	0	1	0	3	0
Trichoptera (l)										
Brachycentridae	0	3	0	3	1	0	0	0	3	0
Glossosomatidae	0	3	0	3	1	0	0	0	3	0
Goeridae	0	3	1	3	1	0	0	3	1	0
Hydropsychidae	0	1	3	1	3	0	0	0	3	0
Hydroptilidae	3	0	0	3	1	0	0	0	3	0
Lepidostomatidae	0	3	1	3	1	0	0	0	3	0
Leptoceridae	0	3	2	3	1	0	0	0	3	0
Limnephilidae	0	0	3	3	1	0	0	0	3	0
Odontoceridae	0	0	3	3	1	0	0	0	3	0
Philopotamidae	0	3	0	0	3	0	0	0	3	0
Polycentropodidae	0	1	3	0	3	0	0	0	3	0
Psychomyiidae	1	3	1	0	3	0	0	0	3	0
Rhyacophilidae	0	1	3	0	3	0	0	0	3	0
Sericostomatidae	0	0	3	3	1	0	0	0	3	0

Appendix: continued.

	Maximum size			Flexibility			Body shape			
	< 5 mm	5-10 mm	> 10 mm	Low	Intermediate	High	Streamlined	Flattened	Cylindrical	Spherical
Mollusca										
Ancylidae	0	3	0	3	0	0	0	0	0	3
Bythinellidae	3	0	0	3	0	0	0	0	0	3
Lymnaeidae	0	2	2	3	0	0	0	0	0	3
Valvatidae	2	3	0	3	0	0	0	0	0	3
Crustacea										
Asellidae	0	2	1	0	3	0	0	3	0	0
Gammaridae	0	0	3	0	3	0	0	3	0	0
Others										
Hydridae	3	1	0	0	0	3	0	0	3	0
Dendrocoelidae	2	3	0	0	0	3	0	3	0	0
Dugesiidae	2	3	0	0	0	3	0	3	0	0
Erpobdellidae	0	0	3	0	0	3	0	1	3	0
Glossiphoniidae	0	0	3	0	0	3	0	3	0	0
Hirudidae	0	0	3	0	0	3	0	3	0	0
Oligochaeta	1	3	3	0	0	3	0	0	3	0

A 3

THE RESPONSE OF BENTHIC MACROINVERTEBRATES TO ARTIFICIAL DISTURBANCE: DRIFT OR VERTICAL MOVEMENT IN THE GRAVEL BED OF TWO SUB-ALPINE STREAMS ?

(Gayraud S., M. Philippe & L. Maridet., 2000: *Archiv für Hydrobiologie*, 147: 431-446)

The response of benthic macroinvertebrates to artificial disturbance: drift or vertical movement in the gravel bed of two Sub-Alpine streams ?

Sébastien Gayraud[1], Michel Philippe and the late Laurence Maridet

With 4 figures and 3 tables in the text

Abstract: In most streams, invertebrate recovery following hydrological disturbance is rapid. For three decades, biologists have assumed that recovery after flooding is facilitated by behavioural migration from refugia, particularly from the hyporheic zone. The relevance of this hypothesis was experimentally tested in two medium-gradient streams with porous beds using a new technique that allows the increase of discharge in a 0.20 m^2 enclosed area. Vertical distribution of benthic macroinvertebrates and drift intensity were compared between disturbed and undisturbed areas. The prediction that after artificial disturbances invertebrate density should decrease on the surface and increase in the hyporheic zone was not supported by the data. Total invertebrate density decreased significantly in the surface layer (0-8 cm) but was not significantly different between disturbed and undisturbed areas in the deep layers (8-60 cm). The same observations were made for most numerous invertebrates such as Chironomidae, Gammaridae and Heptageniidae. The alternative prediction that disturbance should increase drift intensity was supported by field observations. Artificial disturbance enhanced drift intensity and modified drift composition, causing an increase in the relative abundance of Chironomidae pupae and Gammaridae. This study indicates that downward migration of invertebrates within the hyporheic zone during a flood is not always evident and that recolonization may primarily occur by drift from other refugia.

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INTRODUCTION

Scouring during spates dramatically reduces the abundance and the richness of gravel stream macroinvertebrates (RESH et al. 1988, GILLER & Sangpradub 1991, MARMONIER & CREUZÉ DES CHATELLIERS 1991). Despite this impact, the recovery of the macroinvertebrate community is rapid compared to the theoretical recovery time calculated only with the intrinsic growth rate (PALMER et al. 1992). This finding has led biologists to propose a major role for in-stream refugia where invertebrates may survive and from which they can recolonize disturbed areas. Natural streams are characterized by habitat heterogeneity at several spatial scales (TOWNSEND 1989). The mosaic of patchy habitats at a range of discharges (LANCASTER & HILDREW 1993a, b) is important, particularly when discharge is high enough to initiate sediment movement and thus to disturb benthic communities. A variety of potential refugia have been identified or expected (Sedell et al. 1990), such as patches with low shear stress and dead zones (Lancaster & Hildrew 1993a, b), lateral stream margins, banks (Gaschignard-Fossati, 1986), woody debris dams (Palmer et al., 1995) and the hyporheic zone (Clifford 1966, Williams & Hynes 1974, Poole & Stewart 1976, Marchant 1988, Dole-Olivier & Marmonier 1992, Palmer et al. 1992, Maridet 1994, Dole-Olivier et al. 1997).

Williams & Hynes (1974) proposed the “hyporheic refuge hypothesis” to explain the vertical distribution of invertebrates in the Speed River. Few studies have been conducted to test the relevance of the hyporheic refuge hypothesis, most of them providing no direct evidence. After studying the role of the hyporheic zone in both a sandy stream and an experimental channel, Palmer et al. (1992) concluded that the hyporheic zone cannot be considered as a refugial space in all streams. In the streams studied by Palmer et al., annual recurrent floods drastically reduced invertebrate densities in benthic and hyporheic habitats. Thus the vertical movements of the meiofauna did not protect them from flooding impact and did not explain the short recovery time of the community. In a larger river, contrasting results from Dole-Olivier et al. (1997) demonstrated that under certain conditions, invertebrates migrated downwards within the sediments of a gravel bar during natural spates.

The present study was conducted to test the behaviour of benthic macroinvertebrates submitted to an increase in flow velocity and local shear stress occurring during an increase in discharge. As the rarity and unpredictability of disturbance events makes this type of research difficult, a simulation of increasing discharge in natural streams was adopted using a new technique called "Décolofond" (see below). This technique simulates the increase in flow velocity on a 0.20 m^2 enclosed area. The response of invertebrates was examined by comparing their vertical distribution in disturbed and undisturbed areas.

During the increase in discharge, macroinvertebrates exposed to higher shear stress may migrate within the sediment or drift downstream to a more suitable habitat (surface refuge). The prediction of downward migration of invertebrates will be accepted if invertebrate density decreased at the surface (0-8 cm) and increased in the hyporheic zone (8-60 cm). To test the alternative hypothesis of the absence of vertical migration, drift intensity was compared between disturbed and undisturbed areas.

STUDY SITES

The study was carried out in March 1997, in two third-order streams with a medium gradient (approximately 10 m/km) in France. Streams with porous hyporheic zones were chosen according to Maridet & Philippe (1995), who observed that a minimum porosity of at least 4 % was needed to enable colonization by benthic macroinvertebrates.

The Herbasse stream is a small tributary of the River Isère (approximate width 10 m). It has a mean annual discharge of 1.51 m^3/s and a mean two-year flood discharge of 39.9 m^3/s at the gauging station situated 8 km downstream from the study site. The impervious catchment of 187 km^2 is composed of fossil morainic hills, leading to rapid peaks in discharge. The riparian zone is dominated by native deciduous trees. The stream consists of small pool/riffle sequences with cobbles and pebbles in the riffles and pebbles and sand in the pools.

The Galaure stream a tributary of the River Rhône, has a similar width, slope and riparian zone. The catchment is larger (232 km^2) but of similar geology. Mean annual discharge is 2.32 m^3/s and mean two-year flood discharge 37.5 m^3/s at the gauging station situated 20 km downstream from the study site. Substratum grain size is larger than in the Herbasse stream, with cobbles being dominant in both riffles and pools.

MATERIAL AND METHODS

Experimental design

The effect of disturbance was tested by comparing the vertical distribution of invertebrates under disturbed and undisturbed situations. Three pairs of disturbed and undisturbed areas were distributed in each stream. The location of each study site was chosen to represent the most common morphodynamic units. Disturbed and undisturbed areas within each pair were chosen to minimize physical habitat heterogeneity between areas. Hydraulic and substratum variables (flow velocity, water depth, diameter of the largest element of substratum, diameter of the dominant substratum) were then evaluated in the three paired areas. Each pair was located on a cross-sectional transect, perpendicular to the stream flow. Disturbed and undisturbed areas were assigned randomly on the line transect. There was a minimum distance of 4 metres between the disturbed and undisturbed areas to ensure independence.

Artificial disturbance technique

A new technique (Décolofond) was used to simulate natural hydrological variations (Fig. 1). The Décolofond creates a gradual increase of discharge through a transparent P.V.C. channel placed on the stream substratum. The Décolofond is composed of a pump, a regulation tap, and a transparent channel ending in a drift net. The electric pump (Submerged centrifugal pump Pumpex P2001V, power 6800 watts, maximum discharge 20 l/s) is powered by an independent generating unit (BIANCHI 1998). The water is pumped from 5 metres upstream and circulates from the pump to the channel via the regulation tap that controls discharge variations. The channel has an enclosed area of 0.20 m^2 where disturbance is produced. The drift net (mesh of 400 µm) is fixed to the lower end of the channel to collect invertebrates drifting from the disturbed area. A 400 µm filter was fixed to the pump to prevent invertebrates entering the disturbed area via the pump. A channel with similar characteristics was built to create the same experimental conditions for the measurement of the drift from undisturbed areas.

Disturbance consists of an increase in flow rate in the disturbed areas. Velocity was gradually increased (by 0.1 m/s every 15 minutes) from the flow velocity measured on the area before disturbance. The disturbance was stopped when movement of the sand (400 µm-2 mm) was observed on the sediment (critical erosion velocity). Values of initial velocity in the Galaure were 0.35, 0.41 and 0.45 m/s and they were increased to 1.06, 1.05 and 1.20 m/s, respectively. In the Herbasse, initial velocity was 0.30, 0.50 and 0.60 m/s and it was increased to 0.80, 1.10 and 1.10 m/s, respectively. We have no information on velocities during floods. But, as they cause changes in the bottom sediment, natural flood are presumably greater than in the present experiments. Here the stress was on increasing velocities, not on absolute values.

To adjust discharge in the transparent channel, water velocity was measured with an electromagnetic current metre for 30 seconds after each increase of discharge. The current metre was placed 1 cm below the roof of the PVC channel, i.e. 15 cm above the stream bottom. Preliminary measures showed that the boundary layer above the top of the substratum, was 3 cm thick (BIANCHI 1998). We estimated the mean diameter of the stream substratum particles (6 cm in the Galaure and 4 cm in the Herbasse) by the length of the B-axis (width of a particle, i.e. greatest dimension perpendicular to axis A, the greatest length) for a random selection of 150 particles. Hence the measures of velocity in each stream were made above the top of the boundary layer (6+3=9 cm, and 4+3=7 cm, respectively).

The duration of artificial disturbance was approximately 2 hours, so as to simulate the stage of increasing discharge which occurs during flood events in this type of stream (HEROUIN personal communication). Vertical sampling of invertebrates was conducted immediately after the final increase in discharge.

Installation of the transparent channel

Firstly the pump and the regulation tap were placed carefully on the bed upstream from the area. Then the transparent channel and the drift net were attached in both disturbed and undisturbed areas. The installation needed 1 to 4 minutes before the beginning of each experiment. Invertebrates drifting from the site during the installation were collected and counted. Drift intensity was calculated and compared with natural drift intensity (see below) with a Wilcoxon test for paired numeric variables (CONOVER 1980). No significant differences ($P = 0.463$) were observed between natural drift intensity (3.4 ±1.2 individuals $mn^{-1}m^{-2}$) and drift intensity during the installation of the device (5.4 ±2.6 individuals $mn^{-1}m^{-2}$). We concluded that a rapid installation of the transparent channel does not significantly disturb the invertebrate community on the experimental area.

Sampling the vertical distribution of invertebrates

The modified freezing-core technique using liquid nitrogen preceded by electro-positioning (BRETSCHKO 1981, 1985, BRETSCHKO & KLEMENS 1986, MARIDET 1994) was used to collect macroinvertebrates and sediment. For each of the pair, in each area, a 60-cm deep core was taken after the final increase in discharge. The core diameter varied from 18 to 26 cm, with an mean diameter of 21.78±0.59 cm. Five sediment layers (0-8, 8-15, 15-30, 30-45, 45-60 cm) were separated from each core, carried frozen to the laboratory, and stored at -20 °C. Invertebrates were separated from the sediment by elutriation, counted, and identified to major taxonomic groups (Families) according to TACHET et al. (1991). Invertebrate densities were calculated for each layer and expressed as abundance per litre of sediment. The sediment was sieved (12, 8, 5, 2, 1, 0.500, 0.250, 0.050 mm) and the finest fraction (< 50 µm) was separated by continuous-flow centrifugation. Each sieved fraction was dried, weighed, and expressed as a percentage of total dry weight of sediment to calculate distribution factors (MARIDET 1994). Porosity was then calculated for each layer as the ratio of water volume content and total volume of the layer according to STOCKER & WILLIAMS (1972). The volume of water was calculated as the difference between the total weight of the sample and the wet weight of drained sediment (MARIDET 1994).

Drift sampling

During the disturbance, invertebrate drift was sampled simultaneously on both the disturbed and undisturbed areas. Samples were preserved with 10% formaldehyde. Invertebrates were counted and identified to major taxonomic groups to compare with invertebrates within the cores. Drift intensity was calculated as the total number of invertebrates moving downstream from disturbed and undisturbed sites during the experiment and expressed as number per minute per square metre. The relative abundance of each family was calculated for each drift sample and compared with that in the first layer of the corresponding hyporheic samples.

Drift activity varies with velocity, discharge, sunshine, turbidity, predation, and biorhythms of invertebrates (ALLAN 1995). Consequently, all experiments were conducted between 9 a.m. and 5 p.m. to minimize this variability and identify the effect of increasing discharge.

Statistical analysis

We compared invertebrate density, taxonomic richness, and porosity in the hyporheic zone of each stream using analysis of variance (ANOVA). Homogeneity of variance between modalities was tested with the Hartley test. A log(X+1) transformation was used to homogenise variance when necessary. After transformation, we used one-way or two-way ANOVA to compare vertical patterns of density, taxonomic richness, and porosity between streams and sediment layers. All analyses were performed with Statview software© 4.02 for Macintosh.

The Wilcoxon test procedure for paired numeric variables (CONOVER 1980) was used to study the effects of the artificial disturbance on invertebrate density, taxonomic richness and drift intensity. Differences in relative abundance of invertebrates between benthos and drift samples on disturbed and undisturbed areas, and between disturbed and undisturbed drift samples were also examined with the Wilcoxon test.

RESULTS

Vertical porosity pattern

Mean porosity of the sediment (Table 1) decreased with depth in both streams but differed between streams ($P < 0.001$). Porosity in the Galaure was always greater than 4 % in contrast with porosity in the Herbasse which became less than 4 % below a depth of 22.5 cm.

Effect of disturbance on the vertical distribution of the fauna

In our study, total numbers of individuals in frozen and drift samples were 1296 and 4704 in the Galaure, and 1262 and 4915 in the Herbasse, respectively. Total numbers of taxa were 36 in the Galaure and 33 in the Herbasse. In undisturbed areas, invertebrate density decreased significantly with depth in both the Galaure and the Herbasse streams ($P < 0.001$), nevertheless a significant difference between streams was observed in the vertical distribution patterns (Fig. 2). In the Herbasse, the first and second layers contained relative densities of 75.1% and 18.2% respectively, versus 48.5% and 30.4% in the Galaure. Similar vertical patterns occurred following disturbance ($P < 0.001$) but differences in density with depth were attenuated. A Wilcoxon test was then performed on invertebrate density at each layer to further examine the effect of disturbance. The first and second layers of the disturbed areas exhibited a significant decrease in invertebrate density compared to undisturbed areas ($P = 0.030$ and $P = 0.046$, respectively). In the other deeper layers, there were no significant differences in invertebrate density between disturbed and undisturbed areas.

Results for taxonomic richness were different (Fig. 2). The vertical decline was less marked but remained statistically significant ($P < 0.001$) in undisturbed areas of both streams. Richness of the stream benthos was higher in the Herbasse ($P = 0.005$) and it declined gradually with depth, in contrast to the Galaure where richness was lower at the surface, increased to the third layer then decreased (Fig. 2). The Wilcoxon test revealed no significant differences in taxonomic richness between disturbed and undisturbed sites in each layer in either stream.

To further examine the effect of disturbance, the vertical distribution of some particular taxa was investigated. The three most common taxa collected in the first layer were Chironomidae, Gammaridae and Heptageniidae comprising 58.6%, 12.6% and 4.3% of the total abundance in the Herbasse, respectively, and 11.2%, 17.0% and 44.5% in the Galaure. Gammaridae exhibited a response similar to that of the total abundance (Fig. 3) with a statistical decrease in density between treatments in the first layer ($P = 0.046$) and none in the deeper layers. In contrast, obvious variations were observed between streams for Chironomidae (Larvae + pupae) (Fig. 3). Density always decreased in the first layer due to disturbance but appears to have been higher after disturbance in the second layer of the Galaure stream. This possible "stream effect" was due to a high density observed in the second layer of one single core sample.

Finally the distributional patterns of Heptageniidae (typical epibenthic insects) were compared with those of Gammaridae and Chironomidae. There was a significant decrease in the density of Heptageniidae ($P = 0.030$) in the first layer due to disturbance, but not in deeper layers (Fig. 3). As in the Chironomidae, a slight non-significant increase in density may be observed in the second layer of the Galaure, due to one single sample.

Effect of disturbance on drift intensity and benthos structure

Higher flow significantly increased ($P = 0.030$) drift intensity in both streams, but drift intensity in the disturbed and undisturbed treatments differed between streams (Fig. 4). The undisturbed areas of the Galaure had a higher drift intensity than those of the Herbasse (356%); this difference seems to have been attenuated by disturbance (117%). Major groups of invertebrates in the drift are listed in Table 2. Larvae and pupae of Chironomidae made up most of the drift in both streams, with or without disturbance. We tested the homogeneity of relative abundance of major taxonomic groups between benthos and drift samples with Wilcoxon tests (Table 3). No significant differences in relative abundances of the benthos were noted between the undisturbed and disturbed areas. Despite some large differences (e.g. Heptageniidae, Table 2), disturbance did not significantly modify benthos composition.

Conversely, data exhibited differences between drift and benthos composition. Larvae of Chironomidae were relatively more abundant in the drift than in the benthos (+12.4% in the Herbasse, +22.8% in the Galaure) whatever the hydraulic conditions (Table 3). However, disturbance did not alter their relative abundance in either the benthos or in the drift. In contrast, without disturbance Heptageniidae and Gammaridae were relatively more abundant in the benthos than in the drift (Table 3). Disturbance did not significantly affect the relative abundance of Heptageniidae in the benthos and in the drift whereas under disturbance, the relative abundance of Gammaridae increased in the drift (+3.4% in the Herbasse, +8.9% in the Galaure). Chironomidae pupae (Table 3) did not differ significantly between benthos and drift without disturbance, but drift was significantly modified by disturbance (+8.2% in the Herbasse, +4.3% in the Galaure).

DISCUSSION

The hyporheic refuge hypothesis

Our findings, based on disturbances of the magnitude we used, do not support the predictions of the hyporheic refuge hypothesis. In all replicates, we observed a decrease in the total density of the benthos without a parallel increase in most hyporheic samples (an increase only occured in the number of chironomids of one sample). At the same time, the rise in drift intensity is coherent with the drop in benthic invertebrate density.

We examined several variables related to the hyporheic zone and artificial disturbance to interpret our findings. Porosity and size of interstices are obvious limiting factors for invertebrate penetration within hyporheic sediments (STOCKER & WILLIAMS 1972, WILLIAMS 1984). As mean values of porosity were always above 4% in all layers of the Galaure hyporheic zone and between 0 and 15 cm depths in the Herbasse, porosity is unlikely to have been a limiting factor.

Invertebrates have different abilities for vertical migration because of their size or their shape in relation to the size of interstitial spaces. Larvae of Chironomidae are cylindrical, which helps them to move within the interstices. These organisms may be frequently encountered down to

1m deep (DOLE-OLIVIER & MARMONIER 1992). Nevertheless, as in our study, PALMER et al. (1992) observed their low ability to migrate within the sediment under hydraulic stress.

The lack of downward migration in burrowing organisms such as the Gammaridae conflicts with other findings (DOLE-OLIVIER et al. 1997, MARMONIER & DOLE 1986, MARMONIER & CREUZÉ DES CHATELLIERS 1991) but this may reflect differences between experimental situations. Artificial disturbances conducted with the Décolofond do not exactly simulate processes occurring during high flow. Firstly, the duration of the disturbance was calculated according to our hydrological knowledge on this type of catchment. Following PALMER et al. (1992), we assumed that the avoidance behaviour should occur before particle movement, soon after the beginning of disturbance, to enable invertebrates to escape. Nevertheless, the duration and the magnitude of disturbance may not have been long enough to cause downward migration. Secondly, the artificial increase in flow possibly differed qualitatively from natural increases of flow, and light, temperature and turbidity of the water remained constant during our experiment. However such factors may be important in inducing downward migration. Finally, exchanges between surface and hyporheic zones were perhaps underestimated in the present study. The alternation of streambed convexity and concavity creates upwelling and downwelling currents, enhancing water exchanges at a local scale (VAUX 1968). DOLE-OLIVIER & MARMONIER (1992) demonstrated that this hydrological patchiness and these geomorphological characteristics govern the structure of the interstitial assemblage. Thus, the contrasting findings of these studies and the variations between cores in the present study, suggest that downward migration is also governed by hydrological and geomorphological factors rather than by individual behaviour.

Drift composition and disturbance

Average shear stress on the stream bottom varies with mean velocity and a large increase in erosive force is expected during disturbance. Turbulence experimentally measured within the transparent channel of the Décolofond increases due to the increase in mean velocity (BIANCHI 1998). Changes in local shear stress are expected to directly affect the likelihood of organisms to drift (STATZNER et al. 1984). Such hydraulic changes could explain the increase in drift intensity observed in the two streams.

Because of morphological adaptations (flatted body shape), Heptageniidae are often encountered on the largest particles of the streambed (HYNES 1970, STATZNER & HOLM 1989).

Such adaptations may explain their low relative abundance in the drift compared to the benthos whatever the hydraulic conditions. In some of the papers reviewed by STATZNER et al. (1984), no relationships were found between current velocity and drift. During high flow events, the lack of downward migration and low drift intensity suggest that Heptageniidae use the interstices of the stream bottom in the upper layer of the stream (0-8 cm) as a refugial space until the critical erosion velocity is reached. For greater hydrologic events such as natural spates, substratum movements probably drastically reduce the density of Heptageniidae and affect the supply of recolonists.

As for Heptageniidae, the use of stream bottom interstices by Gammaridae (STATZNER & BITTNER 1983, STATZNER et al. 1988) and their low mobility during the day (HUGHES 1970, WALLACE et al. 1975, STATZNER & BITTNER 1983) may also explain their low relative abundance in the drift under natural conditions. As in the present study, other authors (BORCHARDT & STATZNER 1990, HUGHES 1970) have observed an increase in drifting *Gammarus* immediately after an increase in current velocity. HUGHES (1970) observed a decrease in the drift after 40 to 90 minutes of faster flow, suggesting a change of behaviour of *Gammarus* under high shear stress.

Chironomidae larvae seem to enter the drift whatever the hydraulic conditions. No clear relationships are observed under natural conditions between drift and benthic relative abundance. In contrast with NEVEU & ÉCHAUBARD (1975) and the present results, COWELL & CAREW (1976) and NEVEU (1974) observed a higher relative abundance in the benthos under natural conditions. STATZNER et al. (1984) cited some papers that reported a possible positive relationship between drift and discharge. The absence of morphological adaptations for resistance to hydraulic stress in the numerous Chironomidae that lived without attached tubes exposed them to a high probability of dislodgment. During high flow events, drifting Chironomidae may constitute an important supply of recolonists. Pupae of Chironomidae are also characterized by low mobility (VERGON & BOURGEOIS 1993) and by the absence of morphological adaptations to high flow, and may be more prone to dislodgment during disturbance.

Integrating the role of the hyporheic zone during disturbances

Our findings suggest that some invertebrates such as the Heptageniidae and the Gammaridae may use only spaces in the top layer of the stream bottom (0-8 cm) as a refuge over a limited range of flow velocity. Theoretical models of stream refugia may be proposed to explain their behaviour (ROBERTSON et al. 1995). These authors hypothesized that the hyporheic zone may be used as a 'catastrophe avoided' model, which consists of active or passive relocation of invertebrates into habitat affording protection. In such a system, redistribution of invertebrates throughout disturbed habitats happens after disturbance. An example of this functioning may be found in the study by DOLE-OLIVIER et al. (1997) where *Gammarus* passively or actively migrated within the hyporheic zone of gravel bars and could constitute a source of recolonists. However, the present study suggests that an 'incomplete catastrophe' model is more appropriate to explain the role of the hyporheic zone in gravel streams under the magnitude of disturbance we simulated. In this model, invertebrates suffer from high mortality induced by the disturbance except in a subset of habitat patches. Individuals inhabiting these patches are protected but there is no accumulation. As in the 'catastrophe avoided' model invertebrates are relocated throughout the habitat after the disturbance.

Consequently, like BOULTON & FINDLAY (1998) we urge caution in assuming that the hyporheic refuge hypothesis applies widely. But despite the lack of downward migration, the hyporheic zone of gravel streams is likely to be a major source of recolonists because of the high densities observed below 8 cm depth. So, research should now focus on the relationships between density of invertebrates and physical variables of the hyporheic zone in gravel streams.

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Table 1. Percentage porosity of the sediments of the hyporheic zone.

Mean Depth (cm)	Herbasse stream	Galaure stream
3.8	11.7 ±1.3	15.3 ±2.9
11.3	4.3 ±3.0	8.4 ±2.2
22.5	3.8 ±2.0	4.8 ±0.3
37.5	2.6 ±1.0	4.4 ±0.7
52.5	2.7 ±0.6	4.9 ±0.9

Table 2. Percentage (mean ±SE, N=3) of the major taxa in the Galaure (Gal) and the Herbasse (Her) streams. Un. benthos and D. benthos correspond to the first depth core in undisturbed and disturbed areas, respectively. Un. drift and D.drift correspond to the drift samples taken in undisturbed and disturbed areas, respectively.

Taxon		Un. benthos	D. benthos	Un. drift	D. drift
Heptageniidae	Gal	46.8 ±3.4	37.5 ±2.4	6.0 ±0.9	7.1 ±0.5
	Her	3.3 ±2.0	1.4 ±0.6	0.4 ±0.3	0.7 ±0.3
Chironomidae larvae	Gal	7.6 ±3.4	11.2 ±2.6	30.4 ±1.7	30.0 ±1.7
	Her	54.3 ±3.3	52.8 ±3.9	66.7 ±6.0	61.1 ±2.0
Chironomidae pupae	Gal	1.8 ±1.4	1.4 ±0.6	1.3 ±0.4	5.6 ±1.2
	Her	4.9 ±0.0	6.8 ±0.5	7.4 ±0.8	15.8 ±2.0
Gammaridae	Gal	17.7 ±4.3	20.1 ±2.0	3.4 ±0.5	12.3 ±1.4
	Her	12.8 ±2.3	6.5 ±0.3	2.6 ±0.5	6.0 ±0.7

Table 3. Non-parametric comparisons with Wilcoxon matched pairs test for all replicates (N=6) between relative abundances of invertebrates within the benthos and the drift of disturbed (D. bent. and D drift) and undisturbed (Un. bent. and Un. drift) areas.

	Comparison			
Taxon	Un.bent. vs D.bent.	Un.bent. vs Un.drift	D.bent. vs D.drift	Un. drift vs D.drift
Heptageniidae	NS	$p<0.05$ Un. bent. > Un. drift	$p<0.1$ D. bent. > D. drift	NS
Chironomidae larvae	NS	$p<0.05$ Un. bent. < Un. drift	$p<0.05$ D. bent. < D. drift	NS
Chironomidae pupae	NS	NS	$p<0.05$ D. bent. < D. drift	$p<0.05$ Un. drift < D. drift
Gammaridae	NS	$p<0.05$ Un. bent. > Un. drift	NS	$p<0.05$ Un. drift < D. drift

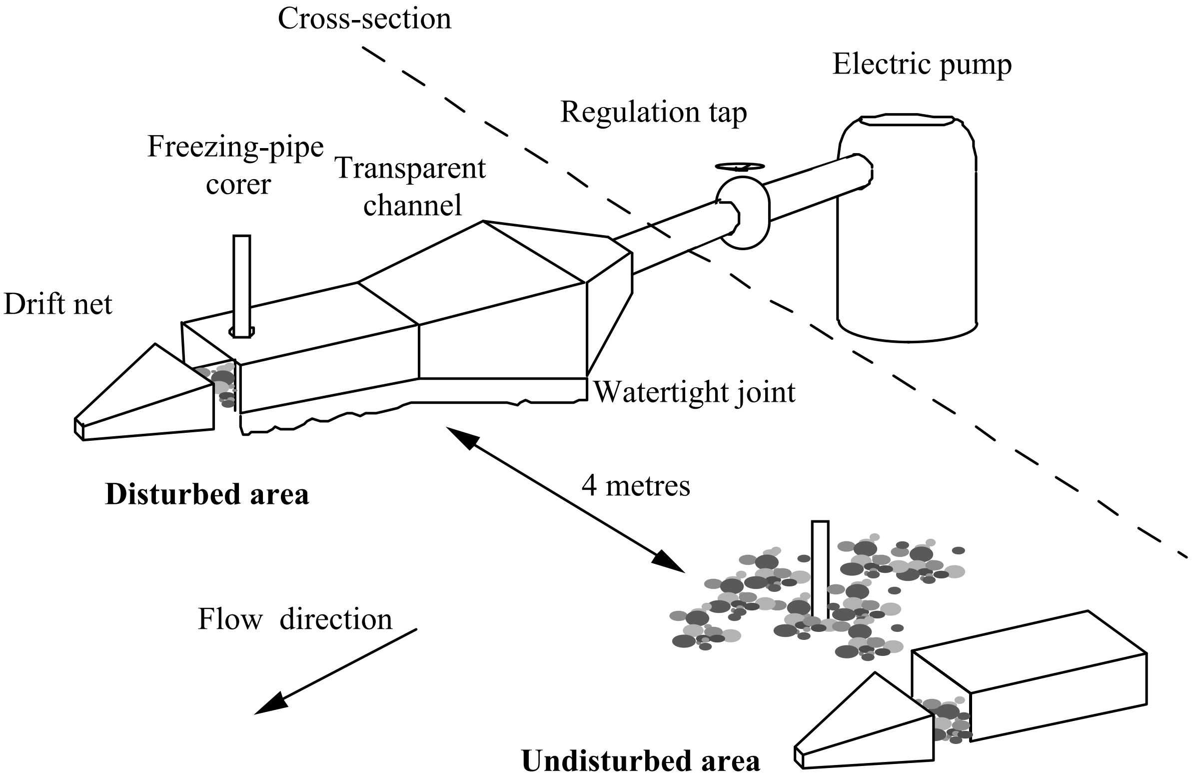

Fig. 1. The Décolofond experimental design showing the location of disturbed and undisturbed areas.

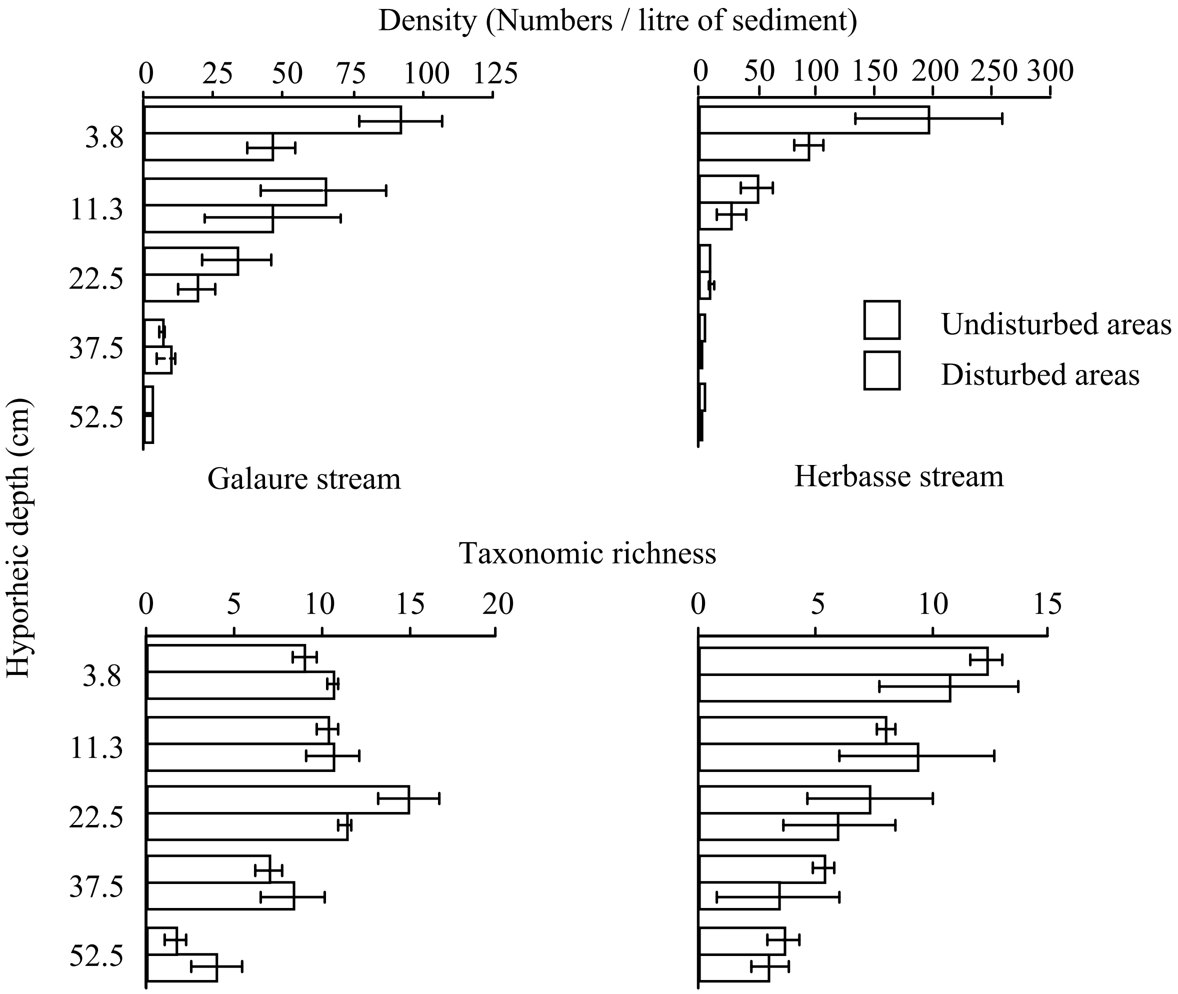

Fig. 2. Effect of disturbance on the vertical distribution of invertebrates and taxonomic richness (mean ±SE, N=3) within the hyporheic zone of the Galaure and Herbasse streams.

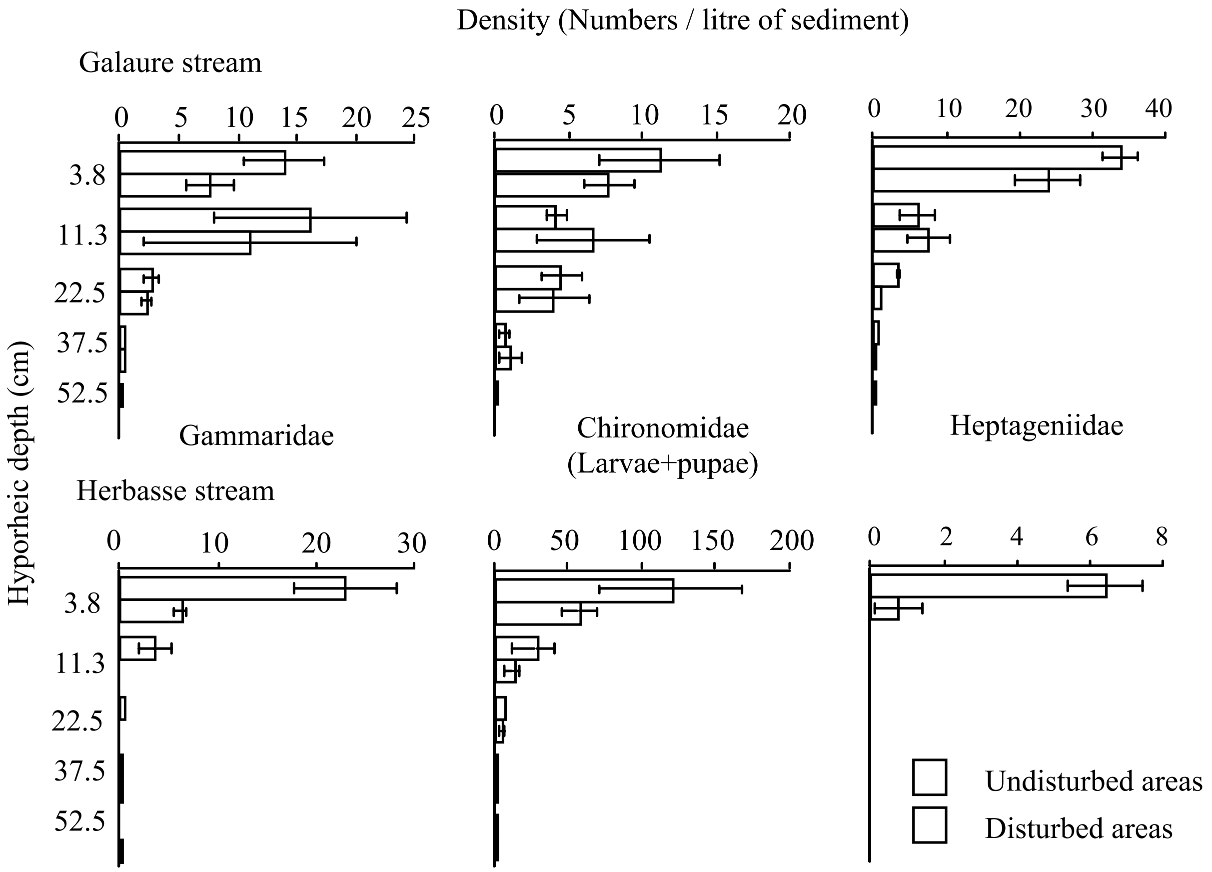

Fig. 3. Effect of disturbance on the vertical distribution (mean ±SE, N=3) of Heptageniidae, Gammaridae and Chironomidae (Larvae+pupae) within the hyporheic zone of the Galaure and Herbasse streams.

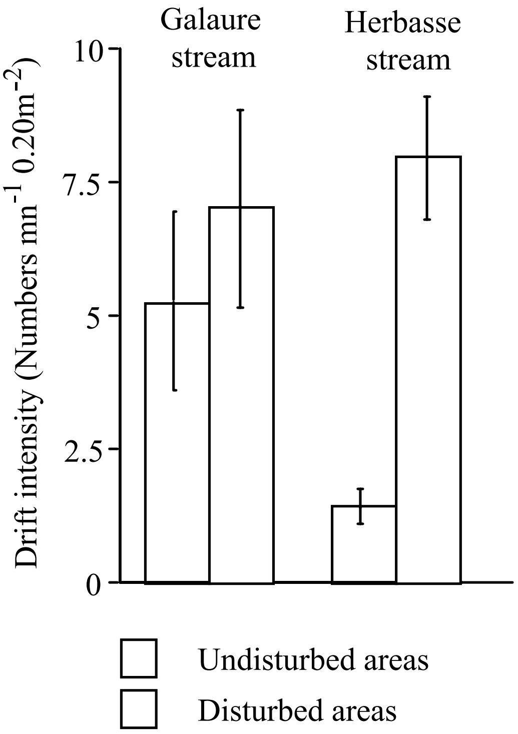

Fig. 4. Effect of disturbance on the drift of invertebrates. Values are means (N=3) with SE bars.

A 4

EFFECTS OF DISTURBANCE REGIME AND PROVISION OF MULTIPLE-SCALE REFUGIA ON STREAM INVERTEBRATES

(Gayraud S., S. Dolédec, M. Philippe & E. Hérouin., en préparation)

Effects of disturbance regime and provision of multiple-scale refugia on stream invertebrates

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Abbreviated tittle: Disturbances, refugia and stream invertebrates

SUMMARY

1. In permanent streams, floods that mobilize the substrate are probably the most disruptive disturbances for the invertebrate community, and biologically relevant variables describing flow variability must be defined in relation to particle movement.

2. In this study, we related the disturbance regime and provision of refugia to the invertebrate community and species trait structures in 9 study sites contrasting by disturbances. Disturbance was described by spate frequency, average spate duration and the yearly average number of days in spate, whereas the provision of refugia was evaluated through interstitial habitat availability, stability of particles, and proportion of the streambed with low shear stress.

3. Disturbance regime strongly influenced the community and species trait structures, in contrast to provision of refugia. More disturbed sites exhibited a significantly higher proportion of species traits: stages outside the stream, terrestrial oviposition, ≥ 1 reproductive cycle per year, filter-feeding and trophic generalist.

4. The average number of days in spate explained a higher proportion of variance in traits than the average spate duration and the average spate frequency, suggesting that disturbance duration played a major role on the community and trait structures.

Introduction

Understanding how benthic community structure changes with its environment is a central question in both theoretical and applied ecology. In this context, the habitat constitutes the basis for mechanisms underlying both species evolution and autoecological processes (Southwood, 1977; 1988). The habitat exhibit variability in time and space and is perceptible from microhabitat to regional scale (Frissell *et al.*, 1986). This multiple-scale habitat acts as a series of spatial filters selecting species traits or strategies (suite of species traits) that maximise the fitness of organisms, through physiological, morphological and behavioural adaptations (Poff, 1997). Thus, environment having similar habitat characteristics should bear species with similar adaptations. In this context, pertinent environmental variables (habitat templet axes) must be defined at the appropriate time and spatial scales with respect to organism characteristics (Townsend, 1989; Reice, Wissmar & Naiman, 1990; Townsend & Hildrew, 1994).

Disturbances play a major role on the community structure and dynamic (Sousa, 1984). In permanent streams, floods that mobilise bed-sediments are probably the most disruptive disturbances for the invertebrate community (Resh *et al.*, 1988) because they affect the substrate arrangement, that is a major component of the invertebrate habitat (Minshall, 1984). Conforming to Townsend' definition (1989) of disturbances, spates are 'relative discrete events in time that remove organisms and open up space or others resources that can be utilised by individuals of the same or different species'. At the scale of the individual, the effects of spates may range from the simple relocation of the invertebrates to a more favourable habitat, to a strong reduction of its likelihood to survive. These effects can result in a drastic reduction of the abundance of individuals, involving changes in the community structure (Badri, Giudicelli & Prévôt, 1987; Scrimgeour & Winterbourn, 1989; Giller & Sangpradub, 1991).

In natural streams, the substrate transport is likely to be a continuous response to the increasing discharge (Petit, 1990). The rise in discharge increases the shear stress applied to the stream bottom and makes particles of increasing size progressively available to the transport. This continuity in the transport process makes difficult the definition of a single threshold above which a spate should be considered as a disturbance. In this paper, we define a disturbance as any increase in discharge that modifies the substrate arrangement and change the invertebrate assemblage at the local scale. Following previous experimental results of Gayraud, Philippe & Maridet (2000), we postulated that the discharge allowing the transport of fine sands (< 500 µm) is sufficient to disturb the invertebrates, *e.g.* through an increase in their drift rate.

During spates, the substrate transport is not spatially uniform since variations in stream morphology and in substrate arrangement can affect the stability of particles (Petit, 1989). This spatial variability results in a patchy habitat, where the more stable patches may act as refugia (Townsend, 1989; Poff & Ward, 1990; Sedell *et al.*, 1990). For a decade a large effort has been conceeded by freshwater biologists to rationalise and to test the effective utilisation of these potential refugia. At the stream scale, the reaches less affected by spates may provide protection to invertebrates against erosion. Furthermore, the hyporheic zone also acts as a patchy refugium and some invertebrates can migrate enough downward within sediments to escape scouring (Dole-Olivier, Marmonier & Beffy, 1997). At the microhabitat scale, areas with low and stable shear stress (Lancaster & Hildrew, 1993; Robertson, Lancaster & Hildrew, 1995; Winterbottom *et al.*, 1997), stream margins (Rempel, Richardson & Healey, 1999), stream banks (Maier, 2001) or woody debris accumulations (Palmer *et al.*, 1996), can also accumulate invertebrates that potentially can recolonise the bed after a spate.

Several recent studies have attempted to relate community structure, species traits or strategies to disturbances and refugium availability. The axes of the templet were defined as measures of the environmental variability in various ways (see Statzner & Borchardt, 1994; Richards *et al.*, 1997; Minshall and Robinson, 1998) or as more elaborated criteria (see Scarsbrook & Townsend, 1993; Townsend, Dolédec & Scarsbrook, 1997a). These studies showed a relation between trends in species traits and the environmental variability. In this paper, following this habitat-based approach, we compare the invertebrate community and species traits structure among 9 stream reaches differing by their disturbance regime and refugium availability.

In this context, we predict that species traits providing a higher probability to survive with respect to erosion processes would be selected in frequently/highly disturbed stream reaches (harsh environments). Invertebrates with a small body size, having a high number of reproductive cycles, with stages outside the aquatic environment, and invertebrates having poor attachment to the substrate, should be selected in harsh environments. We also predict that habitat generalists and trophic generalists should be selected in these habitats. In addition, the availability of trophic resources could be also substantially modified by the disturbance regime; the periphyton biomass may be lowered (Biggs, 1995) and the transport of fine organic matter increased (Wallace *et al.*, 1991) in harsh environments, thus influencing the proportion of trophic groups (Cummins, 1973). In contrast, we predict that the refugium availability should lessen the effects of the disturbance, thus selecting the species traits adapted to utilize these refugia.

Material and methods

Study site characteristics

To fulfill our objective, we selected stream reaches having similar environmental characteristics (reach slope, substrate size, elevation, maximal temperature in summer, trophic level) but differing by their disturbance regime. As the information on sediment transport was not available at the beginning of the study, streams were selected according to the ratio of the 2-year-frequency daily discharge to the median daily discharge (FLOOD2/Q50). We assumed that streams reaches characterised by a high magnitude of the 2-year frequency flood would be those more disturbed (high spate frequency, long spate duration). Since the stream hydrology is controlled by regional patterns of rain fall (see Poff, 1992), it was not possible to find streams with very different hydrological characteristic in the same geographic region (maximal distance between sites is 130 km). Consequently, our 9 3rd order stream reaches encompassed a climatic hydrological gradient across natural geographical areas. Study sites were located at a distance < 30 km from sources and an elevation < 650 m above see level (Table 1). Despite some differences in the main geology covering the catchment area –*i.e.* limestone/dolomite and mixed-rocks-, the water chemical composition was similar, with high pH (7.8 - 8.6), high specific conductance (> 280 µS.cm-2). Stream reaches were also comparable with respect to reach slope, to proportion of fast flowing habitats -*i.e.* riffles and runs- and to substrate particle-size, but they differ by their lateral wandering -*i.e.* the ratio of floodplain width to bankfull width, mean bed width and median discharge. At last, stream reaches were selected in the absence of pollution susceptible to affect the aquatic life (Anonymous, 1996).

The median daily discharge Q50 and characteristics of the disturbance regime were computed from daily discharge data measured between 1990 and 1999 at fixed gauging stations close to our sites. Seven of our study sites (Bez, Drome, Eygues, Galaure, Gere, Herbasse, Ouveze) were located at a distance < 10 km upstream a gauging station managed by the French Ministry of the Environment. Daily discharge in these sites was estimated from the monitored discharge after corrections by the ratio of catchment areas at the gauging station and at the study site. For the two streams that were not continuously gauged, discharge values were estimated from the correlation between the discharge measured in the study site and the discharge monitored at the gauging station located on the nearest catchment. To check the accuracy of the discharge estimates in these two sites, we compared them to discharge measured over the period of the study ($n = 10$, $r^2 > 0.68$).

Assessment of the disturbance regime

In this paper, the disturbance was defined in relation to the threshold of discharge needed to move fine sands. We calculated this critical discharge combining usual hydraulic engineer equations (1 and 2) and power law functions (3) as follows:

$$Rc = \theta c \times (Gs - 1) \times D50 / S \qquad (1)$$

$$Dc = Rc / 0.9 \qquad (2)$$

$$Qc = \mathrm{a} \times Dc^{\,\mathrm{b}} \qquad (3)$$

where *Rc* is the critical hydraulic radius, θc is the critical shear stress (0.035 according to Milhous & Bradley, 1986; Milhous, 1998), *Gs* is the specific gravity of the bed material (2.65 kg.l-1), *D50* is the median size of the bed material surface (m) and *S* is the slope of the energy line (m.m-1). The slope was estimated by the channel slope measured with a dumpy level over 10-20 times the stream width. The critical depth (*Dc*) was derived from the hydraulic radius (*R*c) following the equation (2). The critical discharge (*Qc*) corresponding to the movement of 30% of the armour layer was derived from usual power law (3) linking discharge to mean point depth (Leopold, Wolman & Miller, 1964). The power law was fitted for each study site using outputs of probability distribution models for point depth (Lamouroux, 1998) and point shear stress (Lamouroux *et al.*, 1992).

The analysis of discharge variations with respect to the critical discharge over 10 years (01/01/1990-12/31/1999) provided information on the disturbance regime of the 9 study sites. The disturbance regime, was described by the yearly average number of days in spate (Days), the yearly average frequency of spates (FoD), and the average duration of spates (DoD).

Assessment of refugia at multiple-scales

At the stream scale, the areas upstream the study site that remain undisturbed during a spate and from which invertebrates can recolonise the stream by drift are likely to increase with the distance to the source (Distance). We measured this potential refugium on a geographic map (scale 1/25000^e).

At the reach scale, despite biologists have assumed that invertebrates could migrate downward to escape disturbance, it is likely that migration constitutes a phenomenon restricted to down-welling areas (see Dole-Olivier *et al.*, 1997). Nevertheless, benthic invertebrates living down to 15 cm depth may constitute a source of recolonists since scouring is often limited to 10-15 cm depth for spates occurring 6 times a year (Matthaei, Peacock & Townsend, 1999). We evaluated the interstitial habitat availability (Hyporheos) on sediments samples (15-45 cm depth) collected by freeze-coring (Bretschko & Klemens, 1986). The interstitial habitat availability was measured as the ratio of the volume of interstitial free water to the total volume of the sample. Four cores were collected in two riffles in each study site. In addition to the hyporheic zone, in-stream areas with low and stable shear stress may also provide a refuge during high flow (Lancaster & Hildrew, 1993; Robertson *et al.*, 1995; Palmer *et al.*, 1996). Because it was not possible to measure the distribution of shear stress during high flow, we again used a predictive model which provides the frequency distribution of point shear stress estimated by an FST hemisphere (Statzner, Kohmann & Hildrew, 1991) at different discharge (Lamouroux *et al.*, 1992). We defined this refuge (Deadzone) as the proportion of the bed area where point shear stress was ≤ 8.28 dyn.cm^{-2}, *i.e.* FST ≤ 1.

At the local scale, the area downstream large particles that remain stable during the flood, may also provide refuge for invertebrates. In each study site, the stability of the bed was evaluated by the critical force needed to initiate the particle movement using a spring balance with a hook (Downes, Glaister & Lake, 1997). The critical force was measured on 100 particles with a size > 2 cm, and the potential refuge (Force) was evaluated by the proportion of particles needing a force > 12 N.

Sampling the invertebrate community

The sampling of the invertebrate community of the 9 study sites was conducted at the beginning of the spring over 2 years (1998-1999) with a Surber net (0.03 m^2, mesh size 0.025 mm). Ten samples were randomly allocated in lotic habitats (riffles and runs) of the study sites to assess the spatial variability of the invertebrate assemblage. Samples were preserved in 4% formalin. We generally disturbed the sediments 5 cm deep below the bottom of the armour layer, to collect the invertebrates inhabiting interstitial spaces of the stream bottom. In the laboratory, invertebrates were identified up to family (Oligochaeta, most of Diptera, Sericostomatidae), to sub-family (Chironomidae, Ceratopogonidae, Limnephilidae) or genus level (Ephemeroptera, Plecoptera, Coleoptera, Heteroptera, most of Trichoptera). Animals that were not identifiable because of their small size (young stages) were allocated according to their proportion of identified individuals. We identified 98 macroinvertebrate taxa from the 90 samples. The most common taxa were Orthocladinae (35.14 %), Tanytarsini (7.08 %), Limoniidae (6.83 %), *Psychomia pusilla* (5.95 %), Naïdiae (5.67 %), *Esolus sp.* (3.80 %), *Leuctra sp.* (3.79 %), and *Gammarus sp.* (2.94 %). Thirty-one taxa accounted for 95 % of the overall abundance of the 90 samples.

For the purpose of this study, we examined the invertebrates both in terms of total invertebrate abundance (m^{-2}), expected taxon richness, diversity indices and in terms of species traits. Because the invertebrate abundance varied strongly between study sites, we could not compare directly the taxon richness counts (calculated on the basis of the determination levels described above). Therefore, we used a Monte Carlo method to estimate the expected taxon richness for a minimum abundance (N = 760 in the drome river) similar in all study sites. We performed 100 random sampling of 760 individuals from each study site using Ecosim simulation software (Gotelli & Entsminger, 1996) and we evaluated the expected taxon richness by the average number of taxa.

Selection of species traits

To describe the functional structure of communities, we used 8 of the 22 biological traits proposed by Usseglio-Polatera *et al.*, 2000). Similar traits have been investigated previously in both theoretical (Statzner, Resh & Dolédec, 1944, Dolédec, Olivier & Statzner, 2000) and applied fields (Dolédec, Statzner & Bournaud, 1999; Statzner *et al.*, 2001). The species traits are coded using a fuzzy coding approach that describes the affinity of a taxon to different categories describing a species trait (Chevenet, Dolédec & Chessel, 1994). The information is presented in a fuzzy coded table, where the affinity of each taxon for a category is coded by a number (0-5). The value 0 indicates the absence of affinity and the value 5 indicates a high affinity of a taxon to a category. A complete description of the 22 species traits described by 120 categories is available in the Table 1 of Usseglio-Polatera *et al.* (2000), and the fuzzy coded table is available in Tachet *et al.* (2000). We used the corrected version of Statzner *et al.* (2001).

The selected traits describe morphology, physiology, behaviour or ecological preferences of the invertebrates (Table 2). To describe the trait structure per study site we calculated both the proportion of species having an affinity to each trait category (% of species) and the relative abundance of trait categories in the community (% of individuals). We obtained the relative abundance each trait category by multiplying the ln (X + 1) transformed abundances of taxa in study sites by their affinity to the trait category (in %). In order to limit the number of variables, we derived synthetic variables *e.g.* habitat generalist, or we focused on particular categories (Table 2). For exemple, the trait 'strong attachment of the invertebrate to the substrate' was built by grouping crawlers, burrowers and interstitial invertebrates. We described food and substrate preferences postulating that taxa having an affinity > 0 with > 33% of the categories of a trait were generalist. From this, we obtained 9 variables describing the trait structure of the 90 samples (10 samples × 9 study sites).

Data analyses

The variables describing the potential refugia availability (Distance, Hyporheos, Deadzone, Force) and the disturbance regime (Days, FoD, DoD) were summarised into spatial and temporal axes respectively, following the approach presented in Townsend *et al.* (1997c). The variables were scaled between 0 and 1, and each set of variables was processed separately by a non centred Principal Component Analysis. We used the scores of sites along the first component of these analyses to define their position along the temporal and spatial axis respectively.

The structure of the community was examined by Correspondence Analysis conducted on the transformed abundance of the 62 out of 95 more abundant taxa *i.e.* taxa with a relative abundance > 0.3 % and an occurrence > 2 out 9 study sites. These criteria of selection were applied to avoid the ordination of study sites by rare taxa. The structure of species traits was examined separately on species and individuals proportions having a trait (see above in the text) using normalised Principal Component Analysis. Multivariate analyses were performed with ADE-software (Thioulouse *et al*., 1995).

The relationships between physical variables were quantified by Pearson correlation coefficient. The relationships between biological and physical variables were investigated by linear and non-linear regression models. Because the low number of data (N=9) did not allow to perform satisfactory test of the normal distribution, we examined standardised residuals to detect possible outliers in the y space, and leverage coefficients to detect influent values on the fitting (Sokal & Rohlf, 1998, p. 531). When a possible outlier was detected (whether the analysis was significant or not), the analysis was performed after deletion of the outlier to verify the consistency of the result.

To quantify the association of species traits into the 98 taxa, we used the Φ coefficient which measures the association (0-0 and 1-1 *versus* 0-1 and 1-0) between variables in a 2 × 2 table (Sokal & Rohlf, 1998 p. 741) of the variables coded by binary values (0 = absence of the trait, 1 = presence of the trait). Values of the coefficient near –1 and 1 indicate strong association of the variables, whereas values near 0 indicate poor association.

Results

Measures of disturbance regime and refugium availability

For each study site, the disturbance regime was assessed by the yearly average frequency of spates (FoD), the average duration of spates (DoD) and the yearly average number of days in spate(Days), (Table 3). Study sites exhibited strong variations in terms of number of days in spate (CV Days = 0.71), but lower variations in terms of spate frequency (CV FoD = 0.46), and average spate duration (CV DoD = 0.43). In terms of refuge availability, they mainly differed by the proportion of low shear-stress (CV = 0.88), but exhibited lower variations in terms of the proportion of high force (CV = 0.51), the interstitial space availability (CV = 0.34), and the distance from the source (CV = 0.28). Days was positively correlated both to

DoD ($R = 0.91$; $P < 0.001$) and to FoD ($R = 0.84$; $P = 0.005$), whereas the latter variable was not significantly related to DoD ($R = 0.61$; $P > 0.05$). No significant relationships ($P > 0.05$) were found between variables describing the potential refugia nor among the latter and the variables describing the regime of disturbance.

The variables describing the disturbance regime and the refugium availability were summarised into synthetic axes (Disturbance index and Refugium index, respectively) using non-centred PCA. The Disturbance index exhibited strong positive correlation ($R > 0.85$) with the 3 initial variables, whereas the refugium index exhibited lower correlation ($0 < R < 0.50$) with the 4 variables involved in the analysis. To detect possible confounding effects we examined the links between these synthetic axes and others morphological or hydraulic characteristics that were not involved in the definition of the axes. The Disturbance index was significantly related to stream width ($R = 0.72$, $P = 0.03$), and to the initial criteria used to select the study sites (FLOOD2 / Q50- ($R = 0.81$, $P = 0.008$)) . The Refugium index was slightly related to the proportion of riffles ($R = 0.76$, $P = 0.019$). Study sites were displayed on these spatial and temporal gradients. The relation between the Disturbance index and the Refugium index was complex, since the availability of refuge peaked for an intermediate disturbance index (Fig. 1).

Community structure in relation to the templet

The total invertebrate abundance was poorly correlated to both the disturbance index ($P > 0.05$) and the refugium index ($P > 0.05$), but was positively related to time elapsed since the last disturbance ($R = 0.98$; $P < 0.001$). The expected taxon richness peaked at the intermediate level of disturbance and decreased at low and high level of disturbance as predicted by the intermediate Disturbance Hypothesis. This non-linear link was tested by fitting a second-order polynomial model on the data, but both the quadratic and the linear terms were not statistically significant. The examination of residuals of this regression indicated that the ‘Drôme river’ and the ‘Eygues river’ were possible outliers (studentised residual = 2.44 and –4.25, respectively). The analysis was conducted after the removal of these outliers and a significant second-order polynomial relationship (Fig. 2., $R^2 = 0.62$; $P = 0.03$) was found with the disturbance index. Similarly, the positive relationship predicted by the IDH between the taxon richness and the availability of refugia, was not supported by the data ($P > 0.05$).

We examined variations of diversity indexes, (Shannon index: *H'*, Eveness: *E* and Simpson index: *SDI*) in relation to the axes of the habitat templet. Since the three indexes were highly correlated (*H' vs E*: R = 0.99, P < 0.001; *H' vs D*: R = 0.98, P < 0.001; *D vs E*: R = 0.97, P < 0.001), we only present the relationships with the Simpson index. A second-order polynomial model was fitted on Simpson index versus disturbance index data, but none of quadratic and linear components were significant. As for expected taxon richness the 'Drôme river' and the 'Eygues river' were possible outliers (studentised residual = 2.27 and –4.18, respectively). The analysis was conducted after the removal of these data and a significant second-order polynomial relationship (Fig. 2.; $R^2 = 0.78$; P = 0.002) was found with the disturbance index.

The structure of the community was summarised by the three first axes of a Correspondence Analysis conducted on taxa-by-site matrix. The 62 taxa involved in the analysis represented 98.5 % of the overall abundance. The first two axes explained respectively 27.5% and 20.9% of the community structure. The first axis (CSI) was negatively related to the Disturbance index (Fig. 3., R = - 0.81, P = 0.008) and was not related to the Refugium index (R = 0.01, P > 0.05), suggesting that the community was mainly structured by disturbances. The two other community structure indexes were not related to anyone of the synthetic indexes.

The 62 taxa involved in the analysis were regularly distributed along the CSI, but for readability of the results, we present the more abundant taxa only (relative abundance > 0.3%). Taxa were separated into three groups according to their position along the CSI; group I (CSI > 0.20), group II (0.20< CSI < -0.20), group III (CSI < -0.20). CSI separated insects from non insects. Mollusca, Triclada, Oligochaeta, crustacea and Hydridae (but not Hydracarina) were rather associated to positive values of the index and to lowly-disturbed sites. Insect orders (Plecoptera, Ephemeroptera, Trichoptera, Coleoptera and Diptera) were not strongly separated along the community structure index since they were found in the 3 groups. In contrast, the CSI displayed gradients within most insect orders, and genus or families were distributed as follows:

Ephemeroptera: *Paraleptophlebia sp. / Ephemera sp. / Caenis sp. / Baetis sp. / Ecdyonurus spp. / Seratella sp./ Rhithrogena spp. / Oligoneuriella sp.*

Trichoptera: P. *pusilla / Hydroptila sp. / Tinodes sp.* / Sericostomatidae / *Hydropsyche sp. / Athripsodes sp.*

Coleoptera: *Oulimnius sp. / Orechtochilus sp. / Limnius sp. / Elmis sp. / Esolus sp. / Riolus sp. / Hydrocyphon sp.*

Diptera: Psychodidae / Limoniidae / Clinocoerinae / Corynoneurinae / Athericidae / Tanytarsini / Chironomini / Ceratopogonidae / Tanypodinae / Hemedromiinae / Orthocladiinae / Simuliidae.

Finally, we tested the hypothesis that the availability of refuge could influence the abundance of particular taxa (*Leuctra sp*., *Gammarus sp*., *Baetis sp*.) for which the use of refugia was obvious from the literature. We did not find significant relationships ($P > 0.05$) between the Hyporheos and *Leuctra sp.* and *Gammarus sp.* (density and relative abundance), nor between the proportion of low shear stress and Baetidae, Simulidae and Chironomidae (density and relative abundance).

Species traits in relation to disturbance regime and refugium availability

In a first step, we examined how species traits tended to co-occur in study sites using a normalised PCA conducted on species and individuals proportions having species traits. The first two axes of the analysis conducted on species proportions summarised respectively 55.5% and 25.1% of the species trait structure. We found a strong negative relationship ($R = -0.91$, $P < 0.001$) between the first axis (TSI species) and the Disturbance index (Fig. 4). In contrast, the second axis was not significantly related to both the disturbance index and the refugium index. The same analysis was conducted on the proportions of individuals having species traits. The first two axes summarized respectively 62.6% and 20.3 % of the trait structure. The first axis (TSI individuals) was also strongly related to Disturbance index ($R = -0.96$, $P < 0.001$) (Fig. 4), whereas the second axis was not related to Disturbance or Refugium indexes. Species having a strong attachment to the substrate, and/or being deposit-feeders tended to occur in lowly-disturbed sites, whereas species with stages outside the stream, having terrestrial oviposition, having more than 1 cycle per year and/or being filter-feeders tended to occur in highly-disturbed sites.

We examined how species traits tended to co-occur within taxa, by analysing the association of species traits coded in presence-absence for the 98 taxa. Most of the traits poorly co-occurred ($-0.25 < \Phi$ coefficient < 0.25) within taxa, except for ‘habitat generalist’ and ‘deposit feeders’ traits (Φ coefficient = + 0.45) and ‘trophic generalist’ and ‘filter-feeders’ (Φ coefficient = + 0.33) that were fairly associated.

To quantify the relative importance of the variables we used to describe the disturbance regime (Days, DoD, IoDR) and the refugium availability (Distance, Hyporheos, Deadzone, Highforce), we tested their ability to explain variations in species traits by stepwise regression analysis. Among the 16 variables describing the community trait structure, 10 were significantly related ($P < 0.05$) to one of the three variables: 8 variables exhibited best relationship with the yearly average number of days in spate exhibited (Fig. 5) and 2 variables exhibited best relationship with the mean duration of spates (Fig. 6). Taking the refugium variables separately, the stepwise regression failed to detect a significant relationship with any of the traits.

Discussion

Our objective was to compare community and trait structure occurring in stream reaches differing by their disturbance regime and their refugium availability. Such a comparison is difficult to establish because longitudinal gradients governing the habitat and community characteristics (Illies & Botosaneanu, 1963; Vannote *et al.*, 1980; Statzner & Higler, 1986; Statzner & Borchardt, 1994) must be taken into account. Since the hydrology is strongly related to regional patterns of rainfall (Poff, 1992), our sites having similar morphology were located in three regions. Therefore, despite their similar location along the longitudinal gradient, streams differed by their stream size (min = 4.3, max = 11.9) and their median discharge (min = 0.04, max = 2.92). Nevertheless these differences remain relatively weak in regard to stream size and stream discharge variability in natural systems.

Relative importance of disturbance regime and refugium availability

Many of the species traits we selected exhibited a significant response to disturbance, suggesting that our choice to define the disturbance in relation to the substrate movement was appropriate. Our results support the findings of other studies conducted on invertebrates (Townsend *et al.*, 1997a) and on bryophytes (Muotka & Virtanen, 1995). We defined the disturbance as any hydrological event which modifies the bed by removing fine sediments from within the substrate, which potentially affects the distribution of the invertebrates. According to Gayraud *et al.* (2000), the movement of fine sediments at the surface during the increase in discharge is sufficient to increase the drift rate of many invertebrates and to modify their local abundance within the benthic layer.

To quantify disturbance regime, we used usual hydraulic equations rather than painted tracer particles since the latter method suffered from methodological problems and provides poor estimates of disturbance levels (Downes *et al.,* 1998). The approach we used has the advantages to be well established in the literature (Milhous & Bradley, 1986; Milhous, 1998) and to be easily utilisable by biologists. The approach does not need intensive labour, but only the fitting of a power law function between discharge and point water depth, and the measurement of substrate particle size and stream slope. The disadvantage is that long-term flow records are required to calculate accurate characteristics of the disturbance regime. We are aware that this approach provides only a rough estimate of the true disturbance regime since it simplifies the complexity of both transport mechanisms (Komar, 1987; Petit, 1989) and spatial patterns of erosion and filling (Matthaei *et al.*, 1999). Nevertheless our results suggest that the method is efficient to discriminate sites characterised by different disturbance regime.

Our definition of the disturbance implies that any event exceeding the critical discharge threshold is considered to have the same effect on the invertebrates independently of its magnitude. As a consequence, we did not measured the intensity of the disturbance in space (as it is classically done using the magnitude of the event, see Reice *et al.*, 1990; Townsend, Scarsbrook & Dolédec, 1997c) but in time as the average duration of the event (see Clausen & Biggs, 1997). We found that both the number of days in spate (Days) and the average disturbance duration (DoD) were strongly related to most species traits that were predicted to change in the habitat templet (see Table 2). This result suggests that temporal aspects of spates are important for a better understanding of mechanisms underlying community structure. The major role of these two variables may be explained by the invertebrates behaviour during a flood. Despite the absence of direct measurements in the literature, it is reasonable to assume that most of the invertebrates stop their current activities in order to find protection against the flow. If the favourableness of the habitat is lower in the refugia than in habitat during low flows, stopping or reducing the feeding activity could result in a significant reduction of growth rate or reproductive success of the invertebrates. Consequently, the cost for the invertebrates during spates could be a function of the spate duration and the overall number of days in spate during its development.

In this context, refugia should be important in structuring the community, by selecting the invertebrates through their ability to reach refugia and to exploit resources on these areas.

This assumption was not supported by our data since we did not found a significant relationship between the refugium index and the indexes describing the structure of the community (CSI) and the species traits (TSI species and individuals). This result contrasts with the findings of Townsend *et al.*, 1997a), where significant relationships were found between species traits (habitat generalist, high adult mobility) and a refugium index very similar to the index we used in this study. Such a difference may reside in that we analysed the entire community whereas Townsend *et al.* focused on some insect taxa (35 out of 58 insect taxa). The potential refugia we defined have been already tested in other studies and some evidences were found of the utilisation of stream margins (Maier, 2001), slow patches (Lancaster & Hildrew, 1993; Robertson *et al.*, 1995; Winterbottom *et al.*, 1997), large woody debris (Palmer *et al.*, 1996), and hyporheic zone (Dole-Olivier *et al.*, 1997) by the invertebrates. Chironomidae, *Leuctra nigra*, and *Nemurella pictetii* were found to use areas with low shear stress (Lancaster & Hildrew, 1993; Winterbottom *et al.*, 1997), whereas *Gammarus sp.* was found to migrate downward within the hyporheic zone (Dole-Olivier *et al.*, 1997). Thus, the lack of relationship between the fauna and the availability of refugia is questionable. Despite these evidences of refugia-use strategies by some species, their role and/or their availability during spates could not be sufficient to modify perceptibly the community structure in our streams. Presently, there is few empirical evidences in the literature that refugia influence significantly the dynamic of populations and communities after spates. However, we cannot exclude a possible misevaluation of the availability of refugia since we did not measure the refugium effectiveness during spates. For example, despite the effort made to predict the shear stress distribution at critical discharge, the statistical model could provide biased estimate of low shear stress proportion since it was not calibrated for such a high range of discharge (Lamouroux, pers. com.).

Community organisation in relation to the disturbance regime

The general characteristics of the community were poorly influenced either by the disturbance regime or by the refugium availability. The abundance was not related to this templet but was related to the time elapsed since the last disturbance (Scrimgeour & Winterbourn, 1989). Flecker & Feifarek (1994) found a similar relationship in Andean streams and found that reductions in invertebrate abundance following spates were quickly improved.

We calculated the expected taxon richness using Monte Carlo simulation in order to remove the sample-size effect. The results do not support clearly the theoretical predictions that the taxon richness should peak at the intermediate level of disturbance (IDH; Connell, 1978) and should increase with the refugium availability (PDC; Townsend, 1989; Townsend, Scarsbrook & Dolédec, 1997b). The problem lies in the presence of a possible outlier *i.e.* Drome river. The lateral dispersal of insect females (Petersen *et al.*, 1999) from the less-disturbed Bez study site (see Table 3) located at 100 m of the Drome river may explain the observed taxon richness higher than predicted by the quadratic adjustment.

The community structure index (CSI) separated invertebrates according both the insect/non insect criteria and to genus/family within insect orders. Thus, CSI separates invertebrates having at least one stage outside the streambed. The absence of a clear separation among insect orders and the regular repartition of genus (or families) belonging to the same order support the idea that adaptations to disturbance overlap higher systematic units (order). Other studies have already plotted insect species in relation to spatial habitat variability (Minshall & Robinson, 1998) or in relation to both spatial and temporal habitat variability (Usseglio-Polatera, 1994). The latter found (Fig. 8b, p. 428) that species belonging to the same insect order were also distributed all along the temporal variability axis. This finding is in favour of a lack of phylogenetic relationships.

Species traits and strategies in relation to disturbance regime

The species traits that were selected in relation to the disturbance regime describes their relationship to the substrate, their ability to escape the aquatic environment and to use the trophic resources within the aquatic environment. We found that invertebrates having strong relationships with the substrate (crawlers, burrowers, interstitial invertebrates) were less abundant in highly disturbed environments. Individuals having at least one stage outside the stream are more abundant in highly-disturbed stream, probably because their chance to survive is increased as they spend less time in the disturbed aquatic environment (Gray & Fisher, 1981; Townsend *et al.*, 1997a). This assumption was supported by the increase in individuals ovipositing in terrestrial habitat, suggesting that the egg stage is particularly sensitive to erosion, and that terrestrial environment provide more stable environmental conditions to individuals during their stage outside the stream. We can hypothesise that eggs deposited by some insects on the stream banks (*e.g. Sialis sp.*) are less submitted to the erosion and have consequently a greater chance to produce a new generation than eggs deposited within bed sediments. If the stream banks are obviously less disturbed by spates than the streambed, it is not completely clear how this environment provides a greater egg survival since these stages are also probably submitted to other type of disturbances (*e.g.* erosion by rainfall, predation by terrestrial organisms). These results underline the complexity of mechanisms underlying the persistence of species in aquatic environments. Furthermore, they emphasise the importance of taking into account all the development stages of invertebrates to better understand large spatial patterns and population dynamic of aquatic stages (see Spiers *et al.*, 2000).

We defined trophic generalist as species being associated to up to 30% of the 9 modalities (*i.e.* fine sediment + microorganisms, detritus < 1 mm, plant detritus ≥ 1 mm, living microphytes, living macrophytes, dead animals ≥ 1 mm, living microinvertebrates, living macroinvertebrates, vertebrates) described by the trait 'Preference to food' in Usseglio-Polatera *et al.*, 2000. Despite arbitrary, our variable gave a good description of the invertebrate preferences to trophic resources since the resulting classification was coherent with others studies (*e.g. Baetis sp.* is trophic a generalist and *Epeorus sp.* is a trophic specialist in Mihuc & Minshall, 1995). We found that the proportion of trophic generalists (in terms of % of individuals but not % of species) was related to the disturbance duration. When the spate duration is long in regard to the duration of the aquatic stage, the discontinuity in the feeding activity that may occur during a spate can reduce significantly the growth rate and the fitness of the individuals. Trophic generalists are more adapted to highly-disturbed environments (see Mihuc & Minshall, 1995) where the availability of trophic resources may fluctuate greater than in stable environments. Spates that result in large movement of the bed reduce the periphyton biomass and consequently affect the availability of trophic resources for scrapers (Biggs, 1995; Scrimgeour & Winterbourn, 1989). Similarly, the availability of benthic organic matter is probably reduced in highly-disturbed environments since the transport of fine organic matter is positively related to discharge (Wallace *et al.*, 1991). As a consequence, filter-feeders could take an advantage of living in highly-disturbed environments where the drifting organic matter is probably the most constant trophic resource, whereas the importance of other feeding groups could be lessen.

It was predicted that invertebrates in highly-disturbed study sites would exhibit smaller body size and higher number of reproductive cycles than in lowly-disturbed study sites. The absence in our study of significant links between the disturbance regime and the traits *i.e.* size < 10 mm, number of reproductive cycles per year supports the results of other studies involving invertebrates (Usseglio-Polatera, 1994) or several groups (Resh *et al.*, 1994) in relation to temporal variability.

Many authors have hypothesised that extreme events can be a major selective force in lotic systems (Southwood, 1977; Gray & Fisher, 1981; Townsend, 1989) acting on invertebrates. It is questionable whether the occurrence of these traits is the result of their independent selection or the result of the selection of a suite of traits (a strategy) in response to disturbances. We found that species traits tended to co-occur in our sites *i.e.* their proportion were often correlated, whereas they were poorly associated within taxa (except ‘trophic generalist’ with ‘filter-feeder’, and ‘deposit-feeder’ with ‘habitat generalist’). This poor association of traits contrasts with the classical view of a feed back loop selection that would select an optimal suite of traits maximising the fitness of invertebrates (Southwood, 1977; 1988). However, it suggests that the co-occurrence of species traits in study sites is mainly the result of their independent selection, each of them providing a chance to survive in highly-disturbed environments (Resh *et al.*, 1994; Statzner *et al.*, 1997; Townsend *et al.*, 1997a).

To conclude, this study highlighted the substrate stability as a dominant force structuring the invertebrate communities over climatic or geologic ranges encompassed by study sites. In this context, the number of days in spate during a year and the average spate duration seem particularly important. Thus, taxa having traits well adapted to survive erosion and to continue their current activities (*e.g.* feeding) during spates will be found in a higher proportion in highly disturbed sites. The traits trophic generalist, filter-feeder, terrestrial oviposition, stages oustside the stream and poor attachment to the substrate are selected in these environments.

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Table 1 General characteristics of study sites. Li, Do, Mi code respectively for Limestone, Dolomite and Mixed rock geology.

Characteristics	Stream reaches								
	Bez	Drome	Eygues	Galaure	Gere	Herbasse	Ouveze	Sanne	Vareze
Geology	Li	Li	Li/Do	Mi	Mi	Mi	Li	Mi	Li
Basin (km^{-2})	270	260	147	60	69	168	111	52	63
Distance (km)	30	25	20	25	20	30	20	12	15
Elevation (m)	520	520	610	390	280	200	530	235	340
Slope ($m.km^{-1}$)	9.81	9.80	8.69	8.59	8.10	8.63	10.13	8.04	8.16
Bankfull width (m)	11.9	9.4	7.9	8.3	5.2	8.6	9.8	4.3	4.9
Floodplain width	70	40	30	15	7	15	15	6	10
Riffles (%)	60	59	57	64	57	54	60	51	51
pH	7.8	7.8	8.3	8.2	8.6	8.1	8.3	8.2	8.2
Cd (µS.cm-2)	290	480	380	280	305	480	330	525	295
Carbonates ($mg.l^{-1}$)	170	235	215	150	185	275	220	290	170
Nitrates ($mg.l^{-1}$)	1.3	3.7	0.4	6.0	5.6	12.6	1.0	12.0	3.6
Phosphates ($mg.l^{-1}$)	< 0.03	< 0.03	0.03	0.09	0.06	< 0.03	0.06	< 0.03	< 0.03

Table 2 Definition of the 9 species traits and sign of expected response to disturbance and refugium availability. The species traits are described by percentage of species and percentage of individuals having the trait (see methods for details).

N°	Species traits	Variable tested	Expected response to	
			Disturbance	Refugia
1	Potential size	size < 10 mm	+	-
2	No of reproductive cycles per year	> 1 cycle / year	+	-
3	Aquatic stages	≥ 1 stage outside the streambed	+	-
4	Reproduction	terrestrial oviposition	+	-
5	Substrate relation	strong attachment (crawlers, burrowers, interstitial invertebrates)	-	+
6	Preference to food	food generalist	+	-
7	Feeding habits	filter-feeders	+	-
		deposit feeders	-	+
8				
9	Preference to subtrate	habitat generalist	+	-

Table 3 Measures of disturbance and refugium variables. Days is average number of days in spate during a year. FoD and DoD are the frequency and the average duration of spates. Distance, Hyporheos, Deadzone and Forces are measures of refugium availability. See details in methods.

Characteristics	Stream reaches								
	Bez	Drome	Eygues	Galaure	Gere	Herbasse	Ouveze	Sanne	Vareze
Days	17.9	34.2	26.4	14.8	1.7	8.8	21.6	5.8	6.1
FoD	4.8	6.8	5.8	6.1	1.3	4.8	4.1	2.5	2.6
DoD	3.8	5.0	4.5	2.4	1.3	1.8	5.2	2.3	2.3
Distance	30.0	25.0	20.0	25.0	20.0	30.0	20.0	12.0	15.0
Hyporheos	3.9	2.8	3.9	5.1	4.0	3.8	4.3	0.8	3.6
Deadzone	0.0	0.0	7.0	14.0	3.0	7.0	10.0	18.0	4.0
Forces	27.0	13.0	11.0	14.0	24.0	7.0	32.0	34.0	13.0

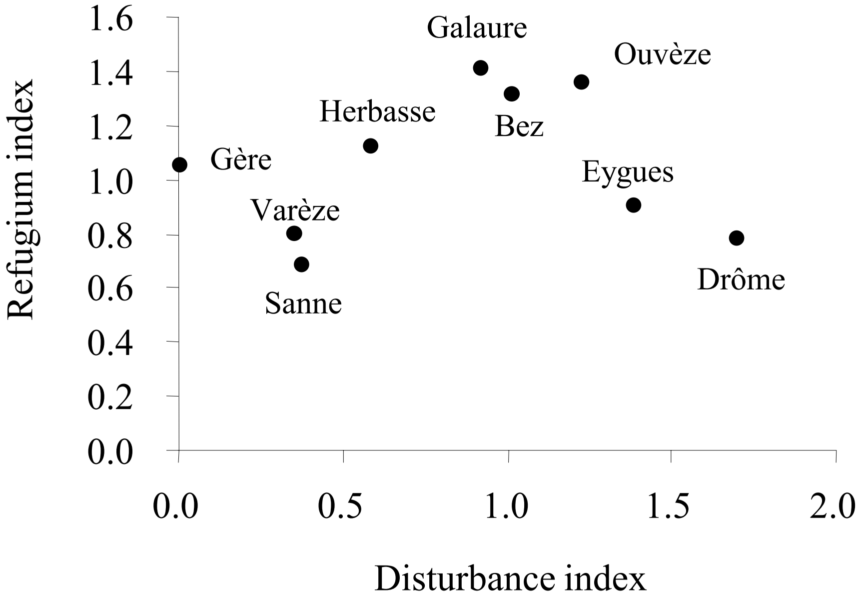


Figure 1: Localisation of stream reaches in the habitat templet.

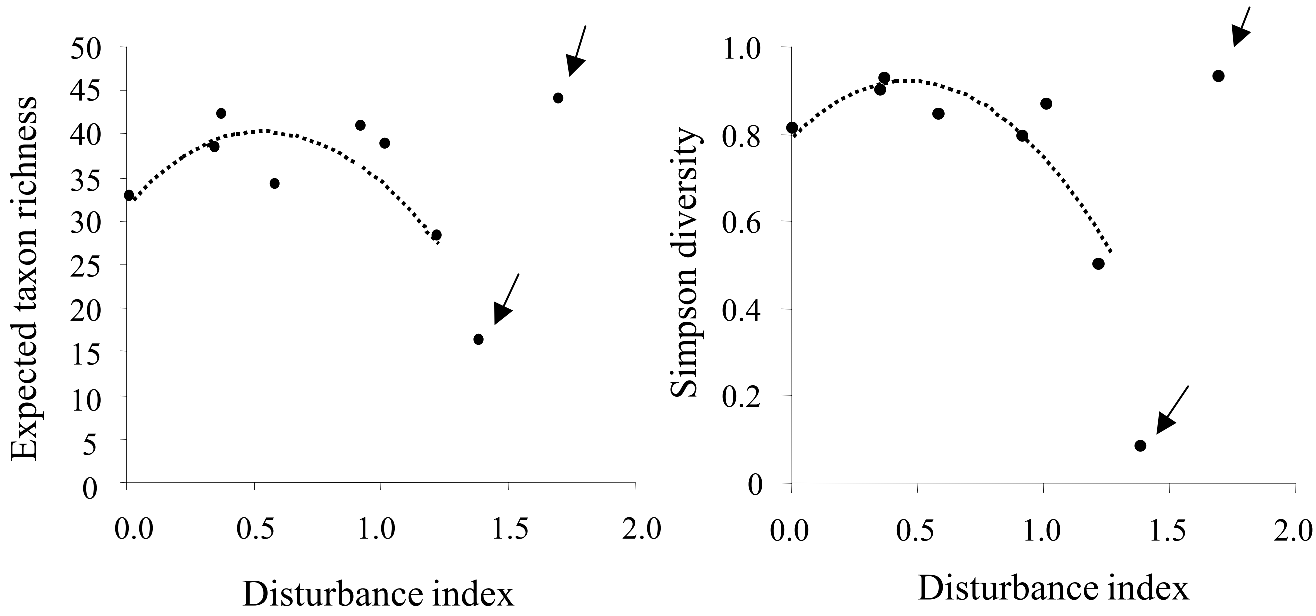


Figure 2: Relationship of the Disturbance index with a) expected species richness (best fit with a second-order polynomial model: $Y = 31.40 + 31.66 X - 28.60 X^2$, $R^2 = 0.62$, $P = 0.03$), and b) Simpson diversity index ($Y = 0.79 + 0.56 X – 0.61 X^2$, $R^2 = 0.78$, $P = 0.002$). Data are fitted after the deletion of outliers indicated by an arrow (see details in the text).

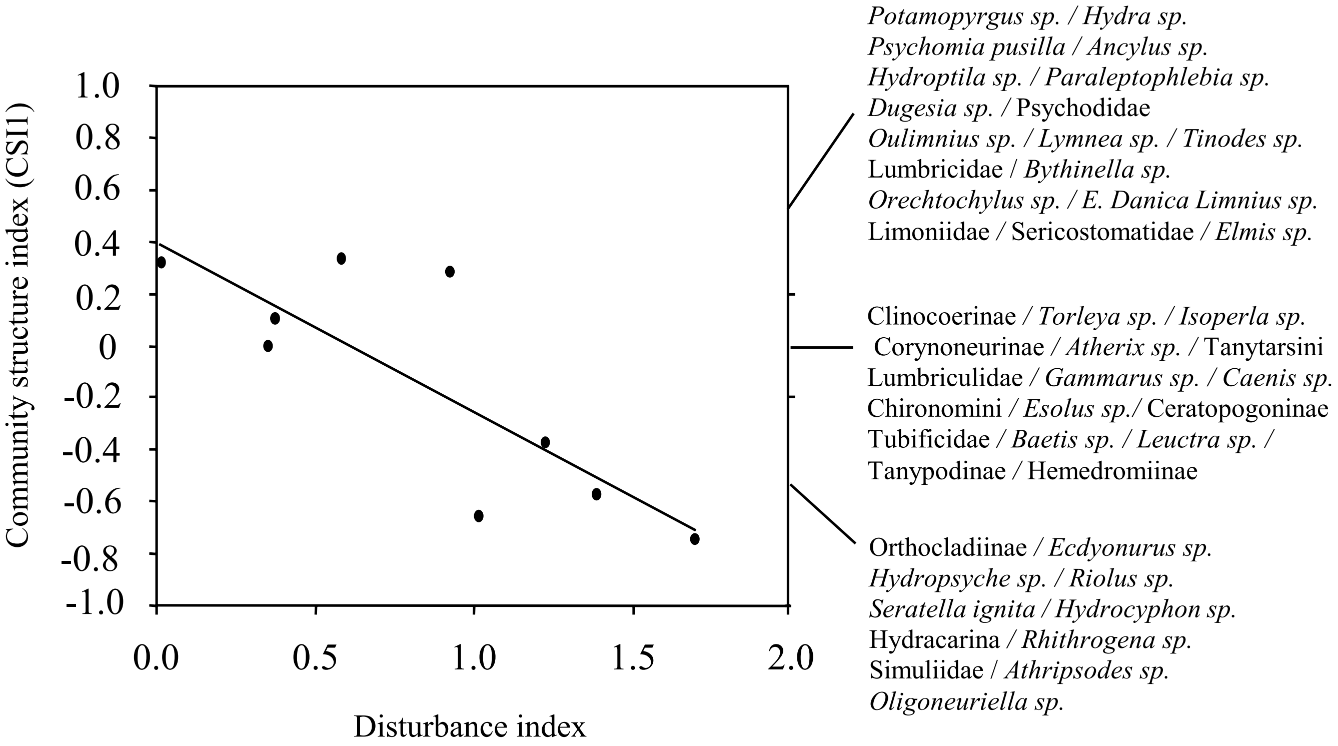
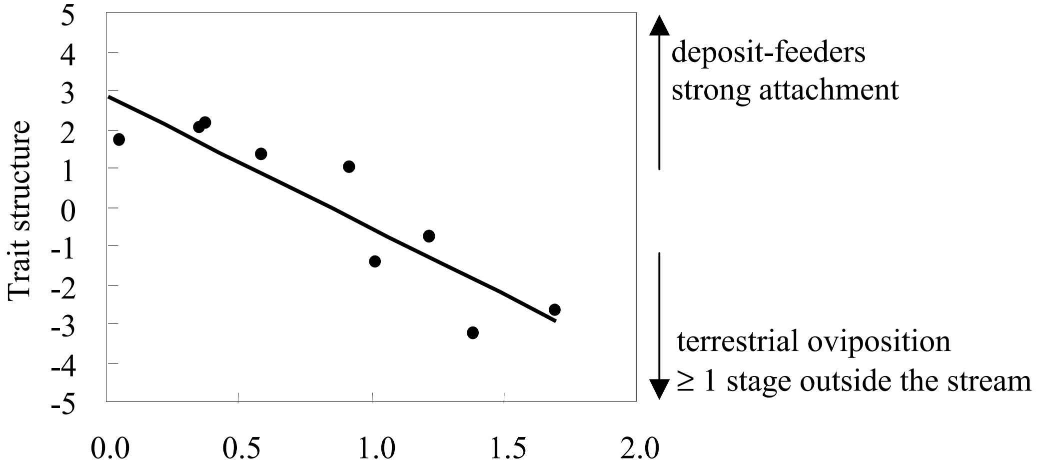


Figure 3: Community Structure Index (CSI) of the 9 stream reaches in relation to the Disturbance index (best fit: Y = -0.65 + 0.40 X, $R^2 = 0.66$, P = 0.008). CSI scores are the coordinates on the first component of a correspondence analysis conducted on taxa abundances. The correspondence of CSI scores with the main taxa included in the analysis is indicated (see details in the text).

a) species



b) individuals

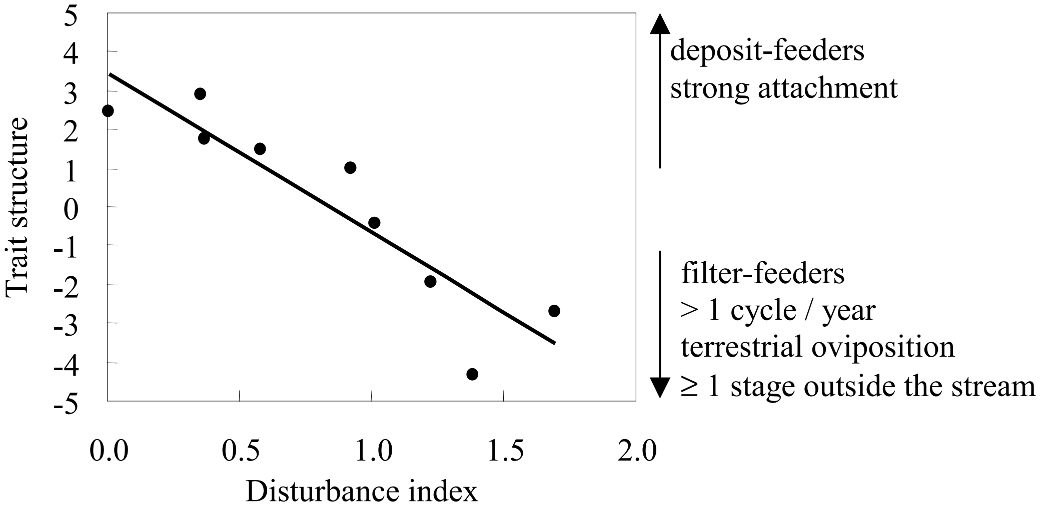


Figure 4: Relationship of the Disturbance index with synthetic indexes of the trait structure described by a) the percentage of species (best fit: $Y = 0.87 - 3.41 X$, $R^2 = 0.81$, $P < 0.001$), and b) the percentage of individuals ($Y = 3.49 - 4.15 X$, $R^2 = 0.83$, $P < 0.001$). Species traits having high correlation coefficients ($R^2 > 0.44$) with the Trait structure index are indicated (see details in the text).

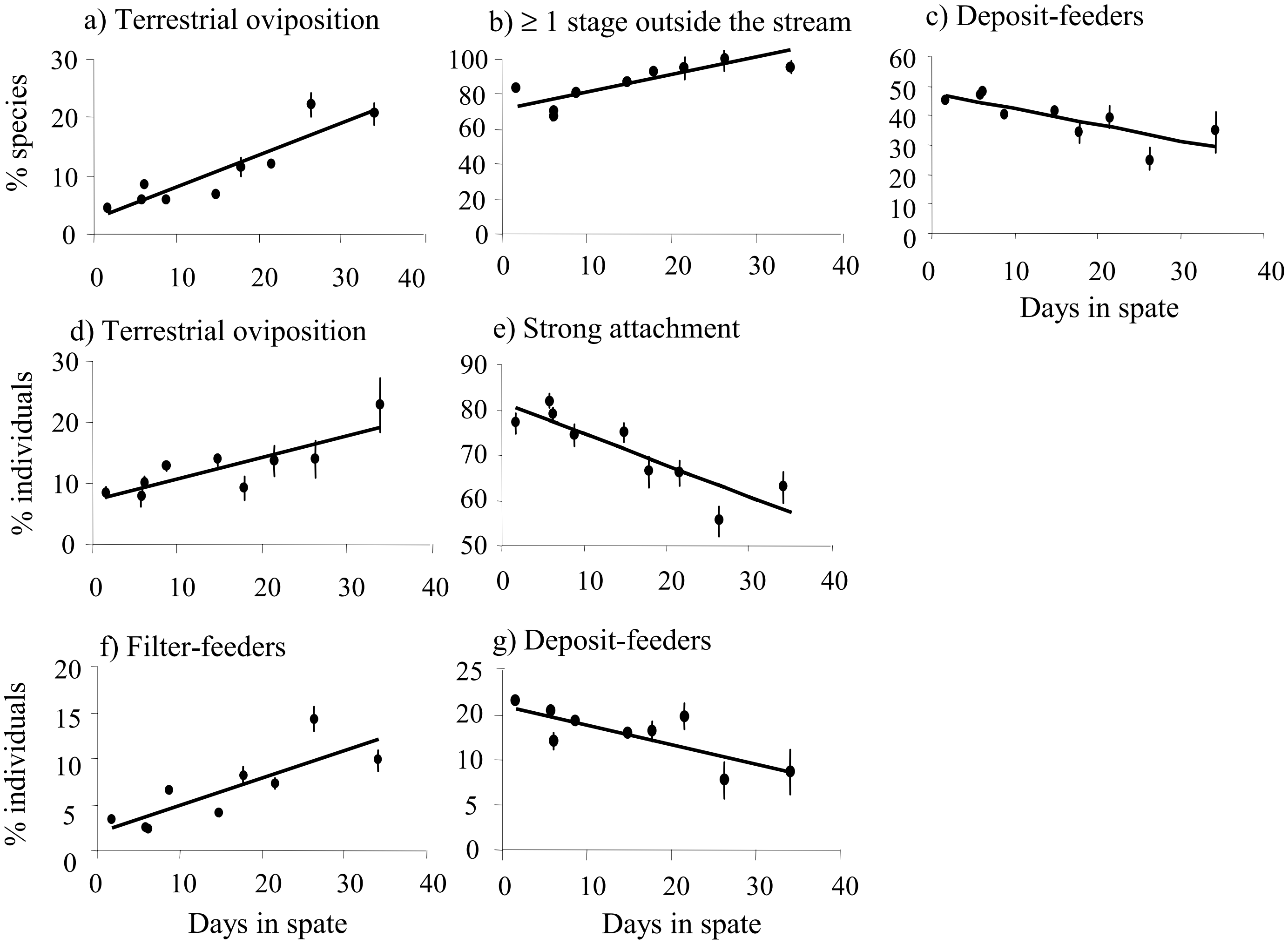


Figure 5: Relationship of the average number of days in spate with the proportion of various species traits: a) terrestrial oviposition (best fit: $Y = 2.53 + 0.54 X$, $R^2 = 0.82$, $P < 0.001$), b) ≥ 1 stage outside the stream ($Y = 73.74 + 0.76 X$, $R^2 = 0.62$, $P = 0.011$), c) deposit-feeders ($Y = 47.64 – 0.54 X$, $R^2 = 0.62$, $P = 0.011$), d) terrestrial oviposition ($Y = 7.05 + 0.35 X$, $R^2 = 0.70$, $P = 0.005$), e) strong attachment ($Y = 81.77 – 0.70 X$, $R^2 = 0.76$, $P = 0.002$), f) filter-feeders ($Y = 18.7 + 0.30 X$, $R^2 = 0.67$, $P = 0.007$), g) deposit-feeders ($Y = 16.14 – 0.22 X$, $R^2 = 0.60$, $P = 0.014$). Mean 1±SE.

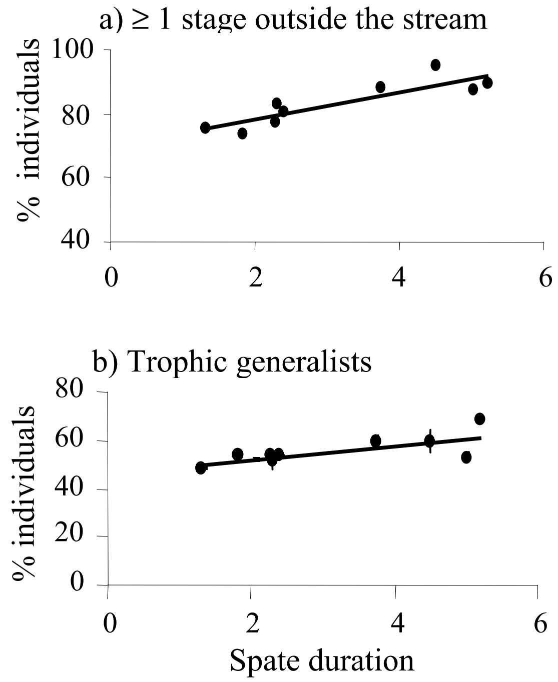


Figure 6: Relationship of the average spate duration with the proportion of a) the proportion of species having ≥ 1 stage outside the stream (best fit: $Y = 69.64 + 4.27 X$, $R^2 = 0.76$, $P = 0.002$), and b) the proportion of individuals being trophic generalists ($Y = 45.32 + 2.98$, $R^2 = 0.55$, $P = 0.023$). Mean 1±SE.

A 5

LE COLMATAGE MINERAL DU LIT DES COURS D'EAU: REVUE BIBLIOGRAPHIQUE DES MECANISMES ET DES CONSEQUENCES SUR LES HABITATS ET LES PEUPLEMENTS DE MACROINVERTEBRES

(Gayraud S., E. Hérouin. & M. Philippe, *Bulletin Français de la Pêche et de la Pisciculture*, sous presse)

LE COLMATAGE MINERAL DU LIT DES COURS D'EAU : REVUE BIBLIOGRAPHIQUE DES MECANISMES ET DES CONSEQUENCES SUR LES HABITATS ET LES PEUPLEMENTS DE MACROINVERTEBRES

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RESUME : Le développement des activités humaines a conduit dans de nombreuses régions à une augmentation du transfert de sédiments fins vers les cours d'eau, multipliant les phénomènes de colmatage. Le colmatage fait référence au dépôt de sédiments organiques ou minéraux et à leur infiltration dans le benthos et l'hyporhéos. Dans cet article de synthèse, le colmatage par les sédiments minéraux est présenté du point de vue de ses mécanismes et de sa variabilité spatio-temporelle dans un schéma d'organisation global du cours d'eau. Le colmatage entraîne une modification des habitats benthique et interstitiel, ainsi que des échanges d'eau et de matières entre la surface et l'hyporhéos. Il affecte la structure du peuplement d'invertébrés en modifiant la structure et la stabilité du substrat, la disponibilité des ressources trophiques et de l'oxygène, ainsi que de la pression de prédation. Les conséquences à court terme sont une augmentation de la dérive et une réduction de l'abondance totale des organismes. Sur le long terme le colmatage affecte la survie, le développement et la croissance des invertébrés ainsi que la biomasse et la productivité du peuplement. Les espèces sensibles adaptées aux substrats grossiers disparaissent au profit des espèces adaptées aux sédiments fins. Les conséquences sur la faune hyporhéique sont peu connues mais l'importance de l'hyporhéos dans le fonctionnement du cours d'eau suggère que son altération pourrait avoir des conséquences importantes en terme de capacité de résilience du peuplement face aux perturbations.

Mots clés : substrat, hyporhéos, sédiment, invertébrés, matières en suspension (MES).

THE CLOGGING OF STREAM BEDS : A REVIEW OF MECHANISMS AND CONSEQUENCES ON HABITATS AND MACROINVERTEBRATE COMMUNITIES

ABSTRACT : The clogging refers to deposition and infiltration of fine organic and inorganic sediments downward within the hyporheic zone. In this review, we presented clogging mechanisms and their spatio-temporal variability in the context of a global stream functioning. Clogging modifies stream bottom and interstitial habitats characteristics and reduces the exchange of water and dissolved substances between the stream surface and the hyporheic zone. Modifications of substrate structure, substrate stability, oxygen and trophic resources and predator influence lead to changes in community structure. In a first step, drift increases whereas the invertebrate abundance drops. In a second step, likelihood to survive, growing, standing crop and productivity are affected. Coarse substrate adapted assemblages are progressively replaced by invertebrates adapted to fine sediments. The studies about consequences of clogging on the hyporheos are scarce, but the major role of the hyporheos on the dynamic of streams suggests that its alteration would strongly decrease the stream resilience capacity after disturbances.

Key words : substrate, hyporheic zone, fine sediments, invertebrates, suspended sediment (SS).

1. INTRODUCTION

Le développement récent des activités humaines dans de nombreuses régions du globe est la cause principale de l'accroissement des transferts de sédiments fins (sables, argiles et limons) vers les cours d'eau (WATERS 1995). Pour ne citer que les principales, l'érosion des bassins versants liée à la déforestation ou aux pratiques culturales, la mauvaise gestion des berges, le déversement des déchets miniers, l'extraction de granulats du lit mineur ainsi que le fonctionnement et l'entretien des barrages et des plans d'eau sont autant de sources de sédiments fins qui conduisent au colmatage des habitats aquatiques (MEADE, 1988 ; WATERS, 1995). A l'heure actuelle, les problèmes posés par les sédiments fins au niveau international sont si préoccupants que leur gestion constitue un critère à part entière dans l'évaluation des débits minima à appliquer pour satisfaire les exigences de la biocénose aquatique. Pour autant, de nombreuses questions se posent encore sur les mécanismes du colmatage et ses conséquences à long terme sur les cours d'eau (WATERS, 1995).

Le colmatage minéral fait référence aux phénomènes de dépôt et d'infiltration de sédiments fins minéraux au sein du lit, ce qui provoque un remplissage des interstices du substrat et conduit à une altération de ses fonctions. Les conséquences biologiques les plus connues de ce type de colmatage sont la réduction des habitats qui conduisent à la réduction des effectifs piscicoles (BJORNN *et al.*, 1977 ; ALEXANDER et HANSEN, 1986) et la réduction de la survie des œufs des lithophiles (CHAPMAN, 1988). La faune piscicole est également affectée par l'intermédiaire des peuplements d'algues et d'invertébrés qui constituent pour celle-ci des ressources trophiques importantes (SCOTT et CROSSMAN, 1973). Chez les macroinvertébrés, le substrat est indispensable à l'accomplissement de nombreuses fonctions biologiques telles que la reproduction, le développement des œufs et l'alimentation (HYNES, 1970 ; MINSHALL, 1984). Il influence leur répartition spatiale au niveau local (CUMMINS et LAUFF, 1969), et la structure (RICHARDS *et al.,* 1993) et la productivité du peuplement (WATERS, 1984) au niveau du cours d'eau. Ces nombreuses interactions avec le substrat rendent les macroinvertébrés particulièrement sensibles au colmatage.

Si le colmatage a été principalement étudié au niveau de l'habitat benthique, sa dimension verticale ne peut plus être négligée aujourd'hui tant le nombre d'études montrant les liens entre la surface et l'hyporhéos s'est accru depuis 3 décennies (BRUNKE et GONSER, 1997). L'hyporhéos constitue un habitat permanent pour les organismes interstitiels (GIBERT *et al.,* 1977 ; MARMONNIER et DOLE, 1986 ; WARD *et al*., 1998), mais également un habitat temporaire (WILLIAMS, 1984), et une zone refuge durant les crues (DOLE-OLIVIER *et al.,* 1997) et les étiages sévères (BOULTON et LAKE, 1992) pour de nombreux invertébrés benthiques.

Les très nombreux travaux (plus de 3000 références ont été sélectionnées en 1991 par RYAN, 1991) tant expérimentaux que de terrain sur l'impact des matières en suspension (MES) et des dépôts de sédiments fins sur les invertébrés ont été synthétisés au travers de revues bibliographiques très détaillées (CORDONE et KELLY, 1961 ; CHUTTER, 1969 ; LLOYD *et al*., 1987 ; RYAN, 1991 ; WATERS, 1995). Cet article a été écrit afin de présenter ces connaissances en nous focalisant sur les mécanismes d'action du colmatage d'une part et en recalant ces mécanismes dans une présentation plus globale des relations entre les invertébrés et le substrat d'autre part. Nous aborderons tout d'abord l'organisation et les propriétés du substrat afin de dégager les paramètres susceptibles d'être affectés par le colmatage, avant de présenter dans une seconde partie les mécanismes de dépôt et d'infiltration des sédiments fins qui conduisent au colmatage. Dans une dernière partie, nous aborderons les conséquences du colmatage sur les organisations structurelles et fonctionnelles des peuplements de macroinvertébrés benthique et hyporhéique.

2. ORGANISATION ET PROPRIETES DES SUBSTRATS

La répartition des particules constituant le lit du cours d'eau est contrôlée par l'écoulement, qui produit ainsi une mosaïque de substrats très diversifiée. On distingue fondamentalement les substrats fins relativement fluides en raison d'une forte teneur en eau, des substrats grossiers plus rigides (Fig.1. ; WARD *et al*., 1998). Ces substrats ont toutefois une organisation commune : les particules de plus grande taille créent une macrostructure (framework) fortement poreuse que viennent combler les particules les plus fines (matrix). Les interstices résultant de cette architecture constituent l'espace interstitiel qui permet le stockage ou la circulation de l'eau, des substances dissoutes, de la matière organique et des organismes vivants (BRUNKE et GONSER, 1997). Par un phénomène d'adsorption, une partie de l'eau interstitielle est piégée par les particules de sédiment (KEMPER *et al*., 1964) tandis qu'une autre fraction est libre et peut ainsi participer aux échanges entre la surface et la zone hyporhéique. L'eau piégée par adsorption est d'autant plus importante que la taille des particules est petite, expliquant la structure particulièrement fluide des substrats fins. En raison de cette relative fluidité, les invertébrés peuvent s'y mouvoir aisément par fouissage en modifiant aisément l'arrangement des particules. Au contraire, la structure plus rigide de substrats grossiers est plus difficilement modifiable par les invertébrés et leur utilisation sera conditionnée par la taille et la quantité des interstices (GAYRAUD et PHILIPPE, 2001). Cette dernière peut être mesurée par l'intermédiaire de la porosité qui représente le volume d'eau interstitielle non piégée par les particules dans un volume de substrat donné (MARIDET, 1990).

D'un point de vue théorique, les substrats constitués de particules sphériques et de taille homogène ont une porosité maximale variant de 26 à 48% selon l'architecture du lit. Dans ce type de substrats, la porosité est indépendante du diamètre des particules (FURNAS, 1931) mais la taille des interstices est directement corrélée au diamètre médian de la distribution granulométrique (WILLIAMS, 1972). Dans le cas de substrat grossiers constitués de particules de taille et de forme variables tel que ceux rencontrés dans les cours d'eau (BRETSCHKO, 1994), la porosité est plus faible (< 30%) et dépend principalement des proportions de chaque classe granulométrique, du tassement des particules (WESTMAN et HUGILL, 1930 ; GAYRAUD et PHILIPPE, soumis), de leur forme (TICKELL et HIATT, 1938) et, dans une moindre mesure, de leur nature géologique en raison des micro-aspérités recouvrant la surface de certaines roches. Globalement, on observe que la porosité des substrats grossiers est d'autant plus faible que la granulométrie est hétérogène et que la proportion d'argiles, de limons et de sables augmente (MARIDET et PHILIPPE, 1995 ; GAYRAUD et PHILIPPE, soumis).

Verticalement, les 20 premiers centimètres du substrat se comportent comme une interface (au sens de BRETSCHKO dans VERVIER *et al.,* 1997) entre le lit profond (zones hyporhéique et souterraine) et l'écoulement de surface. Cette zone d'interface est constituée d'une couche d'armure composée généralement de matériaux grossiers et d'une couche de sub-surface constituée de matériaux plus fins et plus diversifiés. La couche d'armure constitue une protection de la couche de sub-surface contre les contraintes générées par l'écoulement, mais contrôle en même temps, par son degré d'ouverture, l'intensité des échanges d'eau et de matière entre la surface et le lit profond.

Pour un lit homogène du point de vue morphologique, l'écoulement de l'eau dans le milieu interstitiel est laminaire et sa vitesse est contrôlée par la perméabilité du substrat, la viscosité de l'eau ainsi que par le gradient de pression longitudinal (loi de Darcy). La vitesse dans le milieu interstitiel varie de quelques mm/heure à quelques cm/seconde (WILLIAMS et HYNES, 1974 ; ANGRADI et HODD, 1998 ; WAGNER, 1999). La perméabilité qui exprime l'aptitude au déplacement de l'eau dans les sédiments dépend principalement de la porosité du substrat, de la taille des interstices et de la connectivité entre ces interstices. La viscosité dépend uniquement de la température et diminue lorsque celle-ci augmente.

Les irrégularités morphologiques que l'on observe dans les cours d'eau, tant à l'échelle locale (hétérogénéité de la perméabilité, présence de grandes particules) qu'à une échelle plus large (faciès d'écoulement), induisent une composante verticale dans l'écoulement de l'eau au sein du milieu interstitiel (Fig. 2. ; VAUX, 1968 ; HARVEY et BENCALA, 1993 ; ELLIOT et BROOKS, 1997a ; 1997b) qui est prépondérante pour comprendre les mécanismes du colmatage. La présence de particules de grande taille en saillie par rapport au lit induit la pénétration d'eau en amont de ces particules et sa résurgence quelques centimètres en aval (Fig. 2. ; THIBODEAUX et BOYLE, 1987 ; VOLLMER *et al.,* 2000). L'alternance de séquences seuil /mouille (MALAVOI, 1989) crée également des mouvements d'eau complexes au sein du lit. L'eau de surface peut pénétrer de manière localisée dans le lit profond en amont d'un seuil (zone d'infiltration), puis ressortir de manière plus diffuse en aval (zone d'exfiltration) après un transit plus ou moins long au sein des sédiments. La correspondance de ces alternances seuil/mouille avec les bancs de galets (DERRUAU, 1974) se traduit par une pénétration de l'eau en tête du banc et une résurgence localisée en queue de banc (MARMONIER et DOLE, 1986 ; DOLE-OLIVIER, 1998). Enfin, les différences de perméabilité des sédiments, par exemple liées à la présence de couches géologiques imperméables, peuvent également être à l'origine de mouvements d'eau complexes (VANEK, 1997). Les travaux les plus récents indiquent que les micro-irrégularités du lit induisent de forts échanges dans les 20 premiers centimètres du lit, tandis que la pénétration d'eau dans les couches plus profondes serait induite par les irrégularités du lit à large échelle comme l'alternance des faciès d'écoulement (SAENGER, 2000 ; SAENGER et LENK, 2000).

3. DEPOT ET INFILTRATION DES SEDIMENTS FINS

La taille des particules incriminées dans les phénomènes de colmatage apparaît extrêmement variable selon les objectifs des études qui ont été menées (études sur le benthos : < 2 mm ; études sur les frayères de Salmonidés : < 0.8 mm ; études sur l'hyporhéos : < 0.063 mm). Ces particules participent toutes au colmatage mais ces divergences reflètent leur capacité différente à pénétrer le lit des cours d'eau. Au même titre que les sédiments inorganiques, la matière organique particulaire fine participe au colmatage avec toutefois des différences liées à leur faible densité et à leur dégradabilité par la faune (SCHÄLCHLI, 1993 ; BRUNKE, 1999).

3.1. Mécanismes de colmatage et de décolmatage

Le phénomène de colmatage peut être décomposé en plusieurs étapes qui constituent également différents degrés de colmatage du substrat. Les sédiments peuvent simplement se déposer dans les zones où la capacité de transport est réduite (berges, mouilles, annexes du cours d'eau), et/ou bien pénétrer en profondeur dans la zone hyporhéique. Des travaux expérimentaux, permettant de simuler un apport de sédiments fins important et localisé dans le temps ont permis d'identifier les paramètres influençant le dépôt des sédiments, leur profondeur de pénétration dans le lit et le degré de colmatage atteint (BESCHTA et JACKSON, 1979 ; SCHÄLCHLI, 1992 ; 1993). Le principal paramètre influençant les mécanismes de dépôt et de remise en suspension des fines est la contrainte de cisaillement adimensionnelle (θ) qui représente le rapport entre les forces responsables de l'entraînement des particules et celles responsables de leur stabilité (MILHOUS et BRADLEY, 1986 ; PETIT, 1989 ; MILHOUS, 1998) :

$$\theta = RS / [d50\ (G_s - 1)],$$

où R est le rayon hydraulique de la section de mesure (approximativement égal à la profondeur moyenne), S la pente de la ligne d'énergie, d50 est le diamètre médian des matériaux du lit ou de l'armure et G_s la densité des sédiments en place (kg/litre). SCHÄLCHLI (1992) montre que la phase de colmatage du lit se produit pour une contrainte $\theta < 0{,}056$. Jusqu'à cette valeur, l'augmentation de la contrainte provoque une obturation des interstices par les sédiments fins et une réduction de la conductivité hydraulique. Bien que cela ne soit pas démontré, SCHÄLCHLI suppose que la pénétration des fines serait causée par un accroissement de la turbulence liée à l'augmentation de la contrainte.

On considère que le décolmatage intervient au delà d'une contrainte adimensionnelle $\theta \cong 0{,}056$ (SCHÄLCHLI, 1992). Le phénomène se décompose en trois phases successives. 1) Une phase de nettoyage de la couche d'armure se produit lorsque la contrainte atteint une valeur comprise entre 0,056 et 0,072. Ce nettoyage provoque le départ des particules fines ce qui réduit l'enchâssement des particules les plus grosses qui seront alors mobilisables pour un seuil de contrainte plus bas. 2) La destruction de l'armure intervient lorsque la contrainte atteint la valeur 0,078. En raison du départ des sédiments fins, la conductivité hydraulique du lit atteint alors sa valeur maximale. 3) Le lit est ensuite mobilisé plus ou moins profondément en fonction de la taille des matériaux et de leur compaction, lorsque la contrainte dépasse la valeur 0,078.

Dans les cours d'eau, les valeurs critiques de la contrainte adimensionelle peuvent différer des valeurs présentées précédemment à cause de différences d'ordre géomorphologiques ou liées à l'arrangement des particules (KOMAR, 1987 ; PETIT, 1989). Par exemple, la position de saillie de grosses particules par rapport au niveau moyen du lit permet leur départ pour une contrainte plus faible. Au contraire l'imbrication du matériel augmente la contrainte critique pour les particules de petites dimensions. La forme et l'angle de repos des particules ont également une influence, par exemple le dépôt « en tuilage » et la forme aplatie des particules augmentent la contrainte critique nécessaire à la mobilisation de l'ensemble de l'armure. Parce que l'influence de ces facteurs peut être grande et qu'elle est difficilement quantifiable (voir PETIT, 1989), il en résulte une difficulté importante pour calculer avec précision le débit qui permettrait de décolmater le lit (MILHOUS, 1998).

3.2. Infiltration dans la zone hyporhéique

La profondeur de pénétration des particules est influencée par la taille des particules transportées (BESCHTA et JACKSON, 1979), l'homogénéité des particules qui constituent l'armure (BEYER et BANSCHER, 1975 dans BRUNKE 1999) et la taille des pores (FROSTICK *et al.,* 1984). Les auteurs considèrent que lors d'un apport ponctuel de sédiments fins, la profondeur maximale de pénétration varie entre 2,5 et 5 fois le d90 (diamètre non dépassé par 90% des particules) de l'armure, en fonction du diamètre des sédiments fins et des conditions d'écoulement. Dans des conditions expérimentales, BESCHTA et JACKSON (1979) puis SCHÄLCHLI (1992), ont montré qu'un apport de sédiments localisé dans le temps n'influence que les 10-15 premiers centimètres car le colmatage de cette zone forme une barrière qui se comporte comme un filtre et empêche la pénétration en profondeur des particules plus fines. Toutefois, compte tenu de la durée et de la répétition des apports de sédiments qui se produisent en milieu naturel, ceux-ci migrent probablement plus profondémment, ce qui conduit à leur stockage en profondeur (LEICHTFREID, 1988 ; SEAR, 1993 ; PANEK, 1994 ; BRUNKE, 1999). De plus, en milieu naturel, le phénomène de filtration ne limite pas la profondeur de pénétration des fines mais conduit à un gradient vertical de sédiments fins (JOBSON et CAREY, 1989), les plus grossiers (0,063-2 mm) étant plus abondants en surface et les plus fins (< 0,003 mm, 0,003-0,063 mm) en profondeur.

Le rôle des crues est important dans la dynamique des sédiments fins. Sur un cours d'eau de Nouvelle-Zélande, MATTHAEI *et al.* (1999) ont montré que les crues survenant 6 fois dans l'année affectaient le lit uniquement sur les 10-15 cm les plus superficiels, suggérant que l'action remaniante des crues est plus forte à la surface du lit qu'en profondeur. Les sédiments constituant l'hyporhéos pourraient n'être remaniés qu'à la faveur d'événements plus rares d'une fréquence proche de celle du débit de plein bord (2 ans ou plus en moyenne), ce qui favoriserait le phénomène de stockage des sédiments fins. De nombreux auteurs (LEOPOLD *et al.,* 1964 ; voir BRAVARD et PETIT, 1997) considèrent d'ailleurs que le débit de plein bord serait optimal pour le façonnement de la géomorphologie du cours d'eau.

Du point de vue spatial, compte tenu des échanges qui se produisent entre la surface et l'hyporhéos, les zones d'infiltration pourraient être plus sensibles au colmatage que les zones d'exfiltration et les zones où l'écoulement est laminaire (JOBSON et CAREY, 1989). En théorie, ces échanges verticaux ont une influence secondaire par rapport aux facteurs cités précédemment (concentration et taille des MES, taille des particules de l'armure…). Néanmoins, en reproduisant en canal expérimental un gradient hydraulique vertical suffisamment fort, SCHÄLCHLI (1992) montre que le colmatage ne se développe pas sur les zones d'exfiltration, contrairement à ce qui se passe dans les zones d'infiltration. De plus, une phase d'exfiltration à la suite d'une phase d'infiltration permet d'expulser les sédiments fins qui se sont accumulés pendant l'infiltration. Afin de tester cette hypothèse, BRUNKE (1999) a mesuré la répartition verticale des sédiments fins dans l'hyporhéos d'un cours d'eau suisse. En moyenne, les zones d'exfiltration présentent une concentration en sédiments fins (organiques et inorganiques) maximale à 0,50 m de profondeur tandis qu'elle est maximale à 1,50 m dans les zones d'infiltration et les zones à écoulement horizontal. Toutefois la forte variabilité spatiale des observations en milieu naturel ne permet pas d'affirmer de manière certaine le rôle du gradient hydraulique vertical dans la distribution des fines.

3.3. Influence de l'activité biologique sur le dépôt de sédiments fins

La faune aquatique peut influencer localement l'arrangement des sédiments lors d'activités comme la reproduction (KONDOLF *et al.,* 1993), les combats pour occuper l'espace ou les déplacements liés à la recherche de nourriture (STATZNER *et al.,* 1996 ; 1999). Lors de la reproduction, les Salmonidae nettoient les zones de ponte et expulsent environ 30-35% des sédiments < 1mm lors de la formation de la frayère (KONDOLF *et al.* 1993). Des organismes de plus petite taille tels que les larves de *Dinocras cephalotes* (plécoptère) réduisent localement la quantité de sédiments fins comblant les interstices de 30% (ZANETELL et PECKARSKY, 1996) à 75% (STATZNER *et al.,* 1996) lors de la recherche de proies. DANIELOPOL (1984) suggère que la digestion de la matière organique fine ou du biofilm bactérien par les invertébrés pourrait réduire les effets du colmatage dans la zone hyporhéique et maintenir élevée la conductivité hydraulique du milieu. Malgré l'absence d'études spécifiques aux milieux aquatiques (mais voir pour le milieu terrestre VAN VLIET *et al.,* 1993) il est aisé de concevoir le rôle dans le maintien de l'espace interstitiel que peuvent avoir les organismes fouisseurs tels que les oligochètes de la famille des Lumbricidae et des Lumbriculidae qui se déplacent en créant des galeries dans le lit. Loin d'être négligeable, cette activité d'ingestion a été évaluée à 12.6 kg de sédiments fins par gramme de biomasse et par an, chez les oligochètes de la famille des Tubificidae (BREKHOVSKIKH et VISHNEVSKAYA, 1994).

4. REPONSE DU PEUPLEMENT DE MACROINVERTEBRES

Les apports de sédiments fins influencent le peuplement de macroinvertébrés, soit de manière directe en exerçant un stress (réduction de la luminosité, action mécanique, éléments polluants éventuels) sur les organismes, soit par l'intermédiaire de la disponibilité des ressources trophiques, de l'oxygène et de l'habitat (Fig. 3). La réduction de la luminosité consécutive au transport par suspension (KIRK, 1985) peut diminuer la production primaire (GRAHAM 1989). En se mélangeant au périphyton (GRAHAM, 1990) et à la matière organique particulaire (SLOANE-RICHEY *et al.,* 1981), les sédiments fins réduisent l'attractivité et la qualité énergétique de ces ressources trophiques (RYDER, 1989). La modification et l'homogénéisation de l'habitat engendrée par le colmatage, *i.e.* la réduction des échanges hydriques, du volume interstitiel et de la taille des interstices, est également prépondérante dans les changements qui interviennent sur le peuplement. Ces changements sont graduels en fonction du degré de colmatage atteint localement, de son étendue spatiale et temporelle, ainsi que des caractéristiques hydrologiques du cours d'eau. Ces dernières contrôlent la capacité de transport solide du cours d'eau et donc sa capacité de retour vers la structure et la dynamique sédimentaire précédant l'apport de sédiments fins.

4.1. Conséquences du transport de fines et du colmatage sur le benthos

Modifications comportementales

L'augmentation du transport de sédiments par suspension et charriage intervenant soit lors d'une crue, soit lors d'un apport ponctuel artificiel (vidange, extraction de granulats) provoque généralement une augmentation de la mobilité des invertébrés par dérive (GAMMON, 1970 ; WHITE et GAMMON, 1977 ; O'HOP et WALLACE, 1983 ; CULP *et al.*, 1986 ; DOEG et MILLEDGE, 1991). La dérive peut être soit la conséquence de l'action mécanique directe des particules (LAPERRIERE, 1983) ou de la turbulence sur les organismes (BORCHARDT et STATZNER, 1990), soit un comportement en réponse à la réduction de la luminosité ou à l'apparition de conditions défavorables (RYDER, 1989). D'un point de vue quantitatif, ROSENBERG et WIENS (1978) ont montré expérimentalement qu'une exposition à une concentration de MES de 8 mg/l (ce qui constitue une augmentation limitée) pendant 2-3 heures induisait une augmentation immédiate de l'intensité de la dérive d'un facteur 3. La réponse des invertébrés n'est pas toujours si nette et pourrait également dépendre de leur rythme d'activité (CULP *et al.,* 1986), ce qui expliquerait l'absence de dérive diurne observée dans certaines études (*e.g.* CIBOROWSKI *et al.,* 1977).

On observe des différences de comportement parmi les invertébrés (principalement les éphéméroptères, plécoptères, trichoptères et coléoptères) qui ont fait l'objet d'expérience. Ainsi, certains plécoptères (*e.g. Peltoperles maria* dans O'HOP et WALLACE, 1983) et de nombreux éphéméroptères (*e.g. Seratella subvaria* dans CIBOROWSKI *et al.,* 1977 ; *Baetis* sp., *Austrophlebioides* sp. dans DOEG et MILLEDGE, 1991 ; *Paraleptophlebia* sp. dans CULP *et al.,* 1986 et ANGRADI, 1999) adoptent un comportement de dérive évident face à l'augmentation de la concentration en sédiments fins. Au contraire les coléoptères tels *Oulimnius* sp. (LENAT, 1984), *Stenelmis sp.* (WHITE et GAMMON, 1977) et des membres de la famille des Helodidae (coléoptères), semblent relativement indifférents à court terme aux fluctuations de la concentration en sédiments fins.

L' accroissement de la mobilité des invertébrés peut se traduire par une sensibilité accrue à la prédation. Par exemple, BRUSVEN et ROSE (1981) montrent que la prédation de *Seratella grandis*, *Heptagenia solitaria*, *Rhyacophila vaccua* et *Hesperoperla pacifica*, par le chabot (*Cottus rhotheus*) est significativement plus forte dans les substrats sableux et les substrats grossiers fortement ensablés.

Réduction de la croissance, de la fécondité et de la survie

Bien qu'aucune étude ne permette de quantifier la mortalité provoquée par l'action mécanique (abrasion) des sédiments fins, les auteurs considèrent généralement que celle-ci est faible et que les changements d'abondance résultent de la dérive. Par contre, la réduction de la qualité nutritionnelle des ressources trophiques (périphyton, matière organique particulaire) pourrait réduire la croissance des invertébrés ainsi que leur fécondité et leur survie (GRAHAM, 1989). Ainsi, RYDER (1989) montre que les larves de *Pycnocentrodes* sp. broutent préférentiellement le périphyton exempt de limon et que la croissance des jeunes stades de ce trichoptère est significativement réduite chez les individus nourris avec du périphyton mélangé avec des limons. La diminution de la concentration en oxygène dissous consécutive à la réduction des échanges entre la surface et le milieu interstitiel peut également influencer le développement et la survie de certains stades de développement (*e.g.* nymphes d'*Hydropsyche*, RUTHEFORD et MACKAY, 1986). Par ailleurs celle-ci affecte différemment les taxons et HARRISON et FARINA (1965) montrent qu'en présence de la même concentration de sédiments fins, les œufs de *Bulinus globulus* ne parviennent pas à maturité tandis que les œufs de *Lymnea natalensis* se développent normalement.

Modifications faunistiques du peuplement

Lorsque le recouvrement surfacique des éléments grossiers de l'armure par les fines varie entre 1/3 et 2/3, la réduction de l'habitat interstitiel disponible pour les invertébrés (LENAT *et al.*, 1981 ; WATERS, 1995) conduit généralement à la diminution de l'abondance des éphéméroptères, des plécoptères et des trichoptères (BJORNN *et al.*, 1977 ; LENAT *et al.*, 1979 ; LENAT *et al.*, 1981 ; RICHARDS *et al.*, 1993 ; ANGRADI, 1999), qui constituent la faune caractéristique des substrats grossiers (HYNES, 1970). Parallèlement, on observe une augmentation de l'abondance et de la biomasse de taxons à tendance fouisseuse tels que les oligochètes, les chironomidae et certains mollusques. Lorsque le recouvrement dépasse les 2/3 de la surface des éléments grossiers, LENAT *et al.* (1981) interprètent cette modification non plus comme une réduction de l'habitat mais comme un changement d'habitat, dans la mesure où la surface favorable à la faune pétricole n'est plus suffisante pour permettre son maintien. Les changements faunistiques évoqués précédemment sont alors amplifiés.

Ces changements faunistiques s'expliquent par des différences de préférence d'habitat entre espèces qui ont été testées expérimentalement (BRUSVEN et PRATHER, 1974 ; MCCLELLAND et BRUSVEN, 1980). Parmi les espèces d'EPT (Ephéméroptères, Plécoptères, Trichoptères) testées, les plécoptères et les trichoptères présentent une préférence très marquée vis-à-vis des substrats non ensablés lorsqu'ils sont soumis à un choix parmi des substrats caractérisés par des niveaux croissants d'ensablement (1/3, 1/2, 2/3), tandis que les éphéméroptères semblent moins sensibles à l'ensablement (notamment *Seratella grandis*, *Rhitrogena robusta*, *Baetis* sp. et *Caenis* sp.*)*.

Ces préférences d'habitat sont basées sur des comportements et des morphologies résultant probablement d'une évolution adaptative (HYNES, 1970). Par exemple, GAYRAUD et PHILIPPE (2001) montrent que les cours d'eau caractérisés par une faible disponibilité en habitat interstitiel, présentent une plus forte proportion d'invertébrés adaptés morphologiquement à pénétrer le substrat (petite taille, morphologie vermiforme) que les cours d'eau ayant une forte disponibilité en habitat interstitiel. De telles adaptations peuvent également être basées sur d'autres exigences écologiques telle que la recherche de ressources trophiques (HYNES, 1970), ou sur des exigences physiologiques telle que le besoin en oxygène (ERIKSEN, 1964).

Conséquences sur l'abondance, la biomasse, la productivité et la diversité du peuplement

A l'échelle de la station, le colmatage se traduit à court terme par une réduction de 10 % (*e.g.* CLAVEL *et al.*, 1977) à 95 % (*e.g.* WAGENER et LAPERRIERE, 1985) de l'abondance initiale (NEWCOMBE et MCDONALD, 1991). Sur le long terme, l'évolution dépend de l'hydrologie. Si les phénomènes d'érosion consécutifs à la re-mobilisation des sédiments fins sont rares, un peuplement stable, abondant et composé d'organismes adaptés aux sédiments fins se mettra en place. Au contraire, une fréquence élevée de mobilisation entraînera d'importantes perturbations de l'habitat qui se traduiront par une abondance très fluctuante des effectifs du même peuplement (LENAT *et al.*, 1981). En terme de biomasse, l'influence du colmatage est plus homogène et se traduit par une réduction plus ou moins marquée selon l'étendue spatiale et temporelle du colmatage (WATERS, 1984 ; WATERS, 1995).

La productivité de certaines espèces peut être réduite en réponse à la réduction de la qualité ou de la quantité des ressources trophiques ou bien en réponse à l'incapacité des invertébrés à utiliser ces ressources. Par exemple la réduction de la taille des interstices du substrat affecte l'abondance d'*Hydropsyche* sp. (GAMMON, 1970) et de *Polycentropus kingi* (NUTTALL, 1972) qui captent tous deux la matière organique dérivante à l'aide d'un filet de soie. MACKAY et WATERS (1986) ont trouvé une forte différence de production (34.9 g.m².an versus 5.8 g.m².an) d'Hy*dropsyche* sp. entre deux stations se distinguant par un degré de colmatage différent (la station en amont d'un barrage étant plus ensablée que la station en aval). RYAN (1991) suggère que l'évolution de la productivité globale du peuplement dépend de l'abondance des ressources énergétiques associées aux sédiments fins. Elle sera accrue si l'augmentation des sédiments fins est accompagnée d'une augmentation de la matière organique particulaire comme cela se produit dans les cas d'érosion des terrains agricoles (LENAT, 1984) ou de déforestation.

Le changement d'habitat résultant d'un apport important de sédiments fins se traduit, à l'échelle de la station, par une réduction de la diversité de la mosaïque constituée par les micro-habitats. La disparition des espèces sensibles adaptées aux substrats grossiers consécutive à ce changement, n'est pas compensée par l'apparition de nouvelles espèces adaptées aux sédiments fins (qui étaient déjà présente en petite proportion) ce qui se traduit globalement par une réduction de la richesse taxonomique (WATERS, 1995 ; *e.g.* NUTTALL, 1972).

4.2. Influence de l'infiltration des sédiments fins sur l'hyporhéos

Il existe à l'heure actuelle peu d'études (*e.g.* BOU, 1977 ; RICHARDS et BACON, 1994 ; BOULTON *et al.,* 1997) permettant de cerner les effets du colmatage de la zone hyporhéique sur sa faune. La zone hyporhéique constitue pourtant un compartiment essentiel dans le fonctionnement des systèmes aquatiques en raison de la diversité et de l'abondance de sa faune ainsi que de son rôle dans la dynamique du système (BRUNKE et GONSER, 1997 ; WARD *et al.*, 1998). De nombreux invertébrés benthiques (*Seratella* sp., *Caenis* sp. *Leuctra major*, *Esolus parralelepipedus*, Ceratopogoninae, Chironomidae, Hydracariens) peuvent y être rencontrés jusqu'à plus de 30 cm de profondeur. De nombreux auteurs (*e.g.* WILLIAMS et HYNES, 1974 ; POOLE et STEWART, 1976 ; GODBOUT et HYNES, 1982 ; WILLIAMS, 1984) estiment que seulement 20-40 % du benthos (en terme d'abondance) est situé dans les 5 premiers centimètres du lit.

L'impact sur la faune hyporhéique se produit également par le biais de la réduction de l'habitat et des ressources trophiques, ainsi que par la réduction du degré d'oxygénation. Plusieurs auteurs (MARIDET *et al.,* 1992 ; RICHARDS et BACON, 1994 ; MARIDET *et al.,* 1996) ont constaté à l'échelle du micro-habitat, la réduction de l'abondance et du nombre de taxons en relation avec la réduction de la porosité ou l'augmentation de la proportion de sédiments fins. Parmi la faune hyporhéique, ce sont principalement les organismes benthiques qui sont affectés par le colmatage tandis que de nombreux taxons strictement hypogés semblent se satisfaire de concentrations en oxygène plus réduites (BOULTON *et al.,* 1997 ; MALARD et HERVANT, 1999). Compte tenu de l'importance de la zone hyporhéique dans le fonctionnement du système (*e.g.* potentiel de recolonisation), son colmatage pourrait donc avoir des conséquences importantes sur la dynamique des invertébrés ainsi que sur les niveaux trophiques supérieurs.

5. CONCLUSIONS ET PERSPECTIVES

Si les mécanismes de colmatage sont bien compris en situation expérimentale, il existe à l'heure actuelle peu de mesures de terrain permettant d'évaluer en quoi ces mécanismes diffèrent dans les systèmes naturels qui sont souvent bien plus complexes. De nombreuses questions se posent sur la dynamique spatiale et temporelle des sédiments fins en relation avec la géomorphologie et l'hydrologie, ainsi que sur les problèmes d'évolution du système et de réversibilité des effets lorsque les apports de sédiments fins sont accrus de manière importante. L'influence des sédiments fins sur l'hyporhéos a été peu étudiée, de sorte que l'on connaît mal leurs conséquences à long terme sur cet habitat. Au contraire, l'impact des sédiments fins sur le benthos a été évalué à de nombreuses reprises, en différentes situations (expérimentales et études de terrain) et pour différents scénarii (pollution par les mines, la déforestation, les carrières, l'extraction de matériaux, les vidanges de barrage). Ces études ont permis une compréhension globale des mécanismes sur lesquels agissent l'apport de sédiment fins. Toutefois, compte tenu de la complexité de la réponse du peuplement d'invertébrés et de la diversité des situations étudiées, il reste difficile d'identifier les mécanismes prépondérants qui conduisent aux changements faunistiques que nous avons présentés. Une piste intéressante qui permettrait d'intégrer cette complexité réside dans l'utilisation de traits biologiques décrivant les caractéristiques morphologiques (*e.g.* taille maximale, forme du corps), physiologiques (*e.g.* durée de vie, modalités de reproduction, organes de résistance) et comportementales (*e.g.* relations au substrat, préférences trophiques) des invertébrés (STATZNER *et al*., 1994 ; DOLEDEC *et al*., 1999 ; STAZNER *et al.,* 2001). Les traits du peuplement qui seront modifiés dans les situations de colmatage permettront d'identifier les principaux mécanismes responsables des changements faunistiques.

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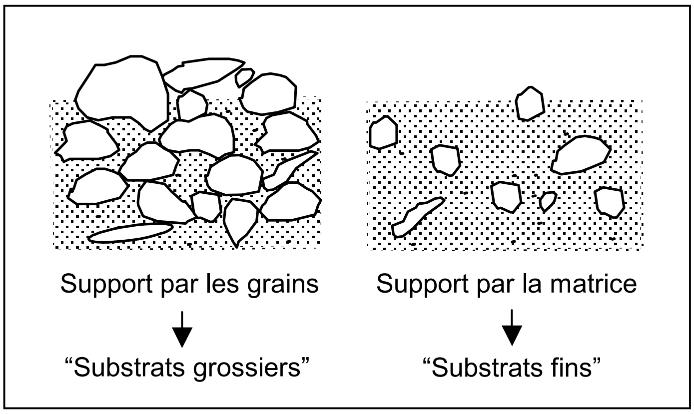

Figure 1 : Deux modes d'arrangement extrêmes des particules au sein du lit sur lesquels est basée la distinction entre substrats fins et substrats grossiers.

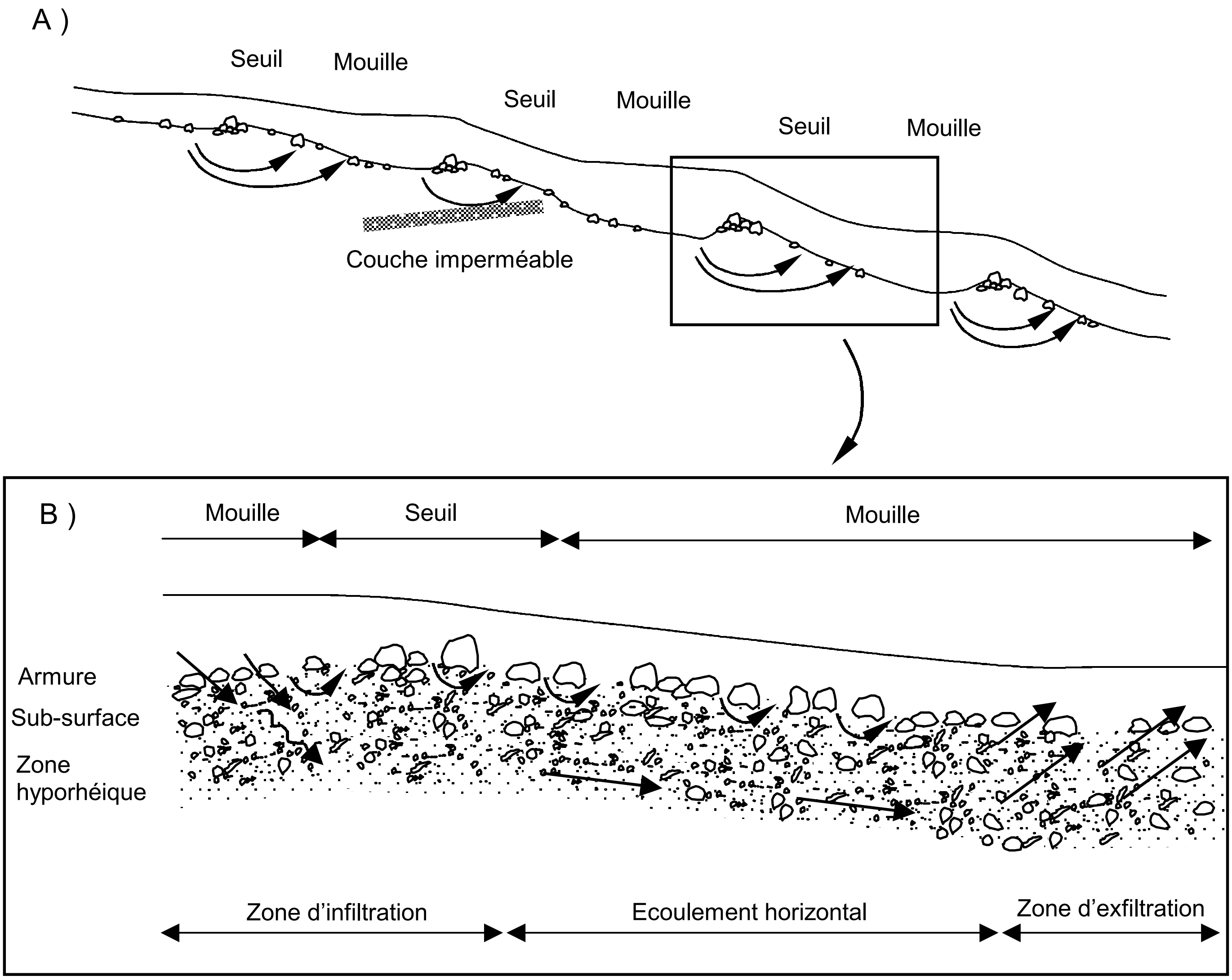

Figure 2 : Mouvements d'eau à plusieurs échelles entre la surface et la zone hyporhéique. A) Echanges hydriques induits par les discontinuités géomorphologiques et géologiques. B) Détail des mouvements hydriques au sein d'une séquence seuil-mouille-seuil.

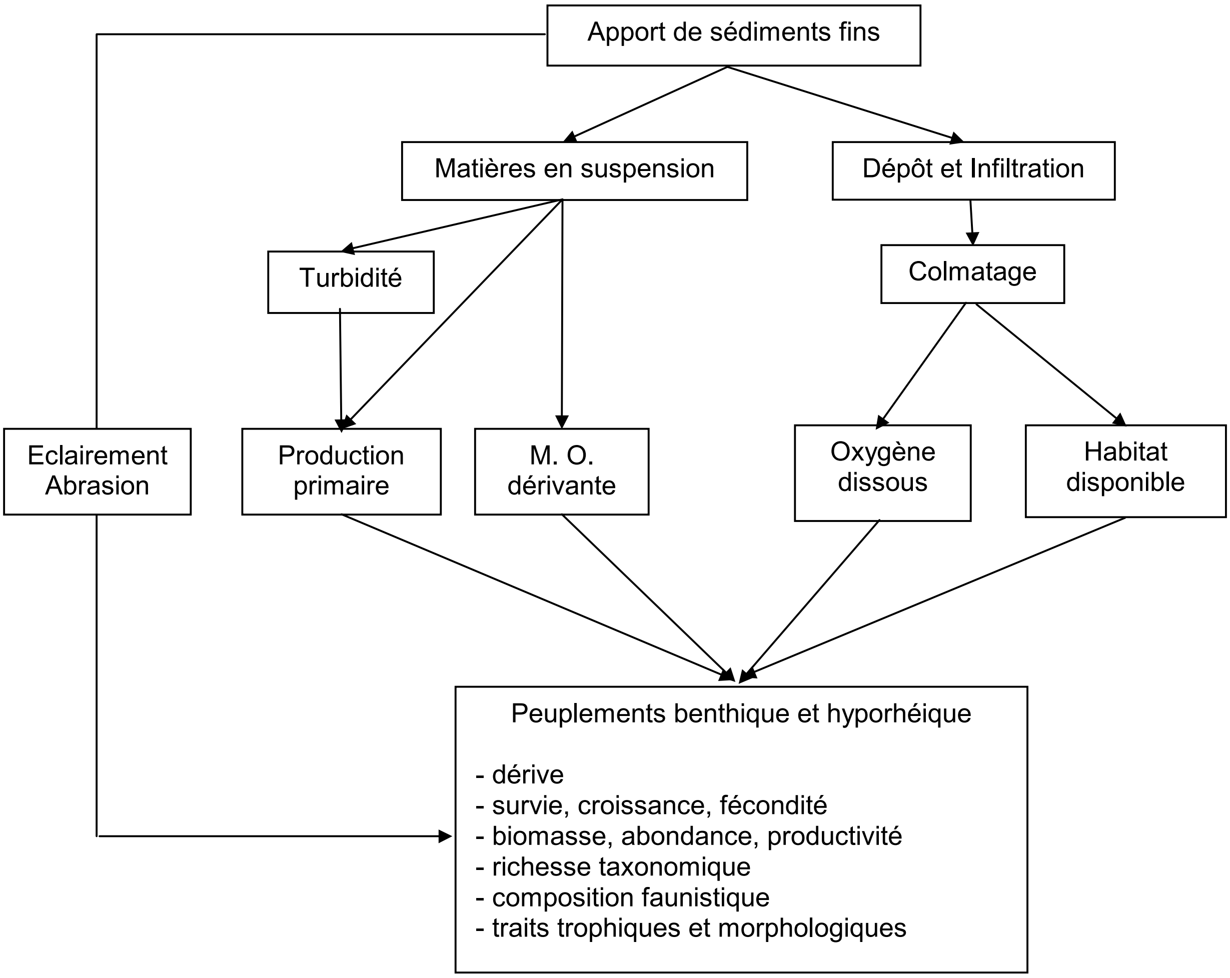

Figure 3 : Schéma récapitulant l'influence des apports de sédiments fins sur le peuplement d'invertébrés et sur son habitat.

A 6

HOW MICROHABITAT PREFERENCES SHAPE INVERTEBRATE COMMUNITY TRAITS IN MULTIPLE STREAM REACHES

(Gayraud S., N. Lamouroux. & S. Dolédec, en préparation)

How microhabitat preferences shape invertebrate community traits in multiple stream reaches

Gayraud S., Lamouroux N., Dolédec S.

Introduction

Habitat template theories relate species traits at the community level to habitat characteristics (Southwood, 1977; Poff and Ward, 1990; Townsend and Hildrew, 1994), suggesting that the spatial and temporal features of the habitat are the major determinants of species-traits observed. Nevertheless, observed correlations between the physical habitat (e.g., water depth and flow variability) and aquatic species traits in regional contexts (e.g., Persat et al., 1994; Resh et al., 1994; Poff and Allan, 1995) were generally not as explicit as what is actually expected from habitat templet theories. Several explanations of this poor explanatory power have been proposed. Among them, the effects of a habitat template on freshwater communities may be constrained by hierarchical environmental filters prevailing at the valley, the basin, or larger scales (Poff, 1997). In addition, species may adapt to their environment by various alternative strategies (Resh et al., 1994). Finally, the spatial and temporal variability of the environment may be perceived differently depending on the variables (and their scaling) used to describe it. As a consequence, using habitat template theories as general predictive tools of community characteristics initially requires precise definition of the major axes of the habitat template.

An attractive mean for identifying the key habitat variables affecting community structure is to analyse habitat preferences within-sites (between microhabitats), and test if they explain between-site differences in community structure. Indeed, the key habitat variables governing the choice of a local habitat by groups of individuals are good candidate for explaining community response to their habitat. At the local scale (generally 0.1 m² or so), analyses of relationships between invertebrate assemblages and their habitat have demonstrated that, within stream reaches, assemblages are influenced by habitat variables such as water depth, velocity, interstitial habitat or combinations of these variables (Gore and Judy, 1981; Statzner et al., 1988; Rempel et al., 2000; Doisy and Rabeni, 2001). At the site scale (generally stream reaches including several pool-riffle sequences), between-site variations in community structure have been associated with position along the longitudinal gradient or differences in average environmental characteristics due to hydraulic, thermic or geomorphic filters (Robertson et al., 1997; Danehy et al., 1999).

It is still unclear how within- and between-sites relationships observed between invertebrates and their habitat are related, and which functions/traits of invertebrate communities are affected by habitat variables. Do microhabitat preferences result in community structure variations between sites (see Lamouroux et al., 1999, for an example with fish), or are other environmental filters (trophic patterns, temperature, zoogegraphy) stronger than microhabitat preferences in structuring invertebrate communities ?

In this paper, we analysed invertebrate microhabitat preferences (for hydraulics and substrate size) within 9 sites at the biological trait level, and tested if these habitat preferences could explain invertebrate trait variations between sites (Fig. 1). For this purpose, we used invertebrate and hydraulics data collected in 9 sites (stream reaches) X 10 microhabitat samples. We tested 1) the influence of microhabitat environmental characteristics on invertebrate traits within sites, 2) the influence of site environmental characteristics at a similar discharge level (the median daily discharge Q50) on invertebrate community traits between sites, and 3) if between site variations in community traits corresponded to those suggested by microhabitat preference analyses. Then, we discuss the power of our results for defining quantitative axes for the physical habitat template of invertebrate communities.

Methods

Study sites

To fulfil our objective, we used data previously collected in 9 3rd order stream reaches located on the Rhône river basin (France). A detailed description of the study sites is available in Gayraud et al. (in prep.). Sites were located at a distance < 30 km from stream sources at an elevation < 650 m above sea level, and were exempt from pollution (Anonymous, 1996). Despite some differences in the main geology covering the catchment area (limestone rock or mixed-rocks), the water chemical composition of sites was similar, with high pH (7.8 - 8.6), and high specific conductance (280 - 525 µS.cm-2). Stream reaches were comparable with respect to reach slope, and to substrate particle-size, but they differ by their width and discharge characteristics (Table 1), and by lateral wandering.

The median daily discharge Q50 was computed from daily discharge data measured between 1990 and 1999 at fixed gauging stations close to our sites. Seven of our study sites were located at a distance < 10 km upstream a gauging station managed by the French Ministry of the Environment. Daily discharge in these sites was estimated from the monitored discharge after corrections by the ratio of catchment areas at the gauging station and at the study site. For the two streams that were not continuously gauged, daily discharge values were estimated from the correlation between the discharge measured in the study site and the discharge monitored at the gauging station located on the nearest catchment. To check the accuracy of the discharge estimates in these two sites, we compared them to discharge measured over the period of the study ($n = 10$, $r^2 > 0.68$).

Microhabitat sampling

At each of the 9 study sites X 10 randomly chosen microhabitats, we sampled invertebrates at the beginning spring 1998 or spring 1999, with a Surber net (0.03 m^2, mesh size 0.025 mm). Samples at a given site were collected simultaneously and preserved in 4% formalin. We generally disturbed the sediments 5 cm deep below the bottom of the armour layer, to collect the invertebrates inhabiting interstitial spaces of the stream bottom. In the laboratory, invertebrates were identified up to family (Oligochaeta, most of Diptera, Sericostomatidae), to sub-family (Chironomidae, Ceratopogonidae, Limnephilidae) or genus level (Ephemeroptera, Plecoptera, Coleoptera, Heteroptera, most of Trichoptera). Animals that were not identifiable because of their small size (young stages) were allocated according to their proportion of identified individuals.

We used the invertebrate trait databases used in Usseglio et al. (2000) and available in Tachet et al. (2000) to describe invertebrate assemblages in microhabitats by their biological traits, using the methods described by Statzner et al. (2001). The functional composition of invertebrate assemblages were described by 69 categories of 13 biological traits related to, e.g., feeding modes, reproduction characteristics and morphology (see Table 2 for a complete list). Briefly (see Statzner et al., 2001), the invertebrate database indicated an affinity associated with each taxon X trait category. To calculate a trait category value for a microhabitat assemblage, we multiplied the ln (x+1) transformed abundance of each taxa by the taxa affinity for the trait category and summed these values. Trait category values were rescaled to sum to 1 for each trait. Therefore, a trait category value is a score that increased from 0 to 1 with the percentage of individuals showing a high affinity for this category.

At each microhabitat, we described hydraulic and roughness conditions using the Froude number FR, the Reynolds number RE, the dominant roughness size DS, and the size of particle embedding largest ones FS. FR and RE are dimensionless combinations of the water column velocity V and the water depth H (each calculated as the mean of measurements made at the four corners of the surber). FR was calculated as $FR = V/(g.H)^{0.5}$, where g is the acceleration due to gravity. RE was calculated as $RE = V.H / \nu$, where ν is the kinematic viscosity of water, considered throughout as equal to 10^{-6} m^2s^{-1}. These dimensionless variables are widely used in stream hydraulics (Yalin, 1992), as they are efficient to compare energetic proporties shared by streams of different size. They have been identified as key habitat factors, at both the microhabitat and the stream reach scales, that influence invertebrate and fish assemblages (Statzner et al., 1988; Quinn and Hickey, 1994; Lamouroux et al., 1999; Doisy and Rabeni, 2001). The Froude number discriminates well riffle-type from pool-type habitats, whereas the Reynolds number increases from bank to midstream habitats with the level of turbulence (Jowett, 1993; Lamouroux et al., 1999). DS and FS were measured by comparing them to a series of squared holes of increasing size made in a PVC plate (Scarsbrook and Townsend, 1993). DS varies between 5 and 192 mm and FS between 0.05 and 24 mm. They were $\log_2$-transformed to reduce their variability and to normalise their distribution.

Analysing microhabitat preferences within sites

We used analysis of covariance (ANCOVA) to reflect how each of our four habitat variables (noted HAB) influenced each of our trait variable (noted TRAIT) across microhabitats within sites. Our ANCOVA model was:

$$TRAIT = C(\text{site}) + Sw * HAB \qquad (1)$$

In this model, C is a constant value (intercept) that depends on the site. It can account for differences in TRAIT between sites, that are not necessarily associated with microhabitat preferences (they can be due to, e.g., temperature or water quality). Sw is a slope parameter which reflects how HAB influences TRAIT within sites. This slope reflects microhabitat preference, because differences in traits between the microhabitats within-sites can confidently be interpreted relative to hydraulics (temperature or water quality conditions are relatively homogeneous in a given site on a given date). We calculated the within-site correlation between HAB and TRAIT to estimate the effect of habitat variables on traits within-sites.

Analysing between-sites relationships between habitat and invertebrate traits.
We analysed relationships between habitat and invertebrate traits at the site level using linear regression. Trait variables were averaged by site to describe invertebrate community characteristics at the site level. The environmental conditions at the site level were described for a similar discharge level: the median daily discharge Q50. Hydraulic conditions were described by the site Froude number and Reynolds number at Q50 (S-FR and S-RE). These variables represent the median value, over time, of the mean hydraulic conditions at the site level. S-FR was estimated by $\text{S-FR} = \text{Q50} / [g^{0.5} . \text{H50}^{1.5} .\text{W50}]$, and S-RE was estimated by $\text{S-RE} = \text{Q50} / [\nu .\text{W50}]$, where H50 and W50 are the reach-average water depth and width at Q50. g is the acceleration due to gravity, and v is the kinematic viscosity of water (considered throughout as equal to 10^{-6} m²s^{-1}). H50 and W50 were estimated using hydraulic geometry relationships (width- and depth-discharge relationships) fitted to standard power functions (e.g. depth = a . discharge ^{b}; see Leopold et al., 1964; Knighton, 1998, p. 171) from 100 depth and 20 width measurements made at two contrasting discharge values in each site (Lamouroux et al., 1999). Hydraulic geometry relationships fit very well to power functions (Leopold et al., 1964), enabling precise estimates of H50 and W50. Substrate dominant size embedding substrate size at the site level (S-DS and S-FS) were measured by averaging the local measurements made on surbers at each site.

Are between-sites relationships explained by microhabitat preferences ?
To test if average habitat conditions of the sites (S-FR, S-RE, S-DS, S-FS) influenced invertebrate traits as suggested by our microhabitat preference analyses, we compared the statistics (significance, correlation) of the between-site regressions with those associated, within-sites, with preferences for microhabitat conditions (FR, RE, DS, FS). Significant relationships of similar sign at both scales indicated that between-site functional variations were consistent with microhabitat preferences.

Results

We identified 98 macroinvertebrate taxa from the 90 samples. The most common taxa were Orthocladiinae (35.14 %), Tanytarsini (7.08 %), Limoniidae (6.83 %), *Psychomyia pusilla* (5.95 %), Naidiae (5.67 %), *Esolus sp.* (3.80 %), *Leuctra sp.* (3.79 %), and *Gammarus sp.* (2.94 %). Thirty-one taxa accounted for 95 % of the overall abundance of the 90 samples.

Analysing microhabitat preferences within sites

Invertebrate had significant habitat preferences for all habitat variables except the dominant substrate size DS. Only categories describing body form and the number of reproductive cycles were not influenced by habitat variables. Other trait categories of local invertebrate assemblages were significantly influenced, within sites, by local habitat variables (FR, RE, DS and FS influenced respectively 17, 22, 0 and 15 of the 69 trait categories, see Table 2). RE and FR were the major variables reflecting habitat preferences. For example, slow/shallow habitats (low RE values) were preferred by invertebrates > 2 cm, subject to passive drift, feeding on fine sediments, absorbers and deposit feeders, and/or swimmers. Riffle-type habitats (high FR values) were preferred by flexible invertebrates, forming statoblasts/gemmules, temporarily attached, feeding on living microphytes, scrapers and/or filter-feeders. Habitats embedded with finest sediment (low FS values) were preferred by inflexible invertebrates, burrowers, feeding on fine sediments, absorber, deposit feeders and/or shredders. In contrast, habitat embedded with largest sediment were preferred by flexible invertebrates, temporarily attached, feeding on living microphytes, scrapers and/or filter-feeders.

Analysing between-sites relationships between habitat and invertebrate traits.

The low number of sites implied that only correlations between habitat and traits above 0.67 were statistically significant. However, habitat characteristics except S-DS also influenced invertebrate traits between-sites (S-FR, S-RE, S-DS, S-FS influenced respectively 12, 7, and 0 of the 15 trait categories, see Table 2). For example, slow/shallow sites (low S-RE values) were characterized by invertebrates with passive drift and/or burrowing. Sites dominated by riffles (high S-FR values) were characterized by invertebrates forming statoblasts/gemmules, with free-isolated eggs, filter-feeders, avoiding feeding on dead animals. Sites dominated by habitats embedded by fine sediment (low S-FS values) were characterized by flexible invertebrates, with flattened body shape, feeding on fine sediment.

Are between-sites relationships explained by microhabitat preferences ?

About half of the significant relationships observed at the site scale were expected from the habitat preference analysis: among the 34 significant relationships observed between-sites, (12 + 7 + 15 with S-FR + S-RE + S-FS), 15 were associated with a significant habitat preference with the corresponding local habitat variable (Table 2). Among these 15 cases, only one revealed an inverse effect of the habitat variable at the two scales (relationship between the proportion of highly flexible invertebrates and finest sediment size).

When considering all tests (significant and non-significant ones), R values associated with the effect of S-FR, S-RE, S-FS between-sites were strongly related to R values associated with the effect of the corresponding local variables (FR, RE, FS) within-sites (especially for the hydraulic variables, see Fig. 2). Therefore, the more a trait variable responded to a local habitat variable (except DS), the more it varied, between-site, with the corresponding site habitat variable (example on Fig. 3). Focusing only on the trait categories that had habitat preferences (54 cases in Table 2), the between-site corresponding correlation was of a similar sign in 50/54 cases. Therefore, habitat preferences were largely confirmed by trends observed at the site scale, even when these trends were not statistically significant.

Discussion

Our results demonstrate 1) that many invertebrate traits are related to the local environment (hydraulics and substrate) at the microhabitat scale, 2) that these microhabitat preferences partly explain the functional variability of invertebrate community across sites, and 3) that other variation in invertebrate community traits, not expected from microhabitat preferences, are related to hydraulics or substrate characteristics across sites.

That many trait categories were significantly related to hydraulic and substrate variables at the microhabitat scale, with generally low within-site variability explained (R between 0.22 and 0.44), reflects the complexity of habitat preferences and the multiplicity of alternative adaptative strategies used by invertebrates. The low variability explained is also due to the fact that, at the surber scale, invertebrates assemblages are partly unsteady and/or random. At this scale, only trends can be observed. Nevertheless, local-scale relationships between traits and hydraulics were generally interpretable and matched previous observations (essentially for trophic traits, Quinn and Hickey, 1994; Doisy and Rabeni, 2001). Invertebrates living near the banks rather than in the centre channel (low RE) were generally < 2 cm (avoiding turbulent lift), and were those subject to passive drift. They could be swimmers (no drift risk) and feeded on fine sediments, deposits or by predation, behaviors hardly achievable in highly turbulent conditions associated with high RE. Invertebrates living in riffle-type, stressful conditions (high FR) benefit from being temporarily attached, and can easily feed on living microphytes by scraping and/or filtering. Invertebrates with inflexible body preferred habitats embedded by fines, where they can easily move to find food. In contrast, habitats embedded by coarse sediment selected invertebrates with flexible body to move within the large stable interstices.

The links between habitat preferences and habitat-trait relationships between sites (Fig. 3) demonstrate that between–sites variation in community traits could be partly explained by the above-mentioned habitat preferences. However, some traits were related to hydraulics or substrate size between sites though these relationships were not suggested by our habitat preference analysis. These links can be due to habitat requirements prevailing at larger scales that the microhabitat scale, or to environmental filters that are correlated with our habitat variables among sites (e.g., the frequency of bed disturbance is generally higher in sites with high Froude numbers than in others, influencing drift and recolonization). For example, high Froude numbers were negatively associated with the trait 'feeding on dead animals', possibly because high drift levels associated with high FR provide more food than available in depositing habitats.

Overall, our results suggest that at-a-site invertebrate functional composition is both influenced by microhabitat conditions and environmental filters prevailing at larger scales. In this context, the fact that habitat preferences partly explain functional variation in invertebrate communities is important. At the local scale, it is generally easier to identify which local habitat variables are responsible for habitat preferences. In our study, FR and RE had more important effects than substrate characteristics on invertebrate assemblages (at least those near the bed; see Gayraud et al., in prep.), and treir role was generally confirmed at the site scale. More generally, relating processes observed at different scales in multiple sites is an efficient way for separating the respective influence of various environmental characteristics on community structure (Peckarscky et al., 1997). It is an important step towards identifying the main axes of the habitat template of stream communities.

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Table 1. Environmental characteristics of the 9 sites studied. Q50 is the median daily discharge computed over 10 years (1990-1999). W50 and L50 are the wetted width and water depth at Q50. D50 is the median substrate size.

Reaches	Basin area (km-2)	Reach slope (m.km-1)	Q50 (m3.s-1)	W50 (m)	L50 (m)	D50 (cm)
Bez	270	9.81	2.92	10.0	0.44	4.1
Drôme	260	9.80	1.2	9.8	0.22	2.7
Eygues	147	8.69	0.86	9.5	0.24	5.6
Galaure	60	8.59	0.70	9.1	0.26	3.6
Gère	69	8.10	0.11	6.1	0.11	4.2
Herbasse	168	8.63	0.73	8.7	0.31	3.6
Ouvèze	111	10.13	0.51	9.9	0.17	4.3
Sanne	52	8.04	0.04	4.0	0.07	3.9
Varèze	63	8.16	0.09	5.1	0.17	4.1

Table 2. Effects of habitat variables on invertebrate trait categories within sites (between samples) and between sites. Within-sites effects (i.e., microhabitat preferences) are analysed by covariance analysis on 90 samples. Between sites effects are analysed by regression on 9 sites. We provide the correlation (within-site or between-site) associated with the effect of each habitat variable. Significant correlations (P<0.05) are bolded. The proportion of individuals in each trait category (prop., after Ln-transformation of abundances) is also given.

Trait/category	Prop	Within-site correlation				Between-site correlation			
			with				with		
		FR	RE	DS	FS	S-FR	S-RE	S-DS	S-FS
Maximal size									
≤.25 cm	0.01	0.13	-0.02	-0.02	0.00	-0.22	-0.34	0.05	-0.32
>.25-.5 cm	0.17	-0.05	0.11	0.06	-0.08	-0.35	-0.66	-0.15	-0.29
>.5-1 cm	0.40	0.21	**0.41**	-0.07	**0.28**	0.58	0.66	0.36	**0.74**
>1-2 cm	0.27	-0.09	-0.19	-0.01	-0.05	0.55	0.39	0.13	-0.24
> 2-4 cm	0.10	-0.20	**-0.31**	0.04	-0.12	-0.65	-0.64	-0.51	-0.58
>4-8 cm	0.04	-0.04	**-0.24**	0.06	-0.19	**-0.70**	-0.58	-0.28	-0.61
>8 cm	0.01	0.02	**-0.26**	0.01	-0.21	**-0.71**	-0.41	-0.15	-0.44
Body flexibility									
none (<10°)	0.05	-0.10	-0.07	0.11	**-0.35**	-0.55	-0.26	-0.38	-0.61
low (>10-45°)	0.55	**-0.36**	0.09	-0.15	-0.16	0.33	0.33	0.05	**0.85**
high (>45°)	0.40	**0.39**	-0.07	0.11	**0.28**	-0.24	-0.32	0.04	**-0.82**
Body form									
streamlined	0.09	0.13	0.06	0.07	0.07	0.21	0.46	0.04	-0.67
flattened	0.14	0.02	-0.10	0.10	-0.17	0.06	0.41	-0.13	**-0.69**
cylindrical	0.73	-0.03	0.06	-0.17	0.07	0.06	-0.26	0.03	**0.79**
spherical	0.04	-0.10	-0.04	0.19	0.07	-0.57	-0.47	0.10	-0.61
Life cycle duration									
≤ 1 year	0.76	0.04	0.14	-0.01	**0.22**	0.60	0.35	0.20	**0.78**
>1 year	0.24	-0.04	-0.14	0.01	**-0.22**	-0.60	-0.35	-0.20	**-0.78**
Potential number of reproductive cycles									
<1	0.05	-0.03	0.13	-0.10	-0.10	-0.16	0.21	0.00	-0.41
1	0.53	-0.03	0.12	0.08	-0.08	0.30	0.48	0.33	-0.63
>1	0.42	0.03	-0.14	-0.04	0.10	-0.21	-0.44	-0.27	0.62
Aquatic stages									
egg	0.32	0.22	0.21	0.07	0.10	0.12	0.49	-0.07	-0.66
larva	0.40	-0.07	0.14	-0.11	-0.12	0.52	0.65	0.32	0.04
nymph	0.20	-0.04	-0.03	-0.03	0.12	0.20	-0.18	0.12	**0.75**
imago	0.08	-0.13	**-0.27**	0.04	**-0.26**	**-0.75**	-0.52	-0.28	-0.63
Reproduction									
Ovoviviparity	0.05	**-0.41**	**-0.43**	-0.03	-0.20	**-0.76**	-0.63	-0.55	-0.25
Isolated eggs, free	0.08	0.03	0.03	0.00	-0.10	**0.69**	**0.69**	-0.09	-0.49
Isolated eggs, cemented	0.15	0.07	**0.28**	-0.11	0.02	0.20	**0.72**	0.09	-0.12
Clutches, cemented or fixed	0.43	0.18	-0.05	0.17	0.17	-0.38	-0.62	-0.08	-0.65
Clutches, free	0.14	**-0.38**	**-0.28**	-0.09	-0.08	-0.19	-0.53	0.19	0.57
Clutches in vegetation (endophytic)	0.01	0.05	**0.44**	-0.03	-0.12	0.48	**0.89**	0.30	0.03
Clutches, terrestrial	0.10	0.16	0.16	0.00	0.08	0.33	0.02	0.05	0.65

Asexual reproduction	0.04	-0.03	-0.22	-0.03	-0.19	-0.65	-0.43	-0.12	-0.30
Dissemination									
Aquatic passive	0.36	-0.12	**-0.35**	-0.03	-0.11	-0.66	**-0.80**	-0.55	-0.25
Aquatic active	0.22	0.12	**0.33**	0.05	0.11	-0.06	0.58	0.18	0.04
Aerial passive	0.15	0.01	-0.03	0.00	0.09	0.16	-0.25	0.17	0.64
Aerial active	0.26	-0.01	0.09	-0.02	-0.12	0.23	0.31	-0.02	-0.62
Resistance form									
Eggs, statoblasts, gemmules	0.15	**0.32**	**0.27**	0.03	0.01	**0.68**	**0.84**	0.11	-0.22
Cocoons	0.05	-0.02	**-0.26**	-0.08	-0.17	**-0.67**	-0.46	-0.17	-0.31
Cells against desiccation	0.00	-0.20	-0.07	0.00	0.00	-0.64	-0.29	-0.05	0.08
Diapause or dormancy	0.09	-0.07	0.01	0.01	0.00	-0.17	-0.12	-0.37	-0.37
None	0.71	-0.18	-0.09	0.00	0.08	-0.36	-0.64	0.07	0.47
Respiration									
Tegument	0.50	-0.05	0.00	-0.08	0.16	-0.08	-0.17	0.35	**0.82**
Gill	0.39	-0.04	-0.15	0.01	-0.09	0.32	0.40	-0.42	-0.46
Plastron	0.07	-0.04	0.02	0.05	-0.12	-0.41	-0.28	0.07	**-0.84**
Spiracle (aerial)	0.05	0.18	0.19	0.07	0.01	-0.09	-0.20	-0.11	-0.40
Locomotion and relation to substrate									
Flier	0.02	-0.05	0.01	0.08	-0.20	-0.33	-0.22	0.04	**-0.86**
Surface swimmer	0.01	-0.07	0.15	0.10	-0.13	-0.62	-0.58	-0.02	-0.42
Swimmer	0.13	**-0.23**	**-0.43**	-0.04	-0.12	-0.22	-0.35	0.06	**0.67**
Crawler	0.49	0.06	0.08	0.03	-0.08	0.30	0.63	0.06	-0.50
Burrower (epibenthic)	0.12	**-0.39**	-0.07	-0.18	**-0.25**	**-0.69**	**-0.74**	-0.44	-0.01
Interstitial (endobenthic)	0.13	0.12	0.11	-0.10	0.03	-0.15	-0.32	0.01	**0.70**
Temporarily attached	0.11	**0.30**	0.12	0.11	**0.35**	0.38	0.00	0.17	0.28
Permanently attached	0.00	-0.21	-0.03	-0.03	0.06	-0.30	-0.04	-0.06	-0.01
Food									
Fine sediment + microrganisms	0.02	**-0.32**	**-0.42**	-0.05	**-0.28**	-0.44	-0.61	-0.42	**-0.82**
Detritus < 1 mm	0.22	0.21	-0.05	0.04	0.07	0.13	-0.51	-0.10	0.11
Plant detritus ≥ 1 mm	0.12	**-0.34**	-0.12	-0.04	-0.03	-0.41	0.01	-0.39	-0.57
Living microphytes	0.32	**0.43**	**0.31**	0.12	**0.25**	0.56	0.51	0.43	0.39
Living macrophytes	0.10	0.01	**0.27**	-0.03	-0.21	0.26	**0.82**	0.11	0.22
Dead animal > 1 mm	0.03	-0.18	-0.10	0.02	-0.06	**-0.70**	-0.52	-0.41	-0.31
Living microinvertebrates	0.09	-0.09	-0.04	-0.02	0.05	0.20	-0.30	-0.10	0.53
Living macroinvertebrates	0.09	**-0.23**	**-0.27**	-0.10	-0.11	-0.44	-0.57	0.16	-0.14
Vertebrates	0.00	-0.20	-0.10	-0.08	0.00	-0.45	-0.13	-0.19	0.00
Feeding habits									
Absorber	0.01	-0.01	**-0.28**	-0.05	**-0.24**	**-0.79**	-0.57	-0.26	-0.56
Deposit feeder	0.20	**-0.26**	**-0.34**	-0.14	**-0.33**	**-0.75**	-0.61	-0.40	0.01
Shredder	0.18	**-0.29**	-0.03	-0.06	**-0.25**	-0.48	-0.09	-0.21	-0.53
Scraper	0.32	**0.31**	**0.27**	0.13	**0.25**	0.53	0.56	0.37	0.33
Filter-feeder	0.13	**0.33**	0.13	0.09	**0.31**	**0.71**	0.18	0.00	0.11
Piercer (plant or animal)	0.01	0.03	0.14	0.13	-0.14	-0.37	-0.37	0.00	-0.47
Predator (carver/engulfer/swallower)	0.10	**-0.24**	**-0.30**	-0.13	-0.08	-0.38	-0.27	0.15	-0.14
Parasite, parasitoid	0.04	-0.05	0.08	-0.07	0.10	0.19	-0.08	0.06	**0.75**

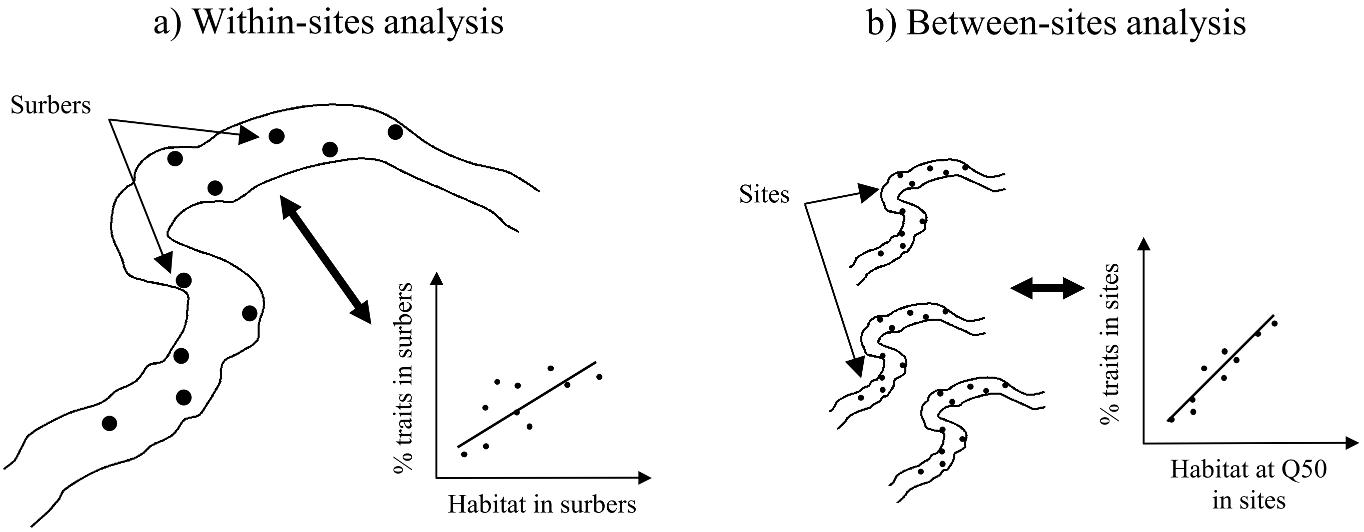

Fig 1. Our methodological approach: In a first step, we focus on habitat preferences by analysing how invertebrate traits respond to habitat variables within-sites (between samples). In a second step, at the site scale, we check if differences in site habitat variables at Q50 shape community traits as suggested by our analyses of habitat preferences.

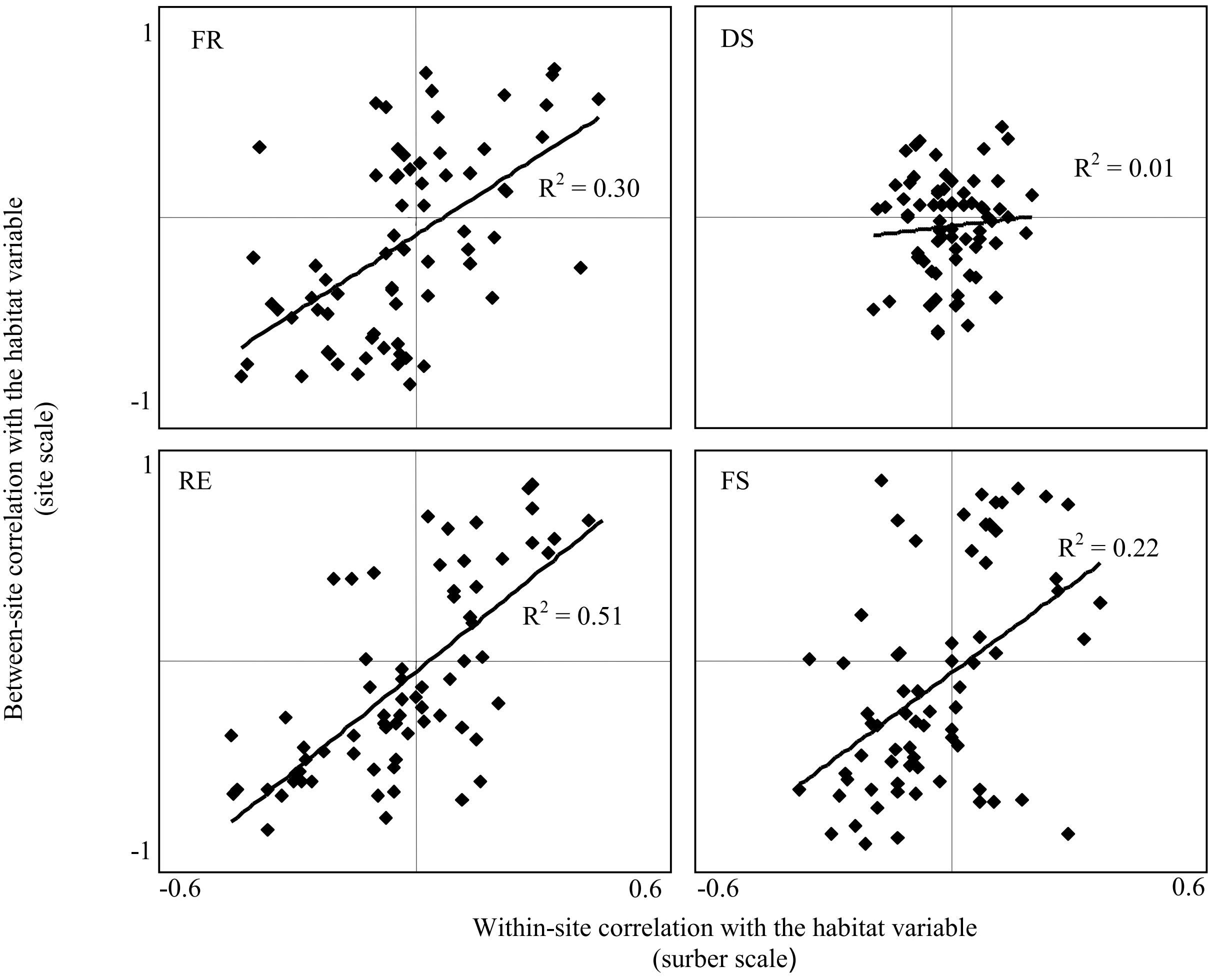

Fig 2. Comparison between the quantitative effect of habitat variables on trait variables between sites (between-sites correlations in Table 2) and their estimates from our analyses of habitat preferences (within-sites correlations in Table 2).

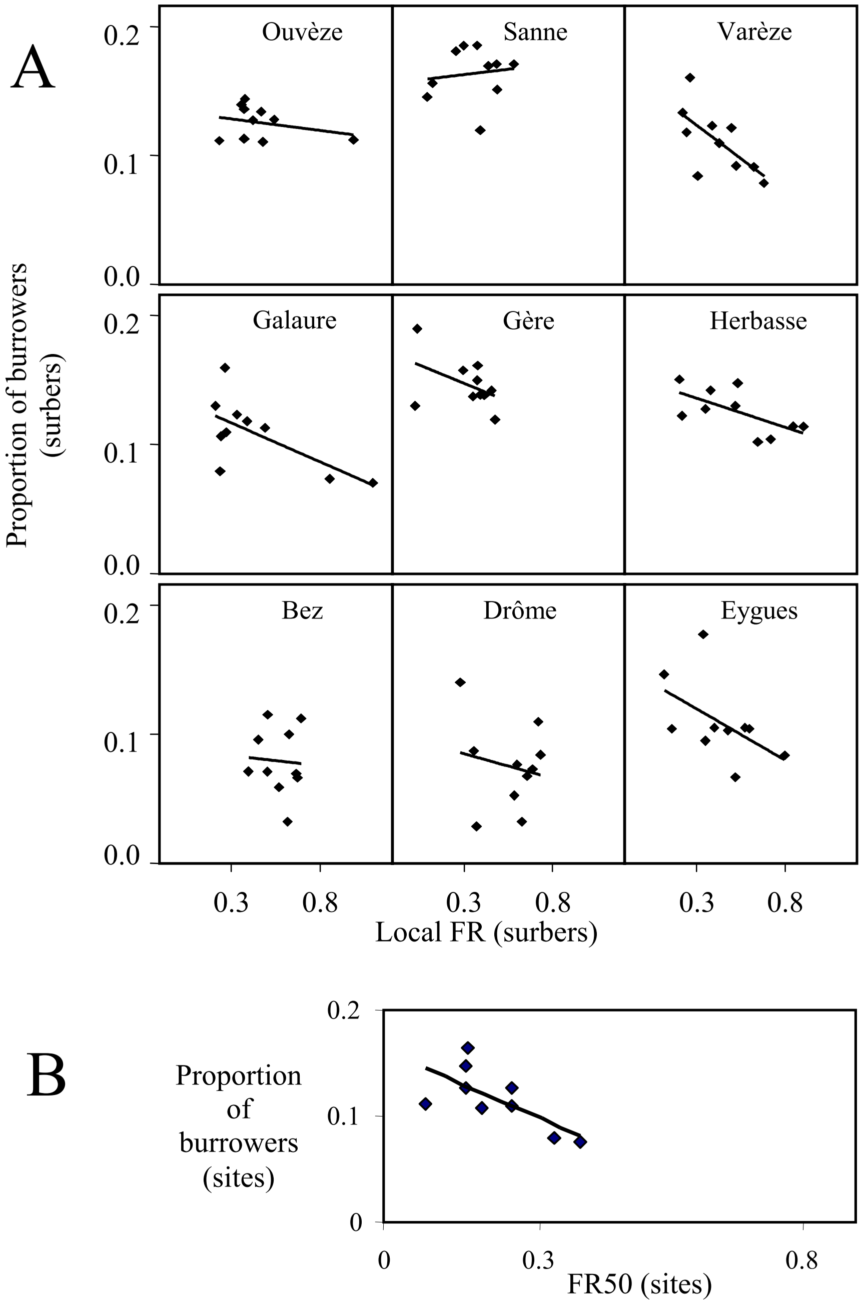

Fig 3. Example of habitat preference upscaling: the relationships between the Froude number and the trait variable 'burrower'. A) within-site relationships and their site-specific regression lines; B) between-site relationship and its associated regression line.

ANNEXE 1

Carottage cryogénique et préparation des échantillons

(Modifié de Maridet, L. (1994): La végétation rivulaire, facteur de contrôle du fonctionnement écologique des cours d'eau : influence sur les communautés benthiques et hyporhéiques et sur les peuplements de poissons dans trois cours d'eau du Massif Central. Thèse de Doctorat, 300p.)

Le carottage

Le carottage cryogénique ou technique du « freezing-core » consiste à congeler à l'aide d'un gaz liquéfié (ici de l'azote liquide) une fraction des sédiments de rivière. Afin d'éviter la fuite des invertébrés devant le front de froid, l'injection d'azote est précédée par la mise en place d'un champ électrique. Ce courant électrique ondulé (450 à 550 V et 3 à 5 A) paralyse ou tue les invertébrés ; d'où le nom de l' « electro-killing ». Ces deux techniques décrites ci-dessous sont adaptées et modifiées des études réalisées en Autriche (Bretschko, 1981 ; Bretschko & Klemens, 1986) et en Angleterre (Carling, 1981).

Six étapes successives sont nécessaires à l'obtention de l'échantillon qui sera ensuite analysé au laboratoire :

1- Dans un premier temps, l'aiguille est enfoncée dans le sédiment jusqu'à une profondeur variable (45 à 60 cm). Autour de l'aiguille, 2 électrodes distantes de 30 à 50 cm l'une de l'autre, sont insérées jusqu'à la même profondeur (Figure 1).

2- Ce dispositif reste en place pendant 48 h afin de permettre la recolonisation de la zone perturbée par les invertébrés.

3- Ce laps de temps écoulé, un champ électrique est créé entre les électrodes pendant 15 mm. Préalablement un déflecteur est placé face au courant pour éviter la dérive des invertébrés de surface paralysés sous l'effet du champ électrique (Figure 1).

4- L'azote liquide est ensuite injecté dans l'aiguille grâce à une surpression créée par un apport d'azote gazeux sous pression. Un détendeur permet de contrôler la pression. Le refroidissement progressif autour de l'aiguille entraîne la formation d'un manchon de sédiments congelés. La congélation du sédiment en surface est facilitée par la présence du déflecteur qui crée une zone d'eau stagnante au niveau du carottage. Ce dispositif évite le réchauffement dû aux forces de frottement dans les zones à forte vitesse de courant (Figure 2).

5- La carotte ainsi obtenue est extraite du lit à l'aide d'un treuil fixé sur un trépied.

6- La carotte est ensuite fractionnée en strates par tranche de 15 cm qui sont conservées congelées jusqu'au laboratoire. Elles sont stockées à – 20°C jusqu'aux traitements et analyses.

ANALYSE DES ECHANTILLONS

Au laboratoire, chaque échantillon correspondant à une strate doit subir un certain nombre de traitements successifs (Figure 3).

1- Détermination du poids (précision : 0.1 g) et du volume (précision : environ 10 ml). Le volume est mesuré par déversement d'eau depuis un cylindre en inox dans lequel l'échantillon est plongé. L'eau déversée est ensuite pesée (précision : 0.1 g).

2- Décongélation et extraction manuelle des grosses fractions minérales pour éviter le broyage des invertébrés. Les particules extraites seront classées et pesées.

3- Prélèvement des macro-invertébrés définis (> 0.5 mm) et des macro-détritus (> 1 mm) par élutriation (le brassage étant réalisé une dizaine de fois). Conservés dans une solution formolée, ils seront ensuite déterminés et dénombrés.

4- Tamisage des sédiments par voie humide avec l'eau utilisée pour l'élutriation. Le temps de tamisage varie de 1 à 2 h suivant l'échantillon (des problèmes de destruction de grains pourraient apparaître pour un temps de tamisage plus important). Les sédiments sont lavés et secoués à l'aide d'une tamiseuse sur le tamis de mailles décroissantes (de 12 mm à 0.05 mm). La fraction < 0.05 mm est extraite par centrifugation continue et est réinjecté en haut de la colonne de tamis pour laver des sédiments.

5- Détermination du poids de chaque fraction granulométrique. Les sédiments sont séchés à 105 °C pendant 24 à 48 h avant d'être pesés (poids sec). Ils sont ensuite humidifiés jusqu'à leur point de ressuyage, égouttés puis pesés à nouveau (poids égoutté).

CALCULS DERIVES

1- La porosité totale est calculée par le ratio du volume d'eau total sur le volume total de l'échantillon. Le volume d'eau est calculé par différence entre le poids total de l'échantillon et la somme des poids des sédiments séchés, en faisant l'hypothèse que l'eau a une masse volumique de 1 kg / litre.

2- La porosité modifiée pour ne prendre en compte que l'eau libre (habitabilité) est calculée par le ratio du volume d'eau libre sur le volume total de l'échantillon. Le volume d'eau libre est calculé par différence entre le poids total et la somme des poids de sédiments égouttés.

3- La distribution granulométrique cumulée est calculée à partir des poids secs des sédiments tamisés. Une macro Excel qui calcule l'ensemble des quartiles est disponible (Macro.granulo3.xls) au Laboratoire d'Hydroécologie Quantitative ainsi qu'auprès des auteurs.

4- Des indices décrivant la distribution granulométrique (index de tri ΦSo, index de symétrie ΦSk, index d'aplatissement ΦKs) sont calculés à partir des centiles Φ-transformés de la distribution .

$$\Phi So = \left(\frac{\Phi 84 - \Phi 16}{2} \right)$$

$$\Phi Sk = \left(\frac{\Phi 84 - \Phi 50}{\Phi 84 - \Phi 16} \right) - \left(\frac{\Phi 50 - \Phi 10}{\Phi 90 - \Phi 10} \right)$$

$$\Phi Ks = \left(\frac{\Phi 90 - \Phi 10}{1.9 \times (\Phi 75 - \Phi 25)} \right)$$

Références :

Bretschko, G., 1981: Vertical distribution of zoobenthos in an alpine brook of the Ritrodat-Lunz study area. - Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie **21:** 873-876.

Bretschko, G. & Klemens, W., 1986: Quantitative methods and aspects in the study of the interstitial fauna of running waters. - Stygologia **2:** 279-316.

Carling, P.A., 1981: Freeze-sampling coarse river gravels. - BGRG Tech. Bull. **29:** 19-29.

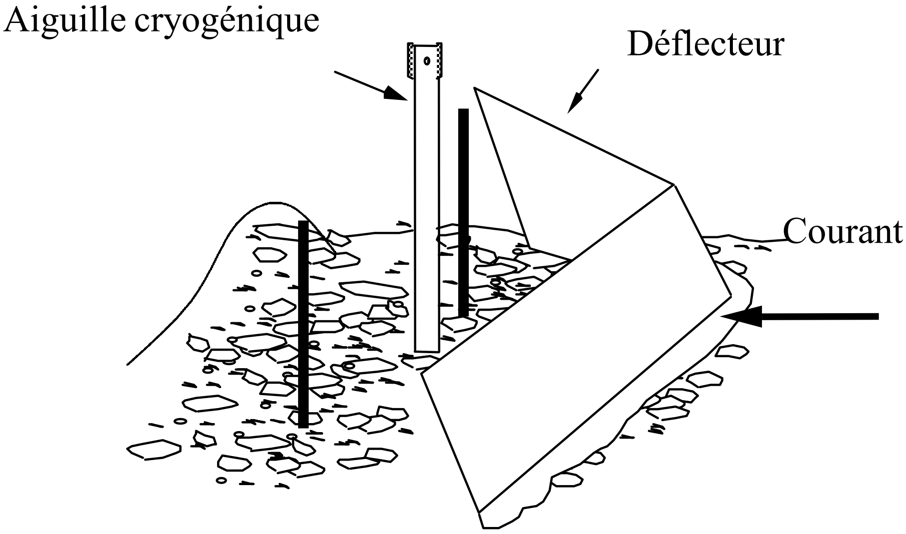

Figure 1. Dispositif utilisé pour l'électro-killing (vue de dessus).

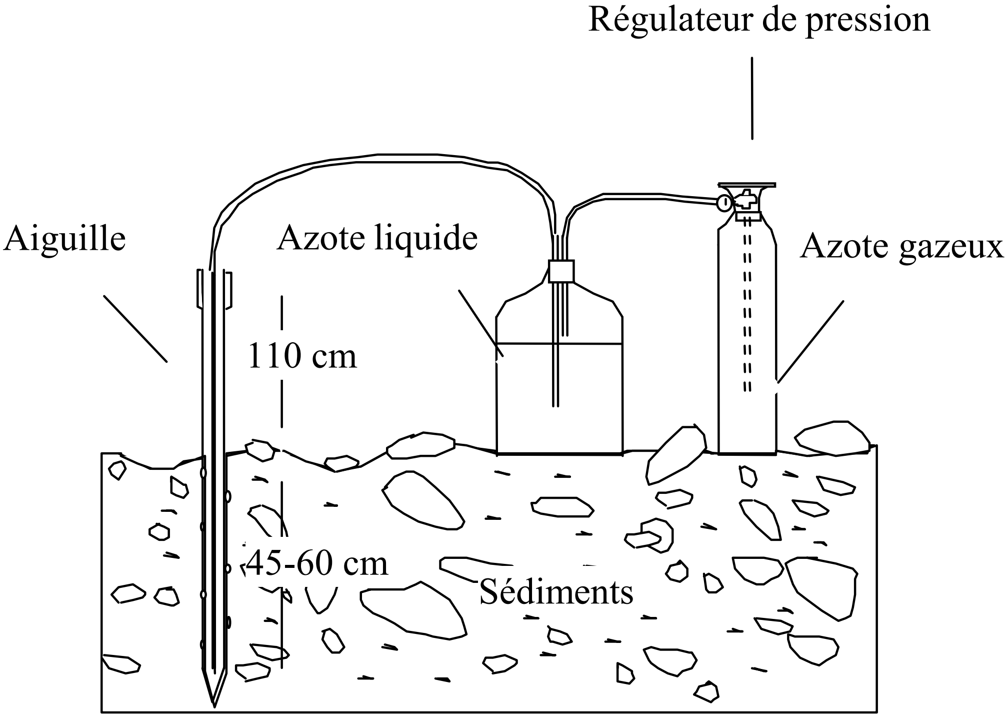

Figure 2. Dispositif utilisé pour le carottage cryogénique (coupe transversale).

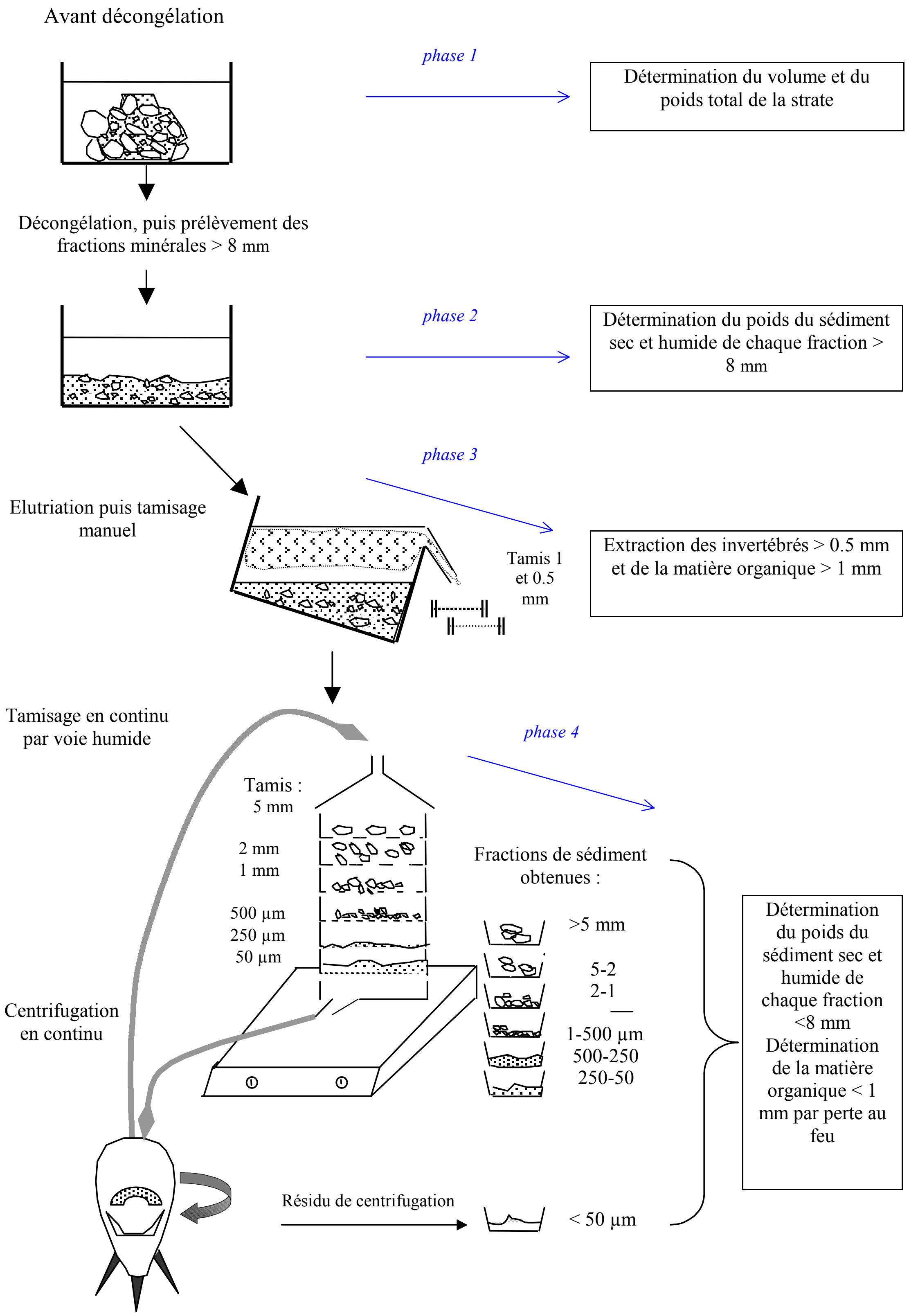

Figure 3. Traitement des échantillons de sédiment réalisé sur chaque strate.

ANNEXE 2

Principales caractéristiques des 17 sites présentés dans l'article A2

Caractéristiques physiques des 17 sites d'étude présentés dans A2. Les sédiments fins, l'habitabilité, les concentrations en particules organiques fines (FPOM) et grossières (CPOM) ont été mesurées sur les échantillons prélevés par carottage. Les concentrations en FPOM et CPOM sont exprimées par rapport au poids total de l'échantillon. L'hétérogénéité (Sorting Index) et le diamètre non dépassé par 84 % des particules (d84) ont été mesurés à partir de 100 particules prélevées à la surface du lit.

	Pente	Sédiments < 2mm	Habitabilité	Hétérogénéité	d84	FPOM	CPOM
	$^{0}/_{00}$	%	%		mm	$^{0}/_{00}$	$^{0}/_{00}$
Le Bez1	9.8	2.4	12.2	2.61	113	0.13	0.70
La Bourne1	10.0	1.8	13.8	3.33	141	0.29	0.04
La Bourne2	6.4	2.5	16.3	3.14	128	0.08	0.10
La Bourne3	5.6	4.0	7.3	4.96	101	0.12	0.14
Le Drac	10.3	1.9	9.8	1.72	70	0.41	0.01
L'Eygues	8.7	8.7	8.0	5.90	93	0.54	0.08
La Galaure1	8.6	6.8	8.0	2.09	98	0.48	0.51
La Galaure2	8.6	2.5	11.7	1.71	98	0.16	0.10
La Gère	8.6	10.3	11.0	5.66	125	0.41	0.27
L'Herbasse	8.0	5.8	14.3	2.47	68	0.75	0.44
La Loire	1.0	11.8	5.3	6.02	70	0.33	0.03
L'Ouvèze	10.1	3.2	9.8	2.44	109	0.25	0.06
L'Ozange	2.7	23.4	4.9	12.52	86	0.03	1.55
La Sanne	8.0	10.4	8.6	3.96	87	0.42	0.02
La Triouzoune	2.9	13.5	5.8	6.93	89	0.02	0.19
La Varèze	8.2	6.6	8.7	3.16	97	0.32	0.06
Le Vianon	18.5	7.4	5.6	6.92	140	0.11	0.37

Caractéristiques faunistiques des 17 sites d'étude présentés dans A2. La densité est exprimée en nombre d'individus par m², et la richesse taxonomique (RT) en nombre de Familles. Les pourcentages des groupes d'invertébrés, Cnidaires, Triclades, Oligochètes, Achètes, Mollusques, Crustacés et des Ordres d'insectes sont présentés.

Site	Densité	RT	Cnid.	Tricla.	Oligo.	Achè.	Mollusc.	Crust.	Ephémé.	Pléco.	Tricho.	Dipt.	Coléo.	Odona.	Hétéro.
Le Bez	8939	21	0.0	0.0	0.6	0.0	0.0	0.0	24.3	18.5	5.1	49.8	1.7	0.0	0.0
La Bourne1	16186	34	1.1	0.9	10.8	0.1	0.2	0.9	10.6	29.1	40.1	5.8	0.3	0.0	0.0
La Bourne2	17107	32	2.2	0.0	7.7	0.0	2.8	0.0	42.9	11.7	9.5	21.5	1.7	0.0	0.0
La Bourne3	11536	32	5.9	0.1	9.5	0.0	0.9	0.3	19.2	24.3	4.9	33.8	1.2	0.0	0.0
Le Drac	4900	15	0.0	0.0	0.1	0.0	0.0	0.0	21.4	6.9	0.5	71.1	0.0	0.0	0.0
L'Eygues	11607	20	0.0	0.0	0.1	0.0	0.0	0.0	1.0	0.4	0.2	98.2	0.1	0.0	0.0
La Galaure1	1413	29	0.0	0.0	10.3	0.8	4.1	0.7	12.6	0.0	14.5	47.0	10.0	0.0	0.0
La Galaure2	39174	38	0.3	0.3	10.1	0.0	1.0	0.6	4.8	7.5	11.9	57.7	5.8	0.0	0.0
La Gère	37182	32	0.1	0.0	4.9	0.0	2.7	0.3	3.5	8.0	1.9	70.1	7.9	0.0	0.0
L'Herbasse	46042	29	0.0	0.1	11.0	0.0	0.9	7.5	6.4	1.2	14.1	54.8	3.9	0.0	0.0
La Loire	1437	19	0.0	0.0	11.0	0.0	0.3	0.1	1.7	0.0	9.0	77.8	0.2	0.0	0.0
L'Ouvèze	5700	25	0.0	0.0	2.0	0.0	0.1	0.0	2.5	1.2	3.5	89.7	0.9	0.0	0.0
L'Ozange	5932	39	0.0	0.0	30.8	0.3	0.3	2.5	6.8	5.8	21.4	26.5	5.7	0.0	0.0
La Sanne	5429	25	0.0	0.0	10.0	0.0	1.7	15.5	33.0	1.4	9.9	23.1	5.3	0.1	0.0
La Triouzoune	5743	38	0.0	0.0	27.5	0.9	2.8	0.0	5.0	1.7	14.8	14.6	32.8	0.0	0.0
La Varèze	7327	29	0.0	1.4	24.4	0.1	0.3	3.7	14.4	5.0	7.3	22.6	20.9	0.0	0.0
Le Vianon	3440	32	0.0	0.0	54.0	0.8	0.6	1.9	8.2	9.7	11.4	6.7	6.6	0.0	0.0

ANNEXE 3

Listes faunistiques pour les sites échantillonnés au cours de la thèse