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DYNAMIQUE SPATIO-TEMPORELLE DES MACROINVERTÉBRÉS
DES DÉBRIS LIGNEUX LENTIQUES

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RÉSUMÉ

Les débris ligneux grossiers (DLG) qui proviennent de la forêt riveraine ajoutent non seulement une certaine hétérogénéité et complexité à la structure des habitats littoraux mais apportent également une quantité substantielle de matériel organique aux écosystèmes aquatiques. Ces DLG ont des effets importants sur la diversité, la structure et la productivité des communautés animales benthiques, notamment les macroinvertébrés, qui sont des acteurs majeurs dans les transferts de matière et d'énergie vers les niveaux trophiques supérieurs.

Nous avons examiné la dynamique spatiale et temporelle des macroinvertébrés associés aux DLG dans un lac de la forêt boréale, de l'est du Québec. Nous avons documenté la densité et la composition des communautés habitant les DLG de thuya (*Thuja occidentalis*), échantillonnés à différentes profondeurs et à différents sites, au printemps, à l'été et à l'automne. Nous avons utilisé la dendrochronologie pour dater le temps de résidence des DLG dans l'eau. La densité et la composition des communautés des macroinvertébrés ont varié entre les saisons d'échantillonnage. Les plus fortes densités en macroinvertébrés ont été observées à l'automne. La saison semble être le principal facteur structurant la communauté des macroinvertébrés associés au DLG. En revanche, la profondeur et le site ne semblent pas avoir d'impact sur la structure de la communauté. Les groupes trophiques retrouvés ont varié selon la saison. Les prédateurs, les racleurs et les collecteurs ont été les plus abondantes au printemps, à l'été et à l'automne respectivement. La plupart des DLG ont été recrutés dans le lac vers la fin du XIXe siècle à cause d'une remontée du niveau d'eau à l'époque pour faciliter la drave. Aucun DLG n'a été recruté dans le lac après cette période.

Bien que cette étude n'ait été effectuée que sur un seul lac de la forêt boréale à l'est du Québec, elle nous a permis de mieux comprendre la dynamique des macroinvertébrés dans les lacs et nous a aussi permis de constater l'impact anthropique dans la forêt boréale lors de la période de coupes forestières intenses.

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INTRODUCTION GÉNÉRALE

Les habitats benthiques littoraux représentent une composante critique des écosystèmes lacustres (Schindler et Scheuerell 2002). Les macroinvertébrés rencontrés dans ces habitats occupent une position particulière dans les réseaux trophiques lacustres. Ils peuvent recycler la matière organique détritique (James et *al.* 2000), servir d'intermédiaire dans le transfert de la production primaire vers les niveaux trophiques supérieurs (Vander Zanden et Vadeboncoeur 2002, Vadeboncoeur et *al.* 2002) et peuvent être exploités directement par l'homme (e.g. crustacés; Covich et *al.* 2004). Malgré tout, le rôle écologique de la zone benthique littorale, notamment son importance sur la structure et le fonctionnement des réseaux trophiques lacustres et sur les échanges de matière organique (MO) entre le milieu terrestre et le pélagos sont encore bien peu connus à ce jour (Vadeboncoeur et *al.* 2002).

Les débris ligneux grossiers (DLG; des troncs et des souches de bois de plus de 5 cm de diamètre à différents stades de décomposition) qui s'accumulent en zone littorale constituent un habitat durable qui abrite diverses communautés végétales et fauniques. Les activités anthropiques peuvent causer des modifications dans la dynamique naturelle de ces communautés, qui auraient des conséquences à court et à long terme sur le fonctionnement des lacs. Pour bien comprendre ces impacts, il devient essentiel de mieux connaître et de mieux comprendre la structure et la dynamique des communautés d'organismes qui colonisent les DLG. À l'heure actuelle, très peu d'études ont porté sur l'importance

écologique des débris ligneux dans les systèmes lentiques et sur les communautés d'invertébrés qui les colonisent.

Zone littorale et couplage entre les écosystèmes aquatique – terrestre

Les lacs sont des écosystèmes complexes, composés d'une mosaïque d'habitats ou de sous-systèmes (Schindler et Scheuerell 2002) (Figure 1). Dans ces systèmes, la zone littorale abrite des habitats extrêmement importants en terme de budget énergétique par leur production primaire et secondaire élevée (Strayer et Likens 1986, Blumenshine et *al.* 1997, James et *al.* 1998, Vadeboncoeur et *al.* 2002). La zone littorale est essentiellement caractérisée par une plus faible profondeur, des eaux plus transparentes et des concentrations en oxygène plus élevées qu'en milieu pélagique (Dussart 1966).
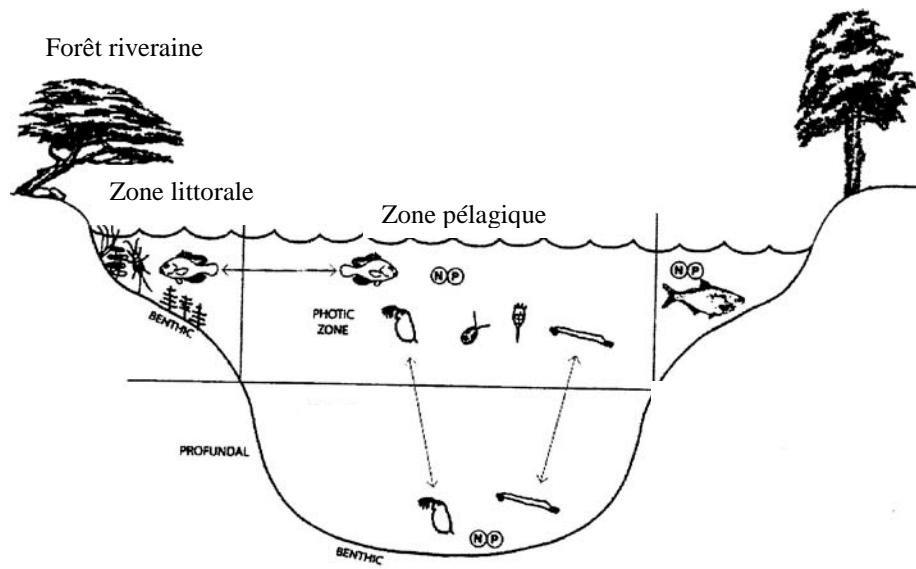
Figure 1. Schéma d'un lac et des différents habitats qui le constituent. La forêt riveraine se situe dans la transition des milieux aquatique et terrestre. Elle est généralement considérée comme faisant partie du système terrestre. Par contre, elle

est intimement liée aux habitats aquatiques par le biais d'organismes terrestres et par les débris ligneux. (Tirée de Schindler et Scheuerell 2002).

Grâce à ces caractéristiques, la faune aquatique est généralement plus riche et diverse dans la zone littorale que dans la zone pélagique des lacs (Wetzel 2001). Malgré son importance, l'influence de la zone littorale sur le fonctionnement trophique et la productivité des systèmes lacustres a souvent été sous-estimée (Wetzel 2001).

Les habitats aquatique et terrestre sont intimement reliés entre eux. Les écosystèmes aquatiques peuvent en effet être alimentés par du carbone organique autochtone produit par le processus de photosynthèse par des organismes autotrophes présents dans l'écosystème mais également par du carbone allochtone produit en dehors puis importé dans l'écosystème (Pace et *al.* 2004, Solomon et *al.* 2008). Des travaux récents, mettant en œuvre la technique de traçage isotopique (i.e., $\delta^{13}C$ et $\delta^{15}N$), ont ainsi montré que les subsides tels que la MO provenant d'environnements terrestres, pouvaient alimenter les réseaux trophiques des lacs oligotrophes et atteindre, voire même excéder, les niveaux de production primaire autochtone (Caraco et Cole 2004, Carpenter et *al.* 2005). Les impacts des apports de subsides allochtones sur les réseaux trophiques lacustres dépendraient par ailleurs de leur forme (dissoute ou particulaire), de la voie d'entrée dans le réseau trophique et des types de consommateurs présents dans le système (Cole et *al.* 2006).

Les débris ligneux grossiers (DLG) qui proviennent de la forêt riveraine constituent une source majeure de matière organique allochtone et d'énergie pour les zones littorale et

pélagique des lacs (Wetzel 2001, Schindler et Scheuerell 2002). Ces DLG complexifient la structure trophique de l'habitat aquatique littoral (Harmon et *al.* 1986).

Structure et fonctions des DLG dans les écosystèmes forestiers

Les DLG sont une composante importante des écosystèmes forestiers (Harmon et *al.* 1986) où ils y remplissent de nombreuses fonctions. Par exemple, les DLG terrestres participent au cycle du carbone et des autres éléments nutritifs (Harmon et *al.* 1986) et servent de substrat et d'habitat pour une grande variété d'organismes (Harmon et *al.* 1986, Masser et Sedell 1994, Richmond et Fausch 1995, Bilbi et Bisson 1998). De nombreuses espèces de bactéries hétérotrophes, d'algues et de champignons utilisent les DLG comme source d'énergie, de nutriment, et comme habitat (Frankland et *al.* 1982, Sippola et Renvall 1999). De même, les invertébrés utilisent et dépendent des DLG comme habitat et comme protection contre les prédateurs (McCafferty 1998, Andrew et *al.* 2000). Quelques vertébrés, comme les oiseaux, dépendent également des DLG pour la fabrication de leurs nids (Fischer et McClelland 1983) et même quelques mammifères, comme le castor, les utilisent pour la construction de barrages (Slough et Sadleir 1977). Enfin, dans certains environnements comme la forêt, des graines peuvent utiliser les DLG comme sites de germination (McKee et *al.* 1982).

Importance des DLG dans les écosystèmes lotique et lentique

Les DLG sont également importants dans les milieux aquatiques (Harmon et *al.* 1986). Ils s'y décomposent beaucoup plus lentement qu'en milieu terrestre (Guyette et *al.*

2002) en raison des concentrations réduites en oxygène (Maser et Sedell 1994) qui limite l'activité biologique des organismes décomposeurs tels que les champignons (Harmon et *al*. 1986). On estime ainsi que le bois de grande taille (>25 cm de diamètre) peut demeurer jusqu'à 10 fois plus longtemps dans les écosystèmes aquatiques que dans les écosystèmes terrestres (Guyette et *al*. 2002).

Les DLG influencent la structure et le fonctionnement des systèmes aquatiques. Leur rôle écologique a surtout été étudié dans les milieux lotiques (e.g. Bilby et Likens 1980; Harmon et *al*. 1986; Robinson et Beschta 1990; O'Connor 1992; Maser et Sedell 1994; Richmond et Fausch 1995). Ils y fournissent les nutriments nécessaires à la survie d'un certain nombre d'organismes (Wallace et Benke 1984), retiennent la matière organique et inorganique (Bilbi et Likens 1980, Bilbi 1981, Ehrman et Lamberti 1992, Wallace et *al*. 1995), dissipent l'énergie dans l'eau et piègent les sédiments (Maser et Sedell 1994). Les DLG accroissent également la diversité des habitats en formant des barrages et des fosses (Robinson et Beschta 1990, Maser et Sedell 1994). Ces barrages sont particulièrement importants en tant qu'habitats pour les poissons (Angermier et Karr 1984) et les invertébrés (Hilderbrand et *al*. 1997). De plus, dans les rivières, les DLG constituent entre 50 et 70% du total de la matière organique disponible pour les microbes et les invertébrés (Maser et Sedell 1994) surtout dans la partie en amont. En général, ce pourcentage varie beaucoup le long du parcours des écosystèmes lotiques, avec une diminution vers la partie en aval.

Les DLG aquatiques comme habitat

Les DLG ont des caractéristiques physiques particulières qui en font un habitat privilégié pour les organismes (Harmon et *al*. 1986). Ces caractéristiques sont par exemple, un substrat dur, des longues périodes de séjour dans l'eau et une surface rugueuse avec plusieurs fissures et cavités fournissant un microhabitat complexe où les organismes peuvent se protéger contre les prédateurs (Hoffman et Hering 2000). Les DLG représentent un habitat relativement stable et une source de nourriture disponible en tout temps (Hoffman et Hering 2000). Ainsi, les DLG peuvent servir de refuge contre la prédation pour un certain nombre d'organismes (Everett et Ruiz 1993) tels que les invertébrés (Hoffmann et Hering 2000) et les poissons comme la truite (*Salvelinus fontinalis*) (Tabour et Wurtsbaugh 1991). Certaines espèces d'invertébrés comme les plecoptères, éphéméroptères, trichoptères, diptères et odonates utilisent les DLG comme habitat de protection au stade larvaire avant d'émerger comme adultes terrestres (Merritt et Cummins 1998). De plus, plusieurs espèces de trichoptères utilisent le bois pour la construction de leur fourreau (Dudley et Anderson 1982). La qualité intrinsèque des DLG (espèce de bois, degré de décomposition et de fissures) est un facteur important pour sa colonisation par les invertébrés (Bowen et *al*. 1998, Magoulick 1998). Les fissures et les rainures très présentes dans le bois à un stade de décomposition avancée seraient utilisées par les invertébrés comme espace refuge contre la prédation (Harmon et *al*. 1986).

Les DLG aquatiques sont aussi un habitat propice pour la colonisation de microorganismes tels que les bactéries hétérotrophes, les algues et les champignons (Sinsabaugh et *al*. 1991, Tank et Webster 1998). Cette colonisation est restreinte à la surface des DLG à cause des conditions d'anoxie présentes dans le bois qui est dans l'eau

(Maser et Sedell 1994). Une fois établis, ces microorganismes forment un biofilm qui peut servir de nourriture à des invertébrés tels que certaines espèces de coléoptères (Anderson et *al*. 1984), d'éphéméroptères, de plécoptères et de trichoptères (Maser et Sedell 1994, McCafferty 1998). En effet, ce biofilm semble être un source d'aliment de haute qualité pour les invertébrés (Hax et Golladay 1993, Eggert et Wallace 2007).

Finalement, les DLG peuvent aussi être utilisés comme site pour le dépôt des œufs et pour l'émergence d'insectes comme certains trichoptères, éphéméroptères et diptères (Hoffman et Hering 2000). Pour déposer leurs œufs, les adultes nagent jusqu'à ce qu'ils trouvent un DLG aux interstices appropriés pour la ponte. Les stades larvaires séjournent dans l'eau et émergent plus tard comme adultes pour vivre dans l'écosystème terrestre (Hoffman et Hering 2000).

Les DLG aquatiques comme source de nourriture

Des analyses de contenus stomacaux indiquent que les DLG peuvent être directement utilisés comme source de nourriture par quelques organismes spécialisés (Pereira et *al*. 1982, Schulte et *al*. 2003). Schulte et *al*. (2003) ont identifié deux espèces de larves de trichoptères qui mangent le bois en éraflant la surface des DLG. Certaines larves de plécoptères peuvent enlever et ingérer la surface la plus molle des DLG et décomposer le bois en le déchiquetant. Finalement, certaines espèces de diptères se nourrissent en mangeant du bois déjà décomposé (McCafferty 1998). Malgré tous ces exemples d'organismes s'alimentant du bois, seulement une petite partie d'entre eux exploite le bois

comme unique source de nourriture, étant donné la piètre qualité alimentaire du bois (Anderson et Cummins 1979). Ainsi, les organismes s'alimentant exclusivement du bois, utilisent fréquemment d'autres méthodes pour couvrir leurs besoins métaboliques. Par exemple, pour compenser leur faible taux de croissance, certains coléoptères, trichoptères et diptères ont un cycle de vie plus long. Certains diptères profitent aussi d'une symbiose avec la flore intestinale pour les aider lors de la digestion du bois et certains organismes sont capables aussi de changer leur régime alimentaire à des stades larvaires plus avancés, lorsqu'une croissance rapide est nécessaire (Harmon et *al.* 1986).

Importance des macroinvertébrés dans les lacs

Les macroinvertébrés remplissent un rôle clé dans la zone littorale des lacs. Ils contrôlent potentiellement la biomasse algale benthique (James et *al.* 2000), recyclent le détritus (Kornijów et *al.* 1995) et sont des acteurs majeurs dans les transferts de matière et d'énergie vers les niveaux trophiques supérieurs (Allan 1995). Les macroinvertébrés sont responsables en particulier de la conversion des productions algale et bactérienne hétérotrophe en biomasse animale, puisqu'étant une composante importante du régime alimentaire de plusieurs espèces de poissons (Graynoth et *al.* 1986, Vander Zanden et *al.* 1997). La prédation des invertébrés par les poissons est un régulateur important de la structure et de la dynamique spatiale et temporelle de ces populations (Wetzel 2001). Ainsi, Francis et *al.* (2007) ont suggéré qu'une diminution dans la densité des macroinvertébrés causerait par la suite une diminution de la population de poissons, qui dépendent directement d'eux pour leur survie alimentaire.

Perturbations d'origine anthropique

Le couplage entre la forêt riveraine et les lacs via les DLG peut être sévèrement altéré par les activités humaines (Christensen et *al*. 1996). Les principales perturbations anthropiques sont : la détérioration de la forêt riveraine résultant de l'intensification de l'exploitation forestière (Linder et Ostlund 1998, Fridman et Walheim 2000); l'apport massif des DLG suite à une augmentation du niveau d'eau dû à la drave et l'enlèvement des DLG associé à l'urbanisation autour des lacs (Marbourg et *al*. 2006, Francis et *al*. 2007). Ces perturbations ont notamment pour conséquence une altération du rythme des apports en DLG dans la zone littorale de ces plans d'eau (Marburg et *al*. 2006, Sass et *al*. 2006).

Projet à l'étude

À l'heure actuelle, très peu d'études ont porté sur l'importance écologique des DLG dans les systèmes lentiques. Sass et *al.* (2006) ont montré l'importance de ces DLG pour les communautés des poissons. Ainsi, suite à l'enlèvement d'une grande partie des DLG dans un lac du Wisconsin, ils ont constaté une forte diminution dans le recrutement des poissons. L'importance écologique des DLG pour les macroinvertébrés a par ailleurs été documentée par Bowen et *al*. (1998). Ils ont étudié la composition d'une communauté de macroinvertébrés associés aux DLG dans la zone littorale de deux lacs en Ontario en été, et ont étudié l'utilisation du biofilm comme source de nourriture pour ces organismes. En introduisant aussi des substrats remplaçant les DLG naturels, ils ont obtenu une colonisation rapide de ces substrats par les macroinvertébrés, avec de densités encore plus

élevées que les densités trouvées sur les DLG naturels. Cela suggérerait toute l'importance écologique des DLG aquatiques pour les macroinvertébrés. Cependant, on ne connaît pratiquement rien du rôle écologique des DLG dans les lacs, notamment leur influence sur le fonctionnement et la structure spatiale et temporelle des communautés de macroinvertébrés.

La présente étude vise donc à documenter la structure des communautés de macroinvertébrés associées aux DLG de l'espèce thuya submergés en zone littorale dans un lac de la forêt boréale.

Les objectifs spécifiques de l'étude sont de :

(1) Documenter la dynamique saisonnière et spatiale des communautés de macroinvertébrés des DLG

Hypothèse 1 : La structure et la composition des communautés de macroinvertébrés des DLG varient avec la saison.

Prédiction 1 : Au printemps, la densité en macroinvertébrés sera maximale dans les DGL suite à une intense colonisation par les insectes. A l'été, la densité en invertébrés dans les DLG déclinera suite à l'émigration des insectes vers l'écosystème terrestre. À l'automne, il y aura encore une augmentation de la densité suite à la recolonisation des DLG par de nouveaux insectes.

Hypothèse 2 : La structure et la composition des communautés de macroinvertébrés des DLG varient avec la profondeur.

Prédiction 2 : Compte tenu que la luminosité et la température diminuent avec la profondeur, le biofilm associé aux DLG diminue également avec elle. Le biofilm est susceptible d'être consommé par les macroinvertébrés benthiques de sort que la densité des communautés des macroinvertébrés associés aux DLG devrait diminuer aussi avec la profondeur.

(2) Étudier la relation entre la structure de la communauté de macroinvertébrés des DLG et le temps de séjour des ces DLG dans l'eau.

Hypothèse 3 : La structure de la communauté de macroinvertébrés des DLG varie avec le temps de séjour des DLG dans l'eau.

Prédiction 3 : Le degré de décomposition des DLG change avec le temps de séjour de ceux-ci dans l'eau, changeant ainsi la structure de la communauté de macroinvertébrés qui y habite.

Enfin, un autre objectif sera de reconstruire la dynamique temporelle des apports de DLG provenant de la forêt riveraine par rapport aux activités humaines durant le 19ème siècle.

Coarse woody debris in the littoral zone of boreal lakes: Life-support structures for macroinvertebrates

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Abstract

Coarse woody debris (CWD) in aquatic ecosystems can influence the structure and productivity of invertebrate communities that utilise wood as habitat. We documented the density and community composition of macroinvertebrates on white cedar (*Thuja occidentalis*) CWD sampled in a boreal lake in Eastern Quebec, Canada, at different depths and sites during spring, summer and autumn. In addition, we used dendrochronology to estimate the time spent by CWD in the water. Macroinvertebrate density and community composition were highly variable in space and time. Season was the main factor structuring taxa composition and their relative densities. Macroinvertebrate density was more than two times greater in autumn than in spring and summer. Predators, scrapers and collectors organisms were the most common functional feeding groups in spring, summer and autumn, respectively. Most CWD entered the lake in the late 19th century, after its level was raised for timber driving by the early logging industry. No CWD entered the lake after this period because of slow riparian forest recovery. These results would assist lake management by providing a better understanding of macroinvertebrate and CWD dynamics in the context of long-term anthropogenic disturbance of forest-lake coupling.

Key words: coarse woody debris, macroinvertebrates, lake ecosystems, forest-lake coupling, spatio-temporal dynamics, riparian forest, littoral, dendrochronology.

Introduction

Coarse woody debris (CWD; regarded here as being all wood material >5 cm in diameter) is an important component of aquatic ecosystems in forested areas (Harmon et al. 1986, Bilby and Bisson 1998). CWD decomposes very slowly once it has entered aquatic habitats (Guyette and Cole 1999) where it can accumulate for centuries. CWD originating from riparian forests provides a complex and unique habitat structure to aquatic ecosystems: it creates habitat heterogeneity in many lakes and rivers (Gurnell et al. 2002, Webb and Erskine 2003), affects the abundance and geometry of pools (Robison and Beschta 1990, Beechie and Sibley 1997) and retains organic and inorganic matter in streams (Bilby and Likens 1980, Bilby 1981, Ehrman and Lamberti 1992). CWD also provides habitat and/or refuge for a range of aquatic organisms including microorganisms (Tank and Webster 1998, Vadeboncoeur and Lodge 2000, Collier et al. 2004), invertebrates (Pereira et al. 1982, Anderson et al. 1984) and fish (Fausch and Northcote 1992, Everett and Ruiz 1993) and serves as direct food source for some invertebrates (Hoffman and Hering 2000, McKie and Cranston 2001).

Terrestrial-aquatic coupling through CWD transfer can be impacted by several anthropogenic activities such as logging of riparian forest, massive input of logs after water level modification and CWD removal. Because CWD may reside in the littoral zone of lakes for centuries, these effects could have long-term impacts on overall lake function (Marburg et al. 2006).

Considerable information is available on the ecology of CWD in forest streams (e.g. Harmon et al. 1986, Andrus et al. 1988, Bilby and Ward 1991, Maser and Sedell 1994,

Beechie and Sibley 1997, Magoulick 1998). On the other hand, much less is known about its ecological function in lake environments (Pieczyñska 1990, Christensen et al. 1996). CWD has been shown to be an important substrate for macroinvertebrates in the littoral zone of two lakes in Ontario, Canada (Bowen et *al.* 1998). However, the dynamics of such communities in space (i.e. according to depth) and time (according to season) is still unknown. Benthic invertebrates are major players in the transfer of littoral energy to upper trophic levels (e.g., fishes) in lakes, as they are responsible for the conversion of benthic primary and microbial production into animal biomass (Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2006). It has been suggested that a decline in the density of benthic macroinvertebrates, as a consequence of anthropogenic activities, would lead to a decline in fish populations which rely heavily on benthic resources (Francis et al. 2007).

The main goal of this study was, therefore, to document the littoral macroinvertebrate communities associated with submerged white cedar (*Thuja occidentalis*) CWD in a boreal forest lake in Eastern Quebec. Specific objectives were (i) to determine whether and how the macroinvertebrate community structure (taxa composition and their relative densities) vary in relation with seasons, depths and sites; (ii) to reconstruct temporal dynamics of CWD inputs from the riparian environment in relation with anthropogenic activities.

Methods

Study area

The Macpès Lake (68° 29'W, 48° 19'N) was chosen in this study because of its accessibility and absence of lakeshore development, which has allowed us to asses only the

anthropogenic impact in the lake due to logging activities in the 20th century. It is located in the Rimouski river watershed in the boreal forest of Eastern Quebec, 25 km south of the town of Rimouski (Fig. 1). The Macpès Lake lies at an elevation of 268 m above sea level, has 10 km of shoreline, a surface area of 18 km^2, a mean depth of 5 m and a maximum depth of 20 m (A. Caron, personal communication). The littoral zone is generally characterized by a steep downward slope of about 45º to a depth of about 5 m. Macpès Lake is oligotrophic and normally ice-covered from late November to early May. The regional climate is subpolar and subhumid. Mean annual air temperature is 2.5°C, with mean monthly minimum (January) and maximum (July) temperatures of -12°C and 18°C, respectively. The mean annual precipitation is 950 mm, with 35% falling as snow (Robitaille and Saucier 1998). The forest vegetation in the study area is composed of mainly white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) (Robitaille and Saucier 1998). White cedar is by far the dominant riparian tree species in this area and frequently forms almost pure stands at shoreline. However, this species is currently absent from the riparian forest at Lake Macpès. The forest industry established in the Rimouski river watershed around 1825 and gained in importance during the 20th century, especially with the construction of two large mills at the Rimouski river's mouth in 1901 and 1903. Surrounding forests were cleared in the late 19th to early 20th centuries and burned during a large and severe fire in 1923. The lake level was raised by about 3-5 m to help float timbers to the mills at the river mouth prior to the 1923 fire, thus causing massive inputs of cedar CWD from drowned riparian trees (see results).

Sample collection

CWD samples were collected by diving at three sites located at least 1 km apart, in May, July, and October 2006, representing the spring, summer and autumn seasons, respectively. At each season, within each site, three white cedar CWD were systematically sampled at five depths (1, 2, 3, 4 and 5 m). White cedar was chosen because it was the dominant species at lake border in the study area during the industrial period. In addition, a previously constructed white cedar tree ring chronology was available to crossdate the live period of cedar CWD over the last 1040 years (D. Arseneault, unpublished results). Cedar was distinguished from other species from its characteristic reddish tint in cross section. In the water, appropriate cedar CWD (i.e. not buried with sediment; containing more than the minimum of about 100 tree rings needed for crossdating; diameter of less than 14 cm to fit in a tube) were gently inserted by a diver into a 50 cm x 14 cm PVC tube. The protruding part of the CWD was then cut using a bow saw. The tube was finally hermetically capped and lifted by hand into a boat and brought to the laboratory. In the water, we noted if the corresponding trees had an attached stump (suggesting a death caused by a raised water level), and char marks (indicating the occurrence of a fire). At each site and on each sampling occasion, temperature, conductivity ($\mu S.cm^{-1}$), dissolved O_2 ($mg.L^{-1}$) and pH were measured with an YSI 556MPS probe (Table 1). In total, we obtained 15 CWD samples per site and 45 CWD per season; except during summer and autumn where we were not able to sample CWD at 5 m in one site because of very high water turbidity and bad weather, respectively.

Laboratory processing

Macroinvertebrates.- Each CWD was gently washed and rinsed 3 times at 24 h washing intervals on a 500-µm mesh, taking care to dislodge invertebrates in crevices. Pooled for all seasons, depths and sites, the first and second washes collected 53% and 80% of all macroinvertebrates sampled, respectively. Macroinvertebrates retained on the 500-µm mesh were fixed in 70% ethanol and identified to the level of order or family using the keys provided by McCafferty (1998), Merritt and Cummins (1998), and Thorp and Covich (2001). To calculate macroinvertebrate density (number of individuals per m^2 of CWD), the surface of each wood sample was estimated by measuring its diameter and length. CWD were exposed to air and dry weight was determined afterwards. CWD volume and density were measured by water displacement and ratio of dry weight to volume, respectively.

Biofilm chlorophyll-a concentration.- Biofilm chlorophyll-a (chl-a) concentration was used as an indicator of the microalgal standing stock on submerged CWD. Two 3.4 x 2.2 cm subsamples of surface biofilm were taken by scraping the surface of each CWD sample with a chisel. These subsamples were placed into small glass sample jars, wrapped in aluminum foil and stored at -20°C for further analysis. One subsample was used to estimate the chl-a concentration and the other to measure the ash-free dry weight (AFDW). Pigment analysis of biofilm was done according to the Holm-Hansen et al. (1965) fluorometric method. Biofilm subsamples were placed into 20 ml scintillation vials with 5 ml of 90% acetone for a 24-h extraction of pigments at 5°C in the dark. Chl-a concentrations were then

measured using a 10-AU Turner Designs fluorometer and calculated according to Riaux-Gobin and Klein (1993). Percentage of moisture content of each biofilm sample was measured by weighing the sample to the nearest 1 mg before and after drying for 48 h at 60°C in a drying oven. Ash free dry weight (AFDW), which is a measure of the organic material, was determined by combusting the dried sample for 5 h at 500°C. AFDW was then calculated by subtracting the ash content from the dry weight.

CWD cross dating

We used dendrochronology to determine the age of white cedar CWD. A cross-sectional disk was cut from each log, air-dried and sanded to reveal the cellular detail of each annual ring. Disks where scanned at 4800 dpi and width of annual growth rings was measured on screen using the OSM software (version 3.35, SCIEM, Vienna, Austria). CWD growth patterns were then crossdated with a master chronology (AD 972- AD 2006) previously developed from Macpès Lake CWD (D. Arseneault, unpublished data). Crossdating was performed using the PAST4 program (version 4, SCIEM, Vienna, Austria), along with COFECHA as a validating tool (version 6.06, Holmes 1983). Date of tree death was estimated from the outermost tree ring found in each sample. Because of CWD erosion, some outermost rings were missing and the actual date of tree death is probably overrestimated (i.e. too ancient) by a few decades. In total, 80 samples out of 127 could be crossdated. Specimens too poorly preserved to allow tree-ring measurements or containing less than 80 rings were omitted.

Statistical analyses

Univariate analyses.- Univariate analyses were made using SAS (version 9.1.2, SAS Institute Inc., Cary, NC, USA). Prior to undertaking analysis of variance (ANOVA), the assumptions of normality and homogeneity of variance were checked for macroinvertebrate density, taxa number, Shannon diversity index (Shannon and Weaver 1949), chl-a concentration and AFDW. Macroinvertebrate density and chl-a concentration required a $\log_{10}(n+1)$ transformation, taxa number and diversity did not require transformations, while AFDW necessitated a rank (non parametric) transformation. The replicate values for each of the above variables were then subjected to three-way crossed ANOVA (involving seasons, depths and sites as factors and including interactions). When ANOVA showed a significant difference ($p<0.05$), Tukey's a posteriori test was used to determine where those differences occurred. An evaluation was made of the relationship between grazing macroinvertebrate densities and chl-a (pooled for depths and sites) using Pearson's correlation. Spearman's rank correlation coefficients were calculated to explore relationships between CWD age and density, taxa number and depth.

Multivariate analyses.- Community structure (regarded as the occurring taxa and their relative densities) was examined using the PRIMER statistical package (version 6, PRIMER-E, Plymouth, UK) (Clarke and Gorley 2001). The Bray – Curtis similarity coefficient was employed to construct a similarity matrix from mean densities of macroinvertebrate taxa in each season, in each depth and in each site. This matrix was then subjected to two dimensional non-metric multidimensional scaling (MDS) ordination.

Permutational MANOVA analysis test (PERMANOVA) were carried out to ascertain whether the composition of the benthic macroinvertebrate communities differed significantly ($p<0.05$) among seasons, depths and sites and if there was an interaction between factors. Taxa contributing to the dissimilarities between density groupings were determined by the similarity percentages procedure (SIMPER). Finally, the effects of single environmental variables on community structure were investigated using the biota and environment matching procedure (BIOENV).

Results

Community composition

CWD samples collected from the three seasons, three sites and five depths contained 21,031 macroinvertebrates belonging to 33 different taxa; the non-insect taxa were identified to the order level, while insect taxa were identified to the family level (Table 2). Chironomidae was the dominant macroinvertebrate taxa during spring and summer, contributing to 56% and 44% of all specimens, respectively. In autumn, Oligochaeta was the dominant taxa (37%), while the contribution of Chironomidae decreased to 27% (Table 2). Ceratopogonidae was the second dominant taxa in spring, but was much less abundant in summer and autumn. In summer, Cladocera, Amphipoda and Elmidae were particularly abundant. Other taxa commonly observed in all seasons included Heptageniidae and Policentropodidae (Table 2).

Densities, taxa number and diversity

Total macroinvertebrate density was highly variable in space and time, ranging from 304 (spring, 4 m, site 1) to 4919 ind.m^{-2} (autumn, 3 m, site 3) (Fig. 3A). Mean density was about two times greater in autumn than in spring and summer, with these latter two seasons displaying similar densities (Table 3, Fig. 3A). A Tukey test revealed that these differences were between autumn and the two other seasons, between 5 m and 1, 2, 3 m and between site 1 and sites 2, 3. A three-way ANOVA showed that mean macroinvertebrate density changed significantly among seasons, depths and sites, with a significant interaction between season and site (Table 4).

The mean taxa number was significantly influenced by season and to a less extent influenced by depth but did not differ among sites (Table 3, Fig. 3B). The mean taxa number was significantly greater in autumn than in spring and summer. Mean diversity was lower in autumn and higher at 1 m in all seasons (Table 3, Fig. 3C). Mean diversity (H') changed significantly among seasons and depths and there was a significant interaction between season and site (Table 4). A Tukey's test revealed that there was a significant difference between spring and the two other seasons, and between 1m and all other depths. Of the environmental variables, both chl-a and AFDW were significantly influenced by season and site (Table 4). Chl-a concentrations were lower in summer than in spring and autumn (Table 3, Fig. 3D) and AFDW was higher in spring than in summer and autumn (Table 3, Fig. 3E). AFDW was also significantly influenced by depth and there was a significant interaction between season and site (Table 4).

Community structure

Season influenced macroinvertebrate community structure. PERMANOVAs test, derived using the mean densities of the three CWD macroinvertebrate taxa sampled at each season, depth and site, revealed that the community structure differed significantly among seasons (Pseudo $F=14.64$, $p=0.0002$), depths (Pseudo $F=2.30$, $p=0.016$) and sites (Pseudo $F=2.2989$, $p=0.040$). Even if depth and sited differed significantly, the components of variation showed that the variation could be attributed mainly to seasons (sq. root=25.32) and neither to depths (sq. root=9.81) nor sites (sq. root=7.81). There was a significant interaction between season and site (Pseudo $F=2.89$, $p=0.006$). Similarly, two-dimensional MDS ordination showed three groups clearly separated from each other when season was used as a factor (Fig. 4A). When depth and site were used as factors, however, samples formed overlapping groups (Figs. 4B and 4C respectively). Once we identified that season was the main factor structuring CWD macroinvertebrate communities, we focused on communities differences among seasons. Analysis of seasonal differences in community structure using SIMPER showed that Chironomidae contributed to dissimilarities throughout all seasons, while Oligochaeta had the greater influence on dissimilarities between spring and autumn (45.13%) and summer and autumn (45.06%), thus clearly typifying autumn (Table 5). Similarly, Ceratopogonidae influenced dissimilarity between spring and summer and spring and autumn, thus typifying spring.

Community structure vs. environmental factors

BIOENV analyses showed that conductivity was the main parameter explaining the community correlation among habitat variables (temperature, conductivity, DO, pH, wood density, chl-a, AFDW, CWD age) and macroinvertebrate community structure (pooled for all seasons, depths and sites as insufficient data were available for testing by factors). However, the correlation was quite low (ρs=0.378).

Functional Feeding Groups

Macroinvertebrates were divided into functional feeding groups according to the descriptions provided in Merrit and Cummins (1998). Macroinvertebrate densities were summed for each functional group and season. The relative importance of functional feeding groups changed among seasons (pooled for depths and sites) (Fig. 5). In spring, macroinvertebrate predators were the most common functional feeding group (47.7%) followed by scrapers (32.6%). Examples of predators include Ceratopogonidae (Diptera) and Policentropodidae (Trichoptera). In summer, scrapers such as Heptageniidae (Ephemeroptera) and Tricorythidae (Trichoptera) were the most abundant group (42.7%) followed by predators (30.0%) (Fig. 4). In autumn, collectors dominated (52.4%), mainly because of Oligochaeta dominance, followed by predators (24.5%) (Fig. 5).

No significant correlation was found between macroinvertebrate grazers densities (scrapers and shedders) and chl-a in spring (Pearson's correlation, r=0.25, *p*=0.097), summer (r=0.11, *p*=0.52), or autumn (r=0.27, *p*=0.096).

Age of CWD

CWD density values were similar in all depths (mean±standard error= 0.295±0.024 g/cm^3), with values ranging from 0.264 (summer, 1m, site 3) to 0.340 g/cm^3 (summer, 1m, site 2). In addition, bark was always absent and all CWD presented a large number of pits dug by macroinvertebrates onto the surface.

Outermost tree rings in CWD were crossdated over a period of 492 years, from AD 1405 to AD 1897. A high proportion (66%) of these crossdated specimens contained an outermost ring formed between 1839 and 1897 (Fig. 6), along with an attached stump, suggesting an episode of massive CWD inputs due to a water level raise at the turn of the twentieth century (considering the loss of the most recent tree rings). No crossdated CWD had an outermost tree ring formed after 1897, also revealing that CWD inputs to the littoral zone almost completely ceased subsequently. In addition, charred CWD indicate two fires that most likely correspond to the well-documented 1923 fire, along with an additional fire event around 1710. This latter fire was associated with a small peak of CWD recruitment (12.6% of the crossdated CWD) (Fig. 6). No significant correlation was found between CWD age and macroinvertebrate densities (Spearman's rank correlation, D=-0.0433, p=0.70), taxa number (D=-0.0562, p=0.62) or CWD depth (D=-0.0810, p=0.47).

Discussion

This study provides important information to fill the knowledge gap on CWD ecology in boreal lakes. Compared with lotic systems, knowledge on macroinvertebrate communities living on lentic CWD is very scarce, a surprising situation given the extreme

abundance of boreal lakes, along with the presumably important role played by CWD invertebrates in transferring energy to the upper trophic levels (Baxter et al. 2005). In fact, we are aware of only one previous study of CWD macroinvertebrates in boreal lakes (Bowen et al. 1998). Although Bowen et al. (1998) have suggested that submerged CWD may be a valuable contributor to macroinvertebrate and biofilm production, they did not study macroinvertebrate dynamics in time and space. Hence, although we have considered only one lake, our study of the seasonal and spatial variations in macroinvertebrate community structure living on CWD in a boreal lake, along with our evaluation of past CWD inputs and abundance, provides much needed information to understand the ecological role of CWD in boreal lakes.

CWD macroinvertebrate community

CWD macroinvertebrate densities were highly variable in space and time, with values varying between 304 and 4919 ind.m^{-2}. On average, mean macroinvertebrate densities on CWD were 1046, 1049 and 2335 ind.m^{-2} in spring, summer and autumn respectively. Such densities are very similar to the 922 and 1249 ind.m^{-2} previously reported for two other oligotrophic Canadian lakes respectively, on white cedar, eastern hemlock and sugar maple (Bowen et al. 1998). In contrast, much higher densities have been measured on artificial substrate in lotic systems. For instance, Spänhoff et al. (2000) reported approximately 10,000 ind.m^{-2} on introduced wood substrates in streams of the northern lowland region of Germany. Nilsen and Larimore (1973) exposed CWD for 6 weeks (October to November, 1966) in an Illinois River, and sampled them weekly. After 5 weeks, they reported

colonization densities of 102,170 ind.m^{-2}. Such differences possibly reflect the fact that artificial substrates have to be colonized by pioneer species (r-selected species) until a stable community is reached. Because natural CWD may have resided in water for several decades, and even centuries, they are likely colonized by a stable community (K-selected species) which underlies a higher interspecific competition (Spänhoff et al. 2000). In addition, the comparatively low densities of invertebrates on wood in lakes (as compared to rivers) may be due to differences in food sources. Many wood-inhabiting invertebrates in rivers are passive filterers and their food is delivered by the current – a factor not relevant for lakes.

Season was the main factor structuring macroinvertebrate community, whereas depth and site had no apparent effect on whole community structure. Similar findings have been reported for lotic systems. Johnson and Kennedy (2003) found that macroinvertebrate CWD assemblages in a Texas river were highly variable spatially and temporally, particularly among seasons. In temperate zones, the insect community emergence typically peaks in early summer (Sabo and Power 2002), and to a lower level in early spring (Nakano and Murakami 2001). In fact, such an emergence peak in spring and summer would explain the lowest Chironomids density in autumn in Macpès Lake. The macroinvertebrates density increase we have observed in autumn is almost entirely due to Oligochaeta's density.

Consistent with taxa values reported by other authors (identified to order or family) (Bowen et al. 1998, Warmke and Hering 2000), we found 33 different macroinverebrate

taxa on CWD in Macpès Lake. Even if depth did not appear to be a factor structuring communities (i.e. influencing the occurring taxa and their relative densities), taxa number and Shannon diversity were affected by depth. A possible explanation is that life conditions were less optimal with increasing depth, possibly reflecting increased fish predation (Wong et al. 1998). A species richness decrease with depth was also observed for invertebrates associated with moving substrates in a pond in USA (Studinski and Grubbs 2007), possibly reflecting the many benefits provided by the shallow margins. Terrestrial fungi, bacteria, and protozoa colonize dry detritus. When it becomes inundated, it feeds a fast-growing biofilm community, which supports macroinvertebrates assemblages (Higgins and Merritt 1999).

Chrironomidae larvae were the most common taxa found in spring and summer, at all depths and sites, which is consistent with observations made elsewhere in streams (Magoulik 1998, Spänhoff et al. 2000), rivers (Nilsen and Larimore 1973, Hax and Golladay 1993) and lakes (Bowen et al. 1998). Many chironomids species have short generation times (Thorp and Covich 2001), resulting in higher densities compared to several other taxa.

In our study, the selected environmental variables (temperature, conductivity, DO, pH, wood density, chl-a, AFDW, CWD age) had no effects on macroinvertebrate community structure, an observation already made in a Central Europe stream (Warmke and Hering 2000) and in a Texas stream (Johnson and Kennedy 2003). In contrast,

Magoulick (1998) reported that wood hardness was an important determinant of invertebrate density in a Michigan stream, with higher densities in soft than firm wood. We did not find any relationship between wood density and community structure, but it must be remembered that wood density did not vary between specimens. In addition, we have considered only one species, white cedar, that is known for its relatively low wood density (Hoadley 1990). Additional studies would be needed to examine whether macroinvertebrate community structure vary among CWD species in boreal lakes.

Homogenity of wood density among CWD samples probably reflect the slow decay of submerged wood, along with the fact that CWD were massively recruited in Macpès Lake during a short time interval. CWD recruitment during a short time period relative to a potentially long residence time in water would have resulted in a CWD population with homogeneous mechanical properties of wood. In addition, the lack of CWD recruitment during the last 100 years in Macpès Lake resulted in the absence of bark in all samples, a factor that has probably contributed to homogenize degree of wood alteration. In aquatic habitats, wood is mainly decomposed from its exterior surface by invertebrates and microbial activity (Hendel and Marxsen 2000), rather than from the interior by fungal activity, as in terrestrial habitats (Rayer and Boddy 1988). The lack of correlation between CWD depth and age may also reflect a well- defined recruitment episode, along with CWD redistribution on the steep littoral slopes.

Functional Feeding Groups

Mean biofilm chl-a concentration was maximum in spring, declined in summer and reached a second, smaller peak in autumn. Declining chl-a concentrations in summer and autumn are probably due to algae senescence (Schindler et al. 1973) and grazing. An autumnal decline of chl-a concentration was also reported by Bowen et al. (1998). Although the biofilm developing on woody debris seems to be the only food source for colonizing grazers (scrapers and shredders) (Spänhoff et al. 2000), similar to previous studies in lakes (Bowen et al. 1998, Smokorowski et al. 2006), we did not find any significant correlation between chl-a concentration and macroinvertebrate grazers densities. Algal biomass may then not be controlled by macroinvertebrate densities. However, it must be considered that chl-a is an indicator of algal standing crop biomass, which is only one component of biofilm. The biofilm consists also of bacteria, fungi and actinomycete-like organisms (Tank and Winterbourn 1995) and of fine particulate organic matter (Winterbourn 1982), which are all potential food sources for invertebrates. Organisms may consume mainly algae (Hillebrand et al. 2002) but also fungi and bacteria (Hoffman and Hering 2000). Further studies should focus on investigating the importance of fungi and bacteria as potential food sources for CWD macroinvertebrates.

Implications of human impact

Our dendrochoronological results revealed massive anthropogenic CWD inputs at the turn of the twentieth century. Although tree mortality and ensuing CWD recruitment cannot be dated precisely due to erosion of the external (most recent) tree rings, several

indices suggest that these massive inputs were caused by the rise of the water level at about 1890 during early industrial logging. First, several CWD had an attached stump indicating that their root system had been completely eroded by raised water level. It was common practise during the log driving period, to raise lake levels by several meters in order to increase the spring time flood wave and facilitate downstream log transport. Second, relicts of an ancient dam at the lake Macpès outlet confirm that the lake level had been manipulated at some point in the past. Third, previous studies revealed that logging activity in this area started around 1890 and continued up to the 1923 fire (Boucher 2002, Sorel 2004). Because lake levels were lowered each spring, previously drowned trees at lake margin could be burned by the 1923 fire, thus explaining the high proportion of charred individuals among the most recent CWD. Removal of large riparian trees during the 1890-1923 logging period, along with the 1923 fire, are two additional disturbances that may have contributed to the abrupt increase and ensuing cessation of the CWD inputs.

Recovery of the riparian wood source would take centuries because of the time necessary for large trees to grow up and generate CWD in the lake. Forest recovery would even be longer if we consider the time needed for white cedar to re-establish dominance at lake margin. Cedar is a late successional species, which takes more than one century to recover after disturbances such as fire and logging (Bergeron et al. 2004). For another Canadian lake, it was reported that macroinvertebrate density was higher in white cedar than in two other CWD species (eastern hemlock and sugar maple) (Bowen et al. 1998), highlighting a possible influential role of white cedar CWD as a substrate for

macroinvertebrates. Because timber floating was a widespread activity in North America and Scandinavia during the 19th and 20th centuries, such long-enduring impacts on CWD recruitment patterns have probably been widespread.

In small oligotrophic lakes such as Macpès Lake, benthic primary production and exogenous sources of carbon, such as CWD, likely fuel aquatic food webs (Vadeboncoeur and Lodge 2000, Pace et al. 2004). Humans are rapidly modifying ecosystems by disrupting the link between lakes and riparian forest ecosystems (Riley and Jefferies 2004). Because CWD can reside for long periods of time in lakes (Guyette and Cole 1999), anthropogenic disturbances of the natural CWD input regime have certainly modified the support capacity for macroinvertebrates of the littoral zone for centuries. These changes in CWD dynamics would have direct consequences on CWD macroinvertebrates communities and are likely to propagate to upper trophic levels.

Conclusion

Our study provides much needed information on CWD and associated macroinvertebrate dynamics in lakes. We showed that while macroinvertebrate community structure can be highly variable in space and time, some general predictions are possible. Season appears to be the a very important factor structuring CWD macroinvertebrate communities, but further studies would help to better understand community structuring processes. In addition, this study reveals that former log driving activities, which were widespread in the boreal zone, may have severely disturbed natural inputs of CWD in lakes.

Accordingly, even if we considered only one oligotrophic boreal forest lake in Eastern Québec, our study is likely to assist lake management planning in lentic systems in the context of long-term anthropogenic impact on forest-lake coupling. Future studies are much needed to asses the potentially long-term, large scale impacts of logging driving activities on CWD inputs and associated lake macroinvertebrates across the boreal zone.

Acknowledgements

Table 1. Physical water characteristics in spring, summer and autumn at the
five depths in Macpès Lake

Physical characteristics	Spring					Summer					Autumn				
	1 m	2 m	3 m	4 m	5 m	1 m	2 m	3 m	4 m	5 m	1 m	2 m	3 m	4 m	5 m
Temperature (ºC)	13.9	13.2	12.8	10.6	8.8	25.1	24.1	23.8	21.9	14.4	10.6	10.6	10.5	10.5	10.5
Conductivity ($\mu S.cm^{-1}$)	152	141	149	140	144	204	201	203	201	186	291	317	235	277	239
Dissolved O_2 ($mg.L^{-1}$)	9.3	9.3	9.2	9.1	8.3	7.1	7.1	7.1	7.1	7.3	9.1	9.1	9.1	9.0	9.0
pH	7.6	7.6	7.6	7.6	7.6	7.5	7.6	7.6	7.6	7.3	7.1	7.1	7.1	7.1	7.1

Table 2. Composition (%) of macroinvertebrate taxa found on CWD

Taxa		Spring	Summer	Autumn
Cnidaria				
Hydra spp.		0.51	0.19	0.67
Platyhelminthes				
Turbellaria		1.28	1.78	0.86
Annelida				
Oligochaeta		0.08	7.36	37.45
Mollusca				
Gastropoda		0.05	0.66	0.15
Bivalvia		0.04	0.15	0.02
Nematomorpha		0.07	0.31	0.22
Arthropoda				
Arachnida: Acarina		1.47	2.07	0.91
Crustacea				
Amphipoda		1.91	4.71	2.44
Copepoda		0.31	0.51	0.08
Ostracoda		0.63	0.23	0.00
Branchiopoda: Cladocera		0.02	5.73	0.84
Insecta				
Ephemeroptera				
Baetidae		0	0.10	0.01
Caenidae		0.59	0	0.29
Ephemerellidae		0.27	0.45	0.35
Heptageniidae		6.54	7.00	4.75
Leptophlebiidae		0.13	0.33	0.99
Tricorythidae		1.26	0.06	4.44
Odonata				
Corduliidae		0.01	0	0.04
Trichoptera				
Helicopsychidae		0.05	0	0
Hydroptilidae		0.14	0.03	0.26
Leptoceridae		2.50	0.50	2.21
Limnephilidae		0.26	0.21	0.07
Molanidae		0.01	0	0.01
Policentropodidae		3.72	3.54	4.62
Psychomyidae		0.83	1.15	0.36
Neuroptera				
Sysiridae		0.08	0	0.10
Megaloptera				
Sialidae		0.03	0.02	0.01
Plecoptera				
Perlidae		0.03	0.07	0.02
Coleoptera				
Elmidae	larvae	2.58	9.15	5.09
	adult	0.89	1.47	0.64
Diptera				

Ceratopogonidae	larvae	11.32	1.55	2.81
Ceratopogonidae	pupae	0.12	0	0.76
Chironomidae	larvae	56.01	43.85	26.91
	pupae	4.13	4.65	0.01
	adult	0.87	1.56	0
Empididae		1.14	0.52	1.62
Simulidae		0.07	0	0

Table 3. Mean values (±SE) for density, taxa number, diversity (Shannon index),
chl-a and AFDW for all seasons, depths and sites

		Density (individuals.m^{-2})	Taxa number	Diversity (H')	Chl-a (µg .g^{-1} DW)	AFDW (mg)
Season	Spring	1 046 (±112)	10.82 (±0.42)	1.83 (±0.05)	653 (±72)	24.42 (±5.90)
	Summer	1 049 (±75)	11.90 (±0.39)	1.78 (±0.05)	121 (±11)	10.27 (±1.11)
	Autumn	2 335 (±208)	14.82 (±0.41)	1.56 (±0.07)	441 (±45)	16.28 (±2.19)
Depth (m)	1	1 487 (±187)	13.41 (±0.56)	2.01 (±0.05)	339 (±100)	30.17 (±9.72)
	2	1 595 (±174)	13.04 (±0.65)	1.71 (±0.08)	411 (±57)	16.61 (±2.24)
	3	1 509 (±253)	12.00 (±0.64)	1.70 (±0.06)	435 (±73)	14.48 (±1.93)
	4	1 608 (±249)	12.15 (±0.60)	1.56 (±0.07)	457 (±74)	11.40 (±1.68)
	5	890 (±142)	11.18 (±0.57)	1.55 (±0.08)	442 (±93)	11.72 (±2.27)
Site	1	1 090 (±119)	12.35 (±0.53)	1.77 (±0.04)	324 (±46)	16.97 (±1.94)
	2	1 434 (±104)	12.70 (±0.50)	1.73 (±0.08)	421 (±75)	17.99 (±6.93)
	3	1 902 (±237)	12.30 (±0.41)	1.65 (±0.05)	511 (±61)	16.94 (±1.42)

Table 4. Results from the three-way crossed ANOVA for macoinvertebrate density, taxa number, diversity (Shannon index), chl-a and AFDW (* significant values)

Factor:		log(density+1)	Taxa number	Diversity (H')	log(chl-a+1)	AFDW (Ranked)
Season	F	39.69	26.23	13.16	67.01	12.15
df = 2	p	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Depth	F	4.11	2.56	12.78	2.36	4.73
df = 4	p	0.0044*	0.0449*	<0.0001*	0.0601	0.0017*
Site	F	12.1	0.28	2.05	6.98	6.61
df = 2	p	<0.0001*	0.757	0.1359	0.0016*	0.0022*
2-way interaction						
SeasonxDepth	F	0.89	0.34	0.7	1.09	1.89
df=8	p	0.5309	0.9487	0.6935	0.3766	0.723
SeasonxSite	F	5.06	1.82	13.74	0	4.26
df=4	p	0.0011*	0.1328	<0.0001*	1	0.0035*
DepthxSite	F	1.08	1.23	3.31	0.85	0.4
df=8	p	0.3824	0.2904	0.0025*	0.5657	0.9168
3-way interaction						
Season x Depth x Site	F	1.01	1	1.95	1.45	1.71
df=16	p	0.4482	0.4589	0.0326*	0.1503	0.0702

Table 5. Mean dissimilarity (MD) between communities compared by pairs of seasons calculated by SIMPER. Taxons are ranked in order of their numeric dissimilarity contribution (NDC). Percentage contribution ($\delta i\%$) to the average Bray-Curtis dissimilarity and cumulative percentage ($\Sigma\delta i\%$) are also expressed (cut-off to taxons list applied at 70%)

|	Taxa	NDC	$\delta i\%$	$\Sigma\delta i\%$
Spring - Summer	Chironomidae	15.34	32.71	32.71
MD=46.9	Ceratopogonidae	4.92	10.49	43.21
	Oligochaeta	4.38	9.35	52.55
	Elmidae	3.91	8.34	60.89
	Cladocera (Daphnia)	3.03	6.45	67.34
	Heptageniidae	2.38	5.08	72.42
Spring - Autumn	Oligochaeta	26.92	45.13	45.13
MD=59.64	Chironomidae	11.11	18.63	63.76
	Ceratopogonidae	3.35	5.62	69.39
	Elmidae	2.65	4.44	73.83
Summer-Autumn	Oligochaeta	24.70	45.06	45.06
MD=54.82	Chironomidae	8.13	14.83	59.89
	Tricorythidae	2.79	5.10	64.98
	Elmidae	2.28	4.16	69.14
	Policentropodidae	1.97	3.59	72.72
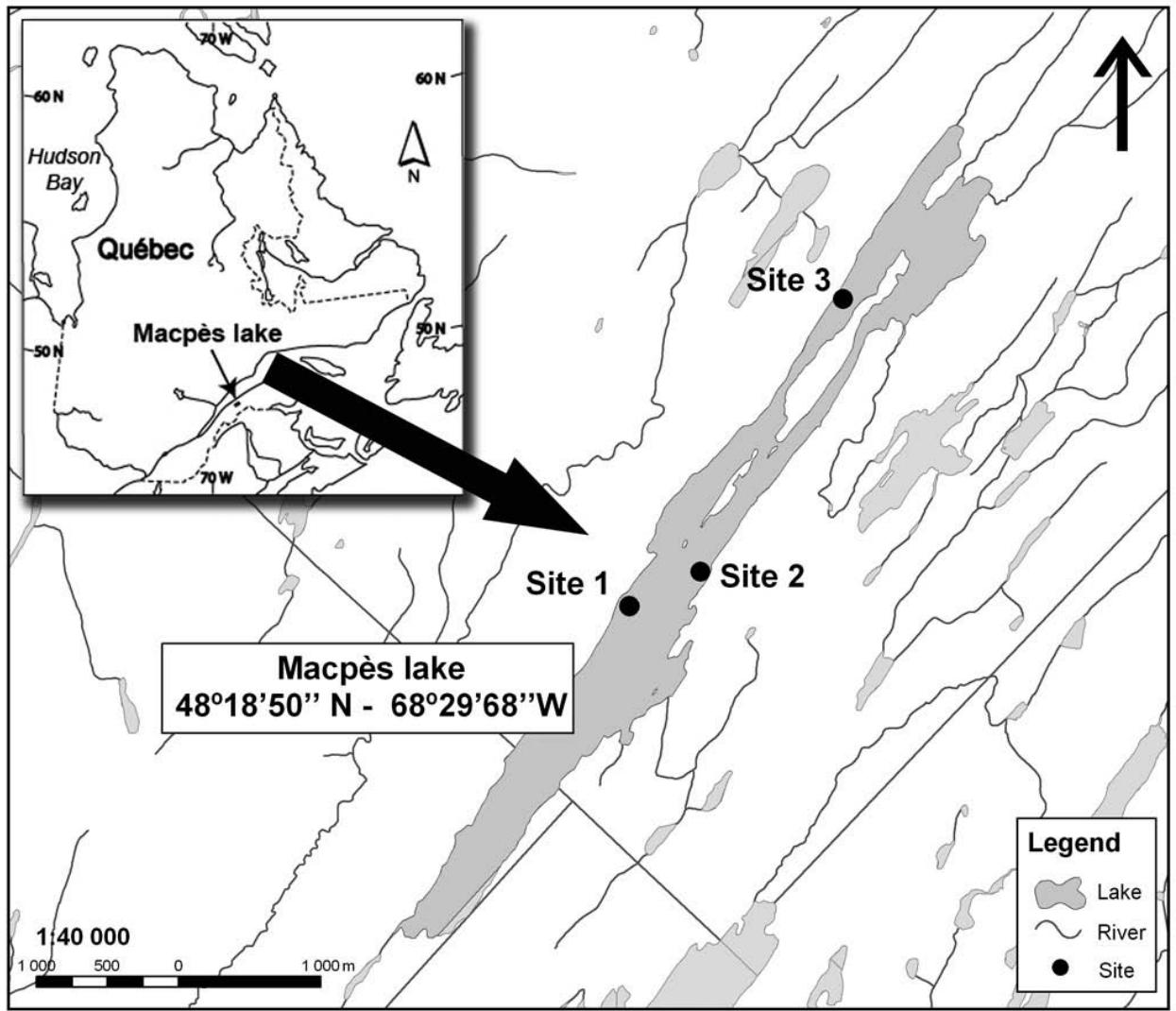
Figure 2. Location of the Macpès Lake in Eastern Quebec (see inset) and the three study sites
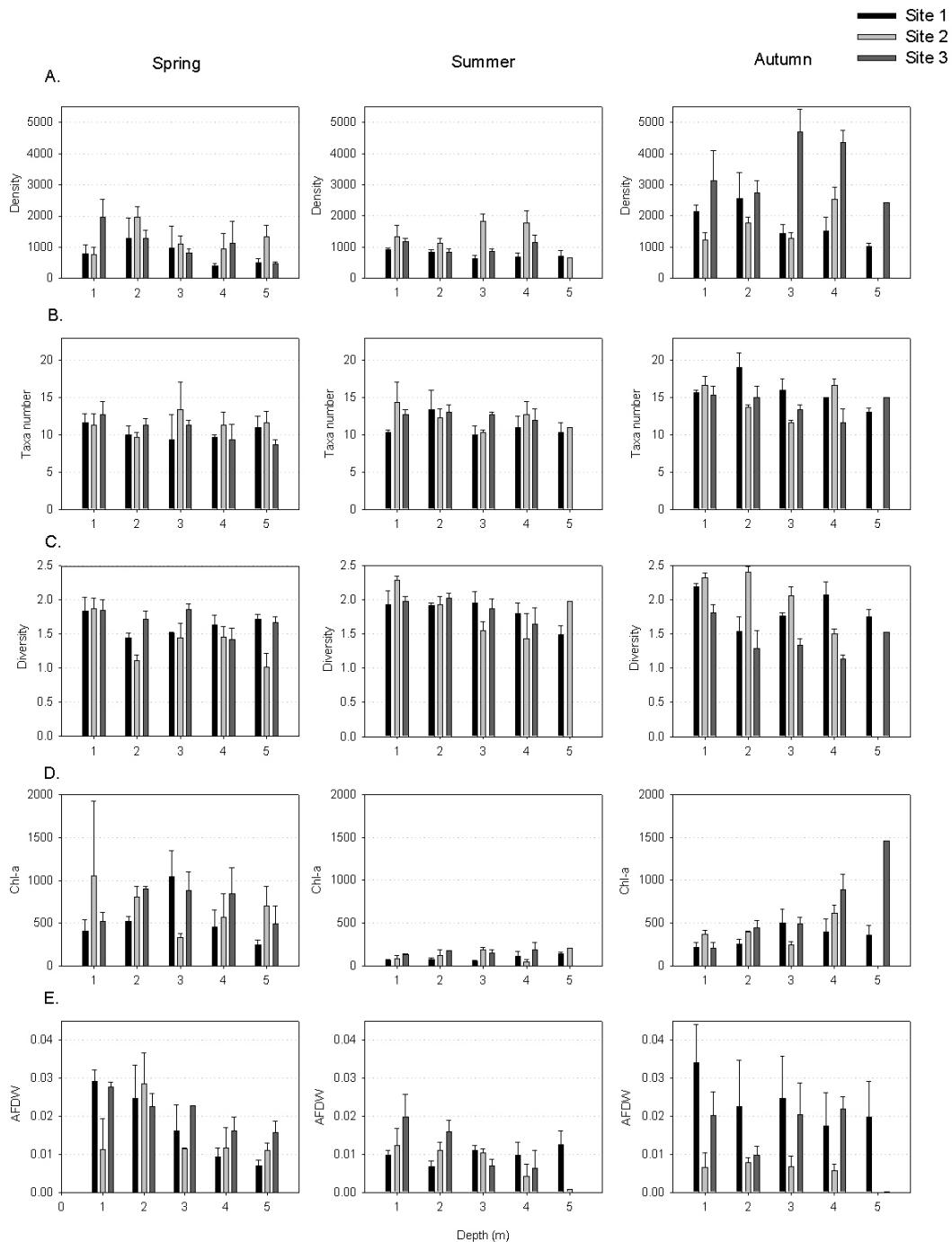
Figure 3. (A) Density (number of individuals.m^{-2}); (B) Taxa number; (C) Shannon diversity index; (D) Chl-a (µg.g^{-1} of dry weight) and (E) AFDW (g) for all depths and seasons. Means ± 1SE are shown.
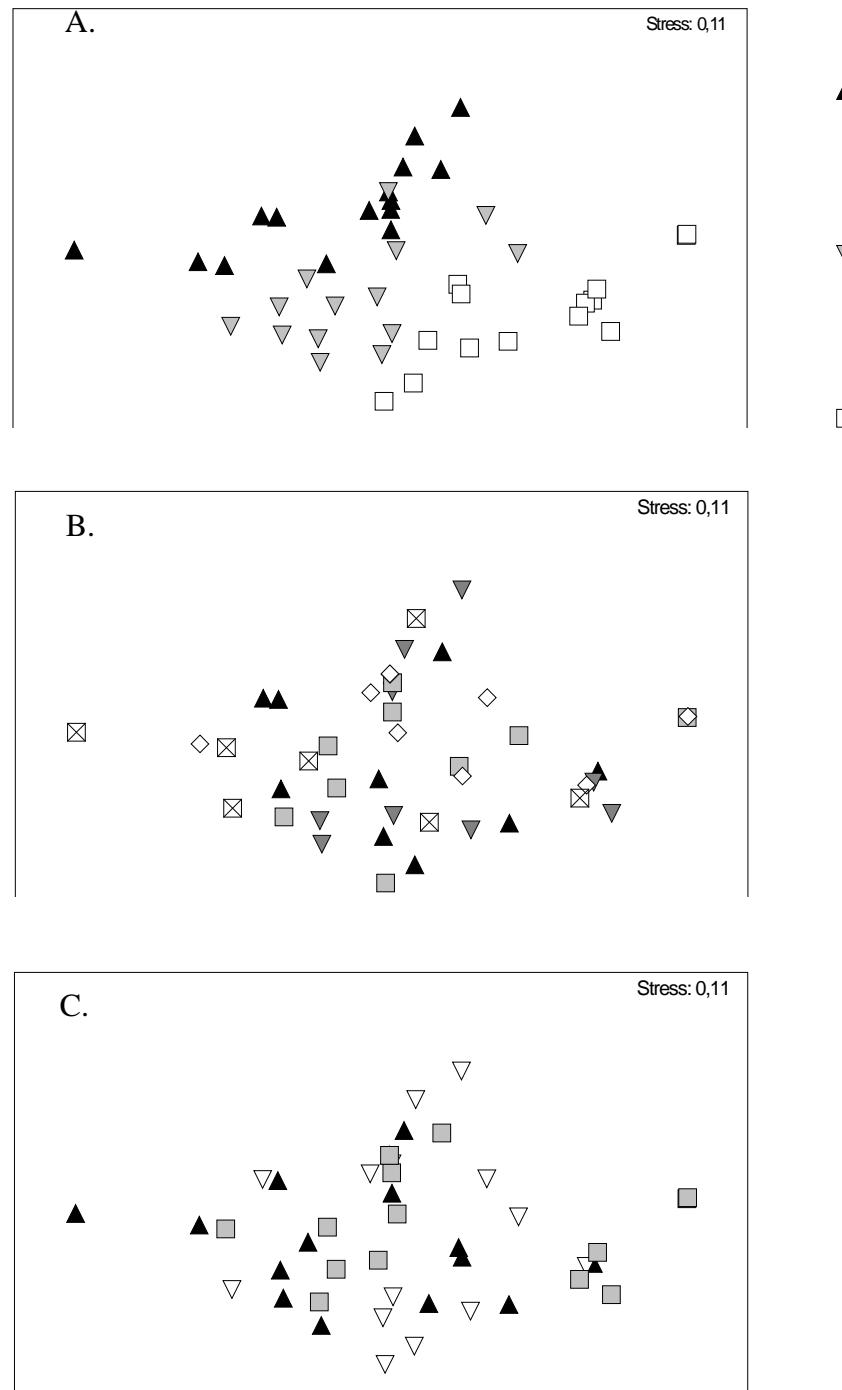
Figure 4. Two-dimensional MDS ordinations of macroinvertebrate community structure among: (A) seasons; (B) depths (m) and (C) sites. Stress = measure of goodness-of-fit
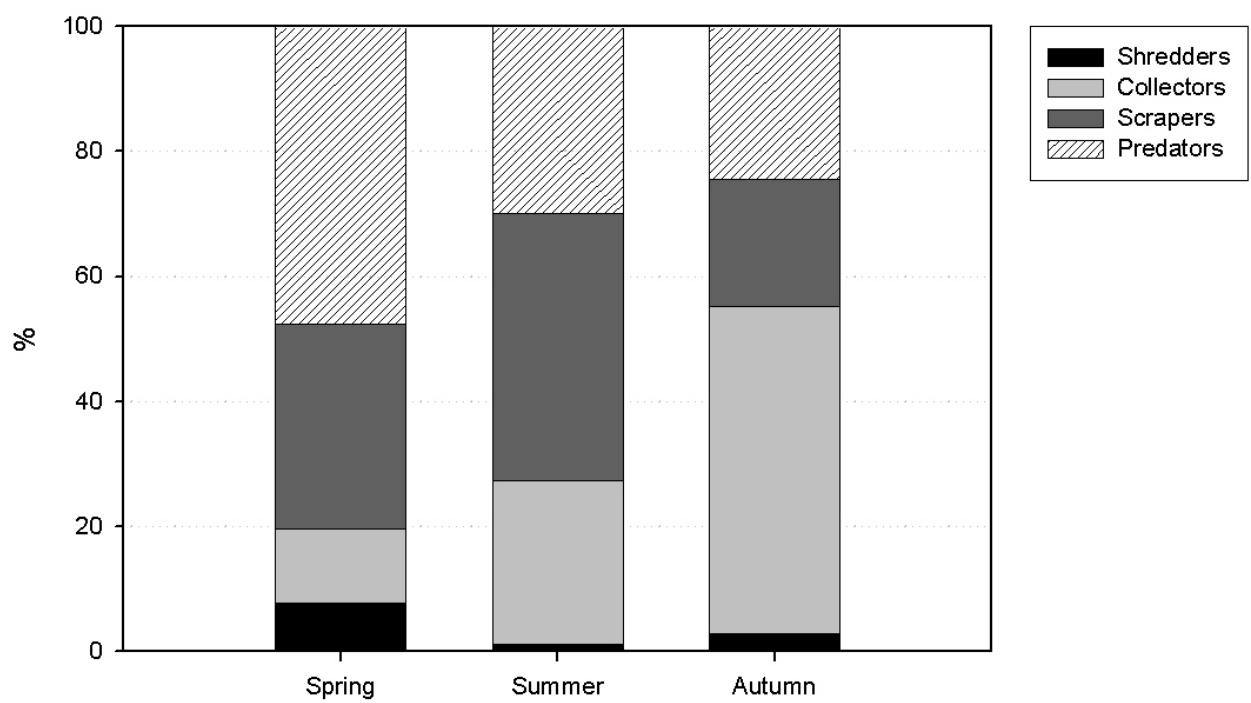
Figure 5. Percent composition of functional feeding groups in spring, summer and autumn
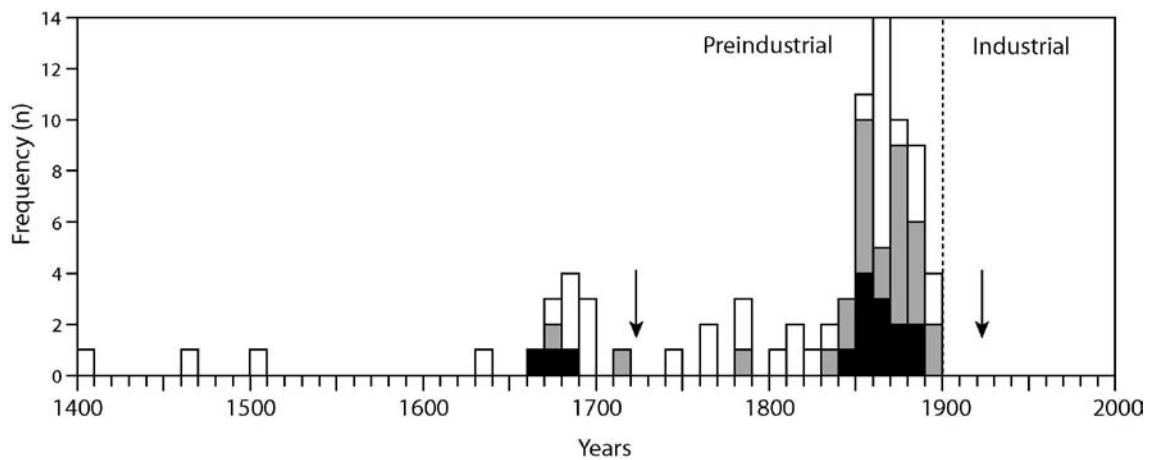
Figure 6. Frequency distribution of outermost tree rings in CWD that could be crossdated using dendrochronology (*n*=80), also indicating individuals with charcoal (black bar) or attached stump (gray bar). Arrows point to the historically documented or presumed fire dates of 1923 and 1720, respectively. The dotted line divides the preindustrial from the postindustrial periods

CONCLUSION GÉNÉRALE ET PERSPECTIVES

Plusieurs études ont été menées sur l'écologie des DLG en milieu lotique. En revanche, il existe très peu d'études portant sur les DLG en milieu lacustre. Ceci peut paraître surprenant, étant donné le grand nombre de lacs que l'on trouve dans le monde, et surtout dans la forêt boréale. Cette étude apporte donc de l'information importante et manquante sur la dynamique des DLG dans les systèmes lentiques. La présente étude nous a permis en particulier de mieux comprendre la dynamique spatiale et temporelle des macroinvertébrés associés aux DLG dans un lac boréal.

La saison s'est avérée être le principal facteur structurant les communautés de macroinvertébrés des DLG. La profondeur et le site n'ont pas montré d'influence sur la structure de la communauté.

Nous avons documenté l'importance du couplage entre les écosystèmes terrestre et aquatique. Les DLG sont une source de matière organique allochtone qui provient de la forêt riveraine et qui remplit différents rôles une fois établis dans la zone littorale des lacs. Nos résultats montrent que ces DLG représentent un lieu de refuge et d'habitat pour les macroinvertébrés.

Les écosystèmes aquatique et terrestre sont couplés pour de longues périodes, le bois se décomposant beaucoup plus lentement dans l'eau qu'en milieu terrestre. Nos résultats

dendrochronologiques montrent comment les impacts anthropiques ont changé à l'échelle séculaire la dynamique naturelle des apports des DLG dans la zone littorale du lac. Ce changement a probablement modifié la capacité de support pour les macroinvertébrés pour les prochains siècles, ce qui aurait des conséquences directes sur les communautés des macroinvertébrés des DLG.

En conclusion, cette étude a montré que même si la structure des communautés des macroinvertébrés peut être très variable, quelques prédictions peuvent être faites. La saison est le principal facteur structurant les communautés. Par contre, cette étude a été effectuée dans un seul lac oligotrophe de la forêt boréale et au cours d'une seule année et avec une seule espèce de DLG. Malgré ces limitations, cette étude nous a permis de mieux comprendre la dynamique des macroinvertébrés dans les lacs et nous a aussi permis de constater l'impact anthropique lors de la période de coupes forestières intenses dans cette région.

Perspectives

Il reste encore beaucoup de connaissances à acquérir concernant le couplage entre les écosystèmes aquatique et terrestre et les communautés de macroinvertébrés des DLG dans l'écosystème lacustre. Pour mieux intégrer les conséquences liées à une perturbation anthropique, comme l'a été les coupes forestières pendant le 19ème siècle, il faut d'abord bien comprendre le système avant ces perturbations. Il serait intéressant d'étudier la structure des communautés de macroinvertébrés des DLG dans plusieurs lacs peu

anthropisés d'une même région permettant ainsi une plus grande généralisation des observations notées. Nous proposons de futures études dans d'autres lacs où les coupes forestières dans la zone riveraine ont été pratiques courantes et sur des lacs non soumis à ces coupes. Ceci nous permettrait éventuellement de mieux mettre en évidence l'impact anthropique de la coupe forestière sur les écosystèmes lacustres et sur les communautés qui y habitent.

Il serait aussi intéressant d'étudier les communautés des macroinvertébrés sur plusieurs années, pour mieux suivre la dynamique temporelle, en comparant les résultats sur plusieurs années. Étudier aussi les macroinvertébrés sur plusieurs espèces de bois nous permettrait d'avoir une vision plus large et plus générale sur les communautés habitant les DLG.

BIBLIOGRAPHIE

Allan, J.D. 1995. **Stream ecology**. Kluwer Academic Publishers. Michigan, USA. 387 p.

Anderson, N.H., et Cummins, K.W. 1979. «Influence of diet on the life histories of aquatic insects». **American Zoologist**, 36, 335-342.

Anderson, N.H., Steedman, R.J., et Dudley, T. 1984. «Patterns of exploitation by stream invertebrates of wood debris (xylophagy)». **Verhandlungen der Internationalen Vereinigung Limnologie**, 22, 1847-1852.

Andrew, N., Rodgerson, L., et York, A. 2000. «Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity». **Austral Ecology**, 25, 99–107.

Andrus, C.W., Long, B.A., et Froelich, H.A. 1988. «Woody debris and its contribution to pool formation in a coastal stream 50 years after logging». **Canadian Journal of Fisheries and Aquatic Sciences**, 45, 2080–2086.

Angermier, P.L., et Karr, J.R. 1984. «Relationships between woody debris and fish habitat in a small warmwater stream». **Transactions of the American Fisheries Society**, 113, 716-726.

Baxter, C.V., Fausch, K.D., et Carl Saunders, W. 2005. «Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones». **Freshwater Biology**, 50, 201–220.

Beechie, T.J., et Sibley, T.H. 1997. «Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams». **Transactions of the American Fisheries Society**, 126, 217–229.

Bergeron, Y., Gauthier, S., Flannigan, M., et Kafka, V. 2004. «Fire regimes at the transition between mixedwood and coniferous boreal forest in Northwestern Quebec». **Ecology**, 85, 1916-1932.

Bilby, R.E. 1981. «Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed». **Ecology**, 62, 1234–1243.

Bilby, R.E., et Bisson, P.A. 1998. «Function and distribution of large woody debris». Dans: **River Ecology and Management**. eds R.J. Naiman and R.E. Bilby. Springer-Verlag, New York, pp. 324–346.

Bilby, R.E., et Likens, G.E. 1980. «Importance of organic debris dams in the structure and function of streams ecosystems». **Ecology**, 61, 1107–1113.

Bilby, R.E., et Ward, J.W. 1991. «Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington». **Canadian Journal of Fisheries and Aquatic Sciences**, 48, 2499–2508.

Blumenshine, S.C., Vadeboncoeur, Y., Lodge, D.M., Cottingham, K.L., et Knight, S.E. 1997. «Benthic-pelagic links: responses of benthos to water-column nutrient enrichment». **Journal of North American Benthological Society**, 16, 466–479.

Boucher, Y. 2002. «**Reconstitution de développement de deux forets du Bas-Saint-Laurent (Québec) en réponse aux perturbations du 20e siècle**». Thèse de maîtrise en gestion de la faune et de ses habitats. Rimouski : Université du Québec à Rimouski,.

Bowen, K.L., Kaushik, N.K., et Gordon, A.M. 1998. «Macroinvertebrate communities and biofilm chlorophyll on woody debris in two Canadian oligotrophic lakes». **Archiv für Hydrobiologie**, 141, 257-281.

Caraco, N.F. et Cole, J.J. 2004. «When terrestrial organic matter is sent down the river : importance of allochthonous C inputs to lakes and rivers». Dans: **Food Webs at the Landscape Level** (eds Polis G. A., Power M. E. and Huxel G.). University of Chicago Press, Chicago, IL, pp. 301-316.

Carpenter S.R., Cole J.J., Pace M.L., Van de Bogert M., Bade D.L., Bastviken D., Gille C.M., Hodgson J.R., Kitchell J.F. et Kritzberg, E.S. 2005. «Ecosystem subsidies: Terrestrial support of aquatic food webs from 13C addition to contrasting lakes». **Ecology**, 86, 2737-2750.

Christensen, D.L., Herwig, B.R., Schindler, D.E., et Carpenter, S.R. 1996. «Impacts of lakeshore residential development of coarse woody debris in north temperate lakes». **Ecological Applications**, 6, 1143–1149.

Clarke, K.R., et Gorley, R.N. 2001. **PRIMER v5: User Manual/Tutorial**. PRIMER-E, Plymouth, U.K.

Cole J.J., Carpenter S.R., Pace M.L., Van de Bogert M.C., Kitchell J.L. et Hodgson J.R. 2006. «Differential support of lake food webs by three types of terrestrial organic carbon». **Ecology Letters**, 9, 558-568.

Collier, K.J., Smith, B.J., et Halliday, N.J. 2004. «Colonization and use of pine wood versus native wood in New Zealand plantation forest streams: implications for riparian management». **Aquatic Conservation: Marine and Freshwater Ecosystem**, 14, 179-199.

Covich, A.P., Austen, M.C., Baerlocher, F., Chauvet, E., Cardinale, B.J., Iles, C.L., Inchausti, P., Dangles, O., Solan, M., Gessner, M.O., Tatzner, B., Moss, B. 2004. «The role of biodiversity in the functioning of freshwater and marine benthic ecosystems». **Bioscience**, 54 (8), 767-775.

Dudley, T.L., et Anderson, N.H. 1982. «A survey of invertebrates associated with wood debris in aquatic habitats». **Melanderia**, 39, 1-21.

Dussart, B. 1966. **Limnologie. L'étude des eaux continentales**. Gauthier – Villars, Paris, France. 677 p.

Eggert, S.L., et Wallace, J.B. 2007. «Wood biofilm as a food resource for stream detritivores». **Limnology and Oceanography**, 52, 1239-1245.

Ehrman, T.P., et Lamberti, G.A. 1992. «Hydraulic and particulate matter retention in a 3rd-order Indiana stream». **Journal of North American Benthological Society**, 11, 341–349.

Everett, R.A., et Ruiz, G.M. 1993. «Coarse woody debris as a refuge from predation in aquatic communities. An experimental test». **Oecologia**, 93, 475-486.

Fausch, K.D., et Northcote, T.G. 1992. «Large woody debris and salmonid habitat in a small coastal British Columbia stream». **Canadian Journal of Fisheries and Aquatic Sciences**, 49, 682–693.

Fischer, W.C., et McClelland, B.R. 1983. **A cavity-nesting bird bibliography – including related titles on forests snags, fire, insects, disease and decay**. Technical Report INT-140. Intermountain Forest and Range Experiment Station, Ogden. Utah. 79 p.

Fortin, J.-C., Lechasseur, A., Morin, Y., Harvey, F., Lemay, J., et Tremblay, Y. 1993. **Histoire du Bas-Saint-Laurent**. Institut québécois de recherche sur la culture, Québec. 860 p.

Francis, T.B., Schindler, D.E., Fox, J.M., et Seminet-Reneau, E. 2007. «Effects of urbanization on the dynamics of organic sediments in temperate lakes». **Ecosystems** [Online First™] doi: 10.1007/s10021-007-9070-0.

Frankland, J.C., Hedger, J.N., et Swift, M.J. 1982. **Decomposer Basidiomycetes, their biology and ecology**. Cambridge Univ. Press, London and New York. pp. 67-90.

Fridman, J., et Walheim, M. 2000. «Amount, structure, and dynamics of dead wood on managed forestland in Sweden». **Forest Ecology and Management**, 131, 23–36.

Graynoth, E., Bennett, L.C., et Pollard, J.C. 1986. «Diet of landlocked sockeye salmon (*Oncorhynchus nerka*) and trout in the Waitaki lakes, New Zealand». **New Zealand Journal of Marine and Freshwater Research**, 20, 537–549.

Gurnell, A.M., Piégay, H., Swanson, F.J., et Gregory, S.V. 2002. «Large wood and fluvial processes». **Freshwater Biology**, 47, 601–619.

Guyette, R.P., et Cole, W.G., 1999. «Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone». **Canadian Journal of Fisheries and Aquatic Sciences**, 56, 496–505.

Guyette, R.P., Cole, W.G., Dey, D.C., et Muzika R. 2002. «Perspectives on the age and distribution of large wood in riparian carbon pools». **Canadian Journal of Fisheries and Aquatic Sciences**, 59, 578-585.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., et Cummins, K.W. 1986. «Ecology of coarse woody debris in temperate ecosystems». **Advances in Ecological Research**, 15, 133-302.

Hax, C.L., et Golladay, S.W. 1993. «Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river». **Freshwater Biology**, 29, 79–87.

Hendel, B., et Marxsen, J. 2000. «Extracellular enzyme activity associated with degradation of beech wood in a Central European stream». **International Review of Hydrobiology**, 85, 95-105.

Higgins, M. J., et Merritt, R.W. 1999. «Temporary woodland ponds in Michigan: invertebrate seasonal patterns and trophic relationships». Dans: Batzer, D. P., Rader, R.B., et Wissinger, S.A. **Invertebrates in Freshwater Wetlands of North America: Ecology and Management**. John Wiley and Sons, New York, pp 279–297.

Hilderbrand, R.H., Lemly, A.D., Dolloff, C.A., et Harpster, K.L. 1997. «Effects of large woody debris placement on stream channels and benthic macroinvertebrates». **Canadian Journal of Fisheries and Aquatic Sciences**, 54, 931–939.

Hillebrand, H., Kahlert, M., Haglund, A.L., Berninger, U.G., Nagel, S., et Wickham, S. 2002. «Control of the microbenthic communities by grazing and nutrient supply». **Ecology**, 83, 2205–2219.

Hoadley, R.B. 1990. **Identifying Wood: accurate results with simple tools**. Taunton Press, Newton Ct. 223 p.

Hoffmann, A., et Hering, D. 2000. «Wood-associated macroinvertebrate fauna in central european streams». **International Review of Hydrobiology**, 85, 25–48.

Holmes, R.L. 1983. «Computer assisted quality control in tree-ring dating and measurements». **Tree-Ring Bulletin**, 43, 69–78.

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., et Strickland, J.D.H. 1965. «Fluorometric determination of chlorophyll». **Journal du Conseil**, 30, 3–15.

James, M. R., Hawes, I., et Weatherhead, M. 2000. «Effects of settled sediments on grazer-periphyton-macrophyte interactions in the littoral zone of a large oligotrophic lake». **Freshwater Biology**, 44, 311–326.

James, M.R., Weatherhead, M., Stanger, C., et Graynoth, E. 1998. «Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand – effects of habitat stability, wind exposure, and macrophytes». **New Zealand Journal of Marine and Freshwater Research**, 32, 287–305.

Johnson, Z.B., et Kennedy, J.H. 2003. «Macroinvertebrate assemblages of submerged woody debris in the Elm Fork of the Trinity River, Texas». **Journal of Freshwater Ecology**, 18, 187–198.

Kornijów, R., Gulati, R.D., et Ozimek T. 1995. «Food preference of freshwater invertebrates: comparing fresh and decomposed angiosperm and filamentous alga». **Freshwater Biology**, 33, 205–212.

Linder, P., et Ostlund, L. 1998. «Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996». **Biological Conservation**, 85, 9–19.

Magoulick, D.D. 1998. «Effect of wood hardness, condition, texture and substrate type on community structure of stream invertebrates». **American Midland Naturalist**, 139, 187–200.

Marburg, A.E., Turner, M.G., et Kratz, T.K. 2006. «Natural and anthropogenic variation in coarse wood among and within lakes». **Journal of Ecology**, 94, 558–568.

Maser, C., et Sedell, J.R. 1994. **From the forest to the sea : the ecology of wood in streams, rivers, estuaries, and oceans**. St. Lucies Press, Delray Beach, Fla. 200 p.

McCafferty, W.P. 1998. **Aquatic Entomology**. Jones and Barlett Publishers, Sudbury, Massachusetts. 448 p.

McKee, A., LeRoi, G., et Franklin, J.F. 1982. «Structure, composition and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park». Dans: **Ecological Research in National Parks of the Pacific Northwest**. (E.E. Starkey, J.F. Franklin et J.W. Matthews, eds.), National Park Service Cooperative Student, Corvalis, Oregon. pp. 22-29.

McKie, B., et Cranston, P.S. 2001. «Colonisation of experimentally immersed wood in south eastern Australia: reponses of feeding groups to changes in riparian vegetation». **Hydrobiologia**, 452, 1–14.

Merritt, R., et Cummins, K.W. 1998. **An introduction to the aquatic insects of North America**. Kendall-Hunt Publishing, Iowa. 441 p.

Nakano, S., et Murakami, M. 2001. «Reciprocal subsidies: dynamic interdependance between terrestrial and aquatic food webs». **Proceedings of the National Academy of Sciences**, 98, 166–170.

Nilsen, H.C., et Larimore, R.W. 1973. «Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois». **Ecology**, 54, 366–374.

O'Connor, N.A. 1992. «Quantification of submerged wood in a lowland Australian stream system». **Freshwater Biology**, 27, 387–395.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van de Bogart, M.C., Bade, D.L., Kritzberg, E.S., et Bastviken, D. 2004. «Wholelake carbon-13 additions reveal terrestrial support of aquatic food webs». **Nature**, 427, 240–243.

Pereira, C.R.D., Anderson, N.H., et Dudley, T. 1982. «Gut content analysis of aquatic insects from wood substrates». **Melanderia**, 39, 23-33.

Pieczyñska, E. 1990. «Lentic aquatic–terrestrial ecotones: their structure, functions and importance. Dans The ecology and management of aquatic–terrestrial ecotones». Dans: **Man and the Biosphere Series Vol. 4**. (R.J. Naiman et H. Décamps eds.). UNESCO and the Parthenon Publishing Group, Park Ridge, N.J. pp. 103–140.

Rayner, A.D.M., et Boddy, L. 1988. **Fungal decomposition of wood**. John Wiley and Sons, New York. 291 p.

Riaux-Gobin, C., et Klein, B. 1993. **Microphytobenthic biomass measurement using HPLC and conventional pigment analysis**. Handbook of methods in aquatic microbial ecology. Lewis Publishers.

Richmond, A.D., et Fausch, K.D. 1995. «Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado». **Canadian Journal of Fisheries and Aquatic Sciences**, 52, 1789–1802.

Riley, R. H., and R. L. Jefferies. 2004. Subsidy dynamics and global change. Dans: **Food webs at the landscape level** (Eds G.A. Polis, M.E. Power, and G.R. Huxel), pp. 410-433. University of Chicago Press, Chicago, IL.

Robinson, E.G., et Beschta, R.L. 1990. «Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA». **Canadian Journal of Fisheries and Aquatic Sciences**, 47, 1684-1693.

Robitaille, A., et Saucier, J.P. 1998. **Paysages régionaux du Québec méridional**. Publications du Québec, Sainte-Foy, Québec. 213 p.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E. et Turner, M.G. 2006. «Fish community and food web responses to a whole-lake removal of coarse woody habitat». **Fisheries**, 31, 321-330.

Sabo, J.L., et Power, M.E. 2002. «River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey». **Ecology**, 83, 1860–1869.

SAS Institute. 2004. **Qualification Tools User's Guide, Version 9.1.2**. SAS Institute Inc., Cary, NC, USA.

Schindler, D.W., Frost, V.E., et Schmidt, R.V. 1973. «Production of epilithiphyton in two lakes of the Experimental Lakes Area, northwestern Ontario». **American Zoologist**, 30, 1511–1524.

Schindler, D.E., et Scheuerell, M.D. 2002. «Habitat coupling in lake ecosystems». **Oikos**, 98, 177-189.

Schulte, U., Spänhoff, B., et Meyer, E.I. 2003. «Ingestion and utilization of wood by the larvae of two Trichoptera species, *Lasiocephala basalis* (Lepidostomatidae) and *Lype phaeopa* (Psychomyiidae)». **Archiv für Hydrobiologie**, 158, 169-183.

SCIEM, 2004. **PAST4 Personal Analysis System for Tree Ring Research, Version 4. Instruction Manual**. SCIEM, Vienna, Austria.

SCIEM, 2005. **OSM. On screen measuring and image analysis. Version 3.35. User manual**. SCIEM, Vienna, Austria.

Shannon, C.E., et Weaver, W. 1949. **The mathematical theory of communication**. University of Illinois Press, Urbana. 117 p.

Sinsabaugh, R.L., Golladay, S.W., et Linkins, A.E. 1991. «Comparison of epilithic and epixylic biofilm development in a boreal river». **Freshwater Biology**, 25, 179-187.

Sippola, A., et Renvall, P. 1999. «Wood decomposing fungi and seed-tree cutting: a 40 year perspective». **Forest Ecology and Management**, 115, 183–201.

Slough, B.G., et Sadleir, R.M.F.S.. 1977. «A land capability classification: system for beaver (*Castor canadensis Kuhl*) ». **Canadian Journal of Zoology**, 55(8), 1324-1335.

Smokorowski, K.E., Pratt, T.C., Cole, W.G., McEacherm, L.J., et Mallory, E.C. 2006. «Effects on periphyton and macroinvertebrates from removal of submerged wood in three Ontario lakes». **Canadian Journal of Fisheries and Aquatic Sciences**, 63, 2038–2049.

Solomon C.T., Carpenter S.R., Cole J.J. et Pace M.L. 2008. «Support of benthic invertebrates by detrital resources and current autochthonous primary production: results from a whole-lake 13C addition». **Freshwater Biology**, 53, 42-54. doi:10.1111/j.1365-2427.2007.01866.x

Sorel, C. 2004. «**Impacts des perturbations anthropiques du XXe siècle sur deux forêts du Bas-Saint-Laurent (Québec)** ». Thèse de maîtrise en gestion de la faune et de ses habitats. Rimouski : Université du Québec à Rimouski.

Spänhoff, B., Alecke, C., et Meyer, E.I. 2000. «Colonization of submerged twigs and branches of different wood genera by aquatic macroinvertebrates». **International Review of Hydrobiology**, 85, 49–66.

Strayer, D.L., et Likens, G.E. 1986. «An energy budget for the zoobenthos of Mirror Lake, New Hampshire». **Ecology**, 67, 303–313.

Studinski, J.M., et Grubbs, S.A. 2007. «Environmental factors affecting the distribution of aquatic invertebrates in temporary ponds in Mammoth Cave National Park, Kentucky, USA». **Hydrobiologia**, 575, 211-220.

Tabour, R.A., et Wurtsbaugh, W.A. 1991. «Predation risk and the importance of cover for juvenile rainbow trout in lentic systems». **Transactions of the American Fisheries Society**, 120, 728-738.

Tank, J.L., et Webster, J.R. 1998. «Interaction of substrate and nutrient availability on wood biofilm processes in streams». **Ecology**, 79, 2168-2179.

Tank, J.L., et Winterbourn, M.J. 1995. «Biofilm development and invertebrate colonization of wood in four New Zealand streams of contrasting pH». **Freshwater Biology**, 34, 303–315.

Thorp, J.H., et Covich, A.P. 2001. **Ecology and classification of North American Freshwater Invertebrates**. Academic Press, San Diego, Calfornia. 1056 p.

Vadeboncoeur, Y., et Lodge, D.M. 2000. «Periphyton production on wood and sediment: substratum-specific reponse to laboratory and whole-lake nutrient manipulations». **Journal of North American Benthological Society**, 19, 68–81.

Vadeboncoeur, Y., Vander Zanden, M.J., et Lodge, D.M. 2002. «Putting the lake back together: reintegrating benthic pathways into lake food web models». **Bioscience**, 52, 44–54.

Vander Zanden, M.J., Cabana, G., et Rasmussen, J.B. 1997. «Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data». **Canadian Journal of Fisheries and Aquatic Sciences**, 54, 1142-1158.

Vander Zanden, M.J., Chandra, S., Park, S.K., Vadeboncoeur, Y., et Goldman, C.R. 2006. «Efficiencies of benthic and pelagic trophic pathways in a subalpine lake». **Canadian Journal of Fisheries and Aquatic Sciences**, 63, 2608–2620.

VanderZanden, M.J., et Vadeboncoeur, Y. 2002. «Fishes as integrators of benthic and pelagic food webs in lakes». **Ecology**, 83, 2152–2161.

Wallace, J.B., et Benke, A.C. 1984. «Quantification of wood habitat in subtropical coastal plain streams». **Canadian Journal of Fisheries and Aquatic Sciences**, 41, 1643–1652.

Wallace, J.B., Webster, J.R., et Meyer, J.L. 1995. «Influence of log additions on physical and biotic characteristics of a mountain stream». **Canadian Journal of Fisheries and Aquatic Sciences**, 52, 2120–2137.

Warmke, S., et Hering, D. 2000. «Composition, microdistribution and food of the macroinvertebrate fauna inhabiting wood in low-order mountain streams in central Europe». **International Review of Hydrobiology**, 85, 67-78.

Webb, A.A., et Erskine, W.D. 2003. «Distribution, recruitment and geomorphic significance of large woody debris in an alluvial forest stream: Tonghi creek, southeastern Australia». **Geomorphology**, 51, 109–126.

Wetzel, R.G. 2001. **Limnology: lake and river ecosystems**. Academic Press. San Diego, California. 1006 p.

Winterbourn, M.J. 1982. «The invertebrate fauna of a forest stream and its association with fine particulate organic matter». **New Zealand Journal of Marine and Freshwater Research**, 16, 271–281.

Wong, A.H.K. Williams, D.D., McQueen, D.J., Demers, E., et Ramcharan, C.W. 1998. «Macroinvertebrate abundance in two lakes with contrasting fish communities». **Archiv für Hydrobiologie**, 141(3), 283-302.