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Plasticité phénotypique des daphnies et réponses de la communauté des crustacés planctoniques au développement résidentiel des lacs du sud du Québec

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Faculté des études supérieures

Cette thèse intitulée

Plasticité phénotypique des daphnies et réponses de la communauté des crustacés planctoniques au développement résidentiel des lacs du sud du Québec

présentée par
Malorie Gélinas

a été évaluée par un jury composé des personnes suivantes

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Bernadette Pinel-Alloul	directrice de recherche
Beatrix Beisner	membre du jury
Joanna Pijanowska	examinateur externe
Pierre Richard	représentant du doyen

Résumé

À l'heure actuelle, l'intérêt grandissant des riverains pour la conservation de leur lacs ou rivières force les écologistes à inclure dans leurs modèles l'intégrité des processus pouvant avoir des répercussions positives ou négatives sur l'ensemble de l'écosystème aquatique. Le zooplancton est au centre des réseaux trophiques des lacs; il relie principalement les algues et les poissons, deux composantes biologiques au cœur des préoccupations des riverains des lacs. La structure ainsi que la dynamique de la communauté zooplanctonique est un indicateur important de l'état trophique d'un lac au niveau régional et même continental puisque la biomasse et la taille des organismes composant la communauté des crustacés zooplanctoniques change en fonction du statut trophique du lac. Plus précisément, la composition de la communauté zooplanctonique joue un rôle clef dans les cascades trophiques ascendantes au niveau des apports en nutriments (phosphore et azote) et de la croissance des algues ou descendantes au niveau de la prédation exercée par les poissons et les invertébrés planctonophages. En particulier, les daphnies assurent une meilleure croissance et survie aux poissons planctonophages et maintiennent la transparence des eaux au début de l'été.

La recherche comporte deux volets majeurs incluant chacun deux articles scientifiques. Dans le premier volet, on a étudié en milieu naturel la plasticité phénotypique des réponses adaptatives des daphnies à la prédation exercée par les jeunes perchaudes de l'année et les invertébrés prédateurs (larves de *Chaoborus* et *Leptodora kindtii*) dans un lac méso-eutrophe du sud du Québec. Nous avons évalué le développement de stratégies morphologiques, démographiques et comportementales chez deux populations de daphnies coexistant dans le lac Brome (Cantons de l'Est, Québec). Nous avons mis en évidence un mécanisme de sélection négative des proies basé sur la taille. Les jeunes perchaudes de l'année sélectionnent préférentiellement les juvéniles des deux espèces de daphnies puis les adultes au cours de leur développement ontogénique et de leur croissance. Les deux espèces de daphnies adoptent des stratégies de défense alternatives selon le type de prédateurs et leur taille. Les deux espèces (*D. pulicaria, D. galeata mendotae*) développent des défenses de type comportemental (migration verticale journalière, grande profondeur de résidence) ou démographique (petite taille à maturité, production d'œufs de durée) comme stratégies anti-prédatrices en présence des jeunes perchaudes tandis que la plus petite espèce (*D. galeata mendotae*) développe des réponses morphologiques (capuchon céphalique proéminent) en présence de prédateurs invertébrés comme les larves de *Chaoborus* et *Leptodora kindtii*. Ce premier volet de la recherche met en évidence la grande plasticité phénotypique des stratégies anti-prédateurs des populations de daphnies en milieu naturel, alors que les études antérieures étaient surtout expérimentales.

Dans le deuxième volet, nous avons évalué la réponse de la communauté des crustacés planctoniques et des populations de daphnies à un gradient de développement résidentiel du bassin versant dans des lacs de la région des Laurentides sujets à une urbanisation récente et rapide depuis les années 1970. Nous avons étudié les variations de la structure et la distribution verticale des crustacés planctoniques et des populations de daphnies en fonction des facteurs naturels tels que la morphométrie des lacs et des bassins versants, l'enrichissement en nutriments et l'augmentation de la biomasse algale, et en fonction des facteurs de perturbation du bassin versant et des rives par le développement résidentiel. Nous avons mis en évidence les effets en cascade du développement résidentiel, mesuré par la densité des résidences et le pourcentage de zones ouvertes sur l'ensemble du bassin, sur la structure et la distribution verticale de 7 groupes fonctionnels de crustacés et de 6 espèces de daphnies. L'enrichissement en phosphore est l'élément intermédiaire primordial dans la cascade d'effets. La structure des groupes fonctionnels de crustacés et des populations de daphnies varie selon le niveau de développement résidentiel. Certains groupes et espèces ont un bon potentiel d'indicateur du niveau de perturbation. Les petites espèces de Cladocères et de daphnies se retrouvent généralement dans les lacs les plus perturbés tandis que les calanoïdes et les grandes espèces de daphnies sont caractéristiques des lacs les plus vierges. La profondeur de résidence des crustacés et des daphnies est contrôlée en priorité par la stratification thermique, photique et chimique des lacs, et aussi par la morphométrie des bassins versants, le niveau de phosphore disponible et la biomasse algale. Les résultats de cette thèse mettent en évidence l'importance de considérer les caractéristiques environnementales naturelles régularisant la communauté zooplanctonique, en même temps que les activités anthropiques afin de mieux caractériser les réponses des lacs du sud du Québec aux changements locaux et globaux.

Mots clés : *Daphnia*, crustacés planctoniques, plasticité phénotypique, prédation, défenses anti-prédateur, facteurs naturels et anthropiques, développement résidentiel, lacs

Summary

Actually increasing awareness of cottagers for the conservation of their lakes and rivers forces aquatic ecologists to integrate all natural and human processes, having positive and negative impacts on aquatic ecosystems, in their models. Zooplankton is a key element in aquatic food webs, linking nutrient and algae to fish, two components of interests for lake users. The structure and dynamic of the zooplankton community is an important indicator of the trophic state of lakes both at regional and continental scales as biomass and size of crustacean species change accordingly to lake trophic status. In particular, crustacean zooplankton community composition plays an important role in bottom-up trophic cascades allowing the energy to flow through nutrient and algal components and in top-down trophic cascades by fish and invertebrate predation. Especially, *Daphnia* species are keystone elements of plankton food webs; they enable survival and growth of fish populations and maintain water clarity during summer.

The research thesis is composed of two major sections, each of them including two scientific papers. In the first section, we studied the phenotypic plasticity of adaptive responses of *Daphnia* facing *in situ* predation pressure by young-of-the-year perch and invertebrates (*Chaoborus* larvae and *Leptodora kindtii*) in a meso-eutrophic lake in southern Québec. We analysed how two *Daphnia* species of different size coexisting in Lake Brome (Eastern Townships, Québec) developed different inducible defences by changing morphological, life-history and behavioural traits. We showed a mechanism of negative size-selection by the young-of-the-year perch toward both juvenile stages of *Daphnia* species before switching to *Daphnia* adult stages during their ontogenic development and growth. Both *Daphnia* species developed alternative anti-predator strategies depending of predator types and of their body size. Both *Daphnia* species developed behavioural traits (diurnal vertical migration, deeper residence depth during daytime) over life-history traits (size at maturity, production of resting eggs) as anti-predator defences when facing young-of-the-year perch. The small *D. galeata mendotae* developed morphological traits (longer helmet) in the presence of invertebrate predators, *Chaoborus* larvae and *Leptodora kindtii*, where the small body size *D. galeata mendotae* showed a longer helmet to cope with the predation pressure. The first section of the thesis illustrated the high phenotypic plasticity of anti-predator strategies developed by *Daphnia* populations in natural conditions within lake ecosystems, when most of previous studies were conducted under experimental conditions.

In the second section, we evaluated responses of crustacean zooplankton communities and *Daphnia* populations to watershed disturbances by residential development in Laurentian lakes subjected to rapid and recent urbanization since the seventies. We studied variations in crustacean community structure and vertical distribution of functional groups and *Daphnia* species in relation to natural changes in lake and watershed morphometry, enrichment in nutrients and algal biomass, and to disturbance by residential development on watershed and shorelines of lakes. We showed cascading effects of residential development and land-cover disturbance, as measured by dwelling density and percentage of open area in forest cover, on the structure and depth selection patterns of 7 crustacean functional groups and 6 *Daphnia* species. Nutrient enrichment in total phosphorus was a key intermediate element in cascading effects. Crustacean community structure and *Daphnia* species assemblages varied with the intensity of residential development. Some groups and *Daphnia* species offered some potential as bio-indicators of disturbance by residential development. Small cladoceran and *Daphnia* species were generally found in the most disturbed lakes, whereas calanoids and large *Daphnia* species occurred in more pristine lakes. Mean residence depth of crustaceans and *Daphnia* species was primarily related to temperature, light and oxygen stratification in the water column, and secondly to watershed morphometry, concentrations of dissolved phosphorus and algal biomass. The results of the thesis emphasises the importance of both natural environmental factors and anthropogenic disturbances as forces driving the responses of crustacean zooplankton communities to local and global changes in Québec lakes.

Keywords: *Daphnia*, crustacean zooplankton communities, phenotypic plasticity, predation anti-predator defences, natural and anthropogenic factors, residential development, lakes

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À

Karène

ma jumelle d’âme

et mon humoriste personnelle préférée

et

Colette

ma mère

cette femme forte au regard taquin que j’admire

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Chapitre 1

Introduction générale

1.1 Généralités sur les réseaux trophiques lacustres

Le zooplancton est une composante clé des réseaux trophiques pélagiques des lacs qui relie les compartiments ascendants et descendants (McQueen et al. 1986; Lazarro et Lacroix, 1995) (Figure 1.1). Les compartiments ascendants sont couramment appelés 'bottom-up' et regroupent les nutriments, les bactéries, les protistes et le phytoplancton. La production des algues dépend en grande partie des nutriments, principalement du phosphore (P) et de l'azote (A), présents et entrant dans le milieu aquatique (Schinder 1977; Dillon et al. 1988). Le zooplancton exerce un grand potentiel de broutage sur les algues (Mazumder 1994). Les compartiments descendants sont nommés 'top-down' et regroupent les poissons piscivores et planctonophages et les invertébrés prédateurs tels les larves de *Chaoborus*, de *Leptodora kindtii* et les crevettes d'eau douce *Mysis*. Le zooplancton sert de nourriture aux poissons planctonophages et aux prédateurs invertébrés (Balvay 1995; Pinel-Alloul 1995). Par son double rôle de brouteur sur le phytoplancton et de proie pour les poissons et les invertébrés planctivores, le zooplancton module les interactions entre les niveaux trophiques et la dynamique des réseaux pélagiques (Sommer et al. 1986).

A

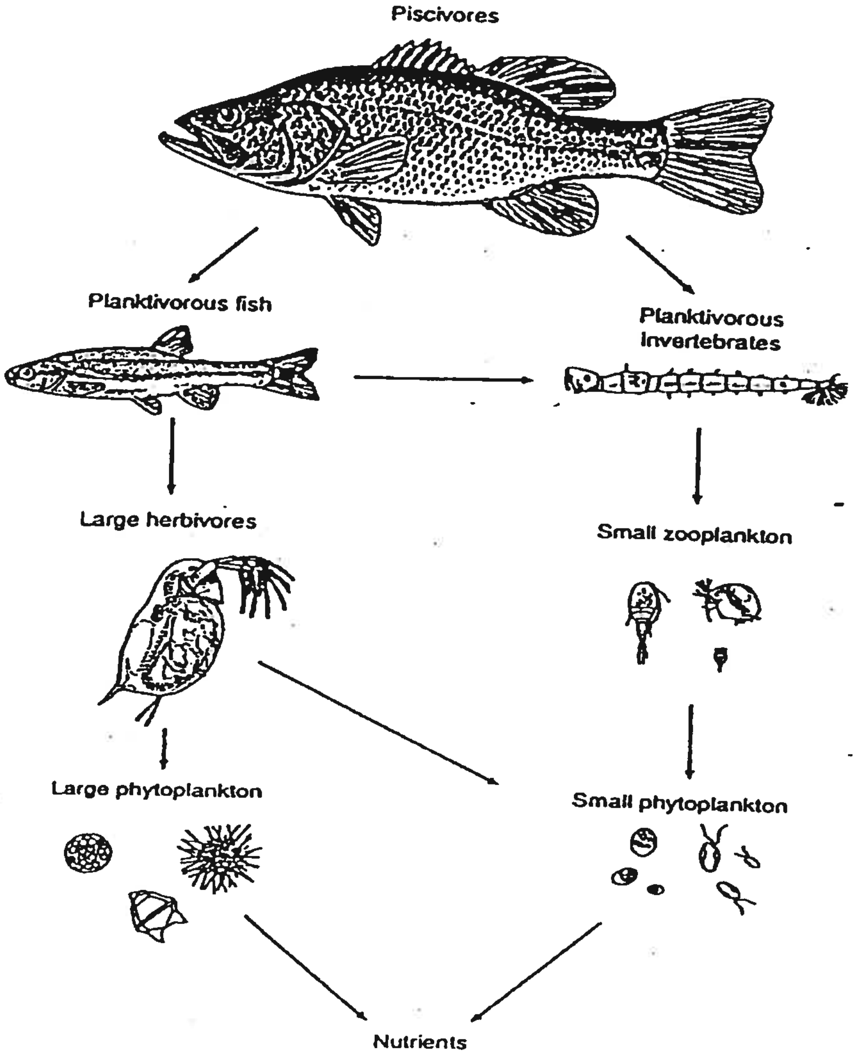

Figure 1.1. Réseau trophique pélagique tiré du libre 'The Trophique Cascade in Lakes' tiré de Carpenter and Kitchell (1993).

La manipulation biologique des réseaux pélagiques est une stratégie employée pour améliorer la qualité de l'eau des lacs. La manipulation des compartiments descendants (poissons) des réseaux pélagiques peut produire une cascade d'interactions trophiques ressentie jusqu'aux niveaux inférieurs (phytoplancton) (Carpenter et al. 1985). En conditions naturelles dans les lacs méso-eutrophes lorsque l'abondance des poissons piscivores est faible, l'abondance de leurs proies, les poissons planctivores sera forte. Ceux-ci pourront alors exercer une forte prédation sur les crustacés zooplanctoniques de grande taille. Ces gros herbivores devenus en trop faible abondance ne seront plus en mesure de contrôler le développement du phytoplancton. En conséquence, la biomasse des algues augmentera et l'eau sera moins transparente (Figure 1.2). Pour augmenter la transparence de l'eau, un signe indéniable de meilleure qualité de l'eau, on peut manipuler les réseaux trophiques en introduisant des poissons piscivores. En augmentant l'abondance des poissons piscivores, on provoque une cascade trophique qui va diminuer l'abondance de leurs proies, les poissons planctonophages. En conséquence, la pression de prédation des poissons planctonophages sur le zooplancton sera réduite. Ceci aura pour effet d'augmenter l'abondance du zooplancton herbivore et le broutage sur le phytoplancton. La baisse de l'abondance des algues suite à ce broutage intense aura pour conséquence d'accroître la transparence de l'eau et d'améliorer la qualité de l'eau. (Figure 1.2).

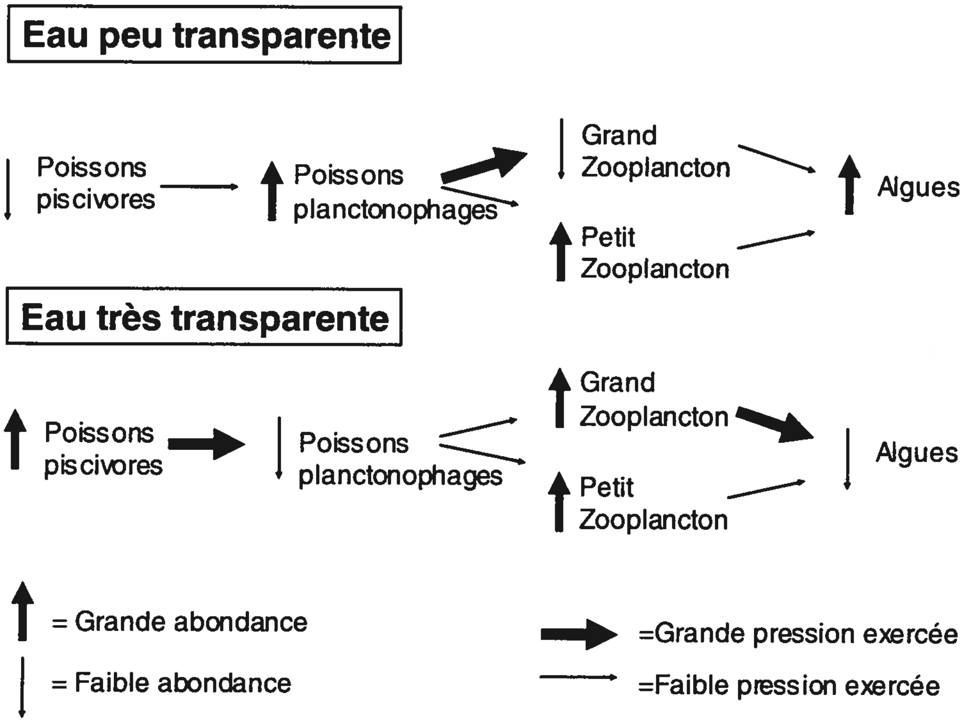

Figure 1.2 : Manipulation biologique en cascade des réseaux trophiques pélagiques.

Au sein de la communauté des crustacés planctoniques, le genre *Daphnia* joue un rôle crucial et intéresse les scientifiques depuis le $17^{\text{ième}}$ siècle (Edmondson 1987). *Daphnia* est une composante dominante des communautés de cladocères planctoniques des lacs. Son rôle réside dans sa grande capacité de filtration de l'eau (jusqu'à 14 ml d'eau individu L^{-1} jour L^{-1} ; Kasprzak et al. 1986) et de broutage du phytoplancton (Cyr 1998; Beisner 2001) De plus, par la grande diversité en taille des particules ingérées, les daphnies sont des herbivores généralistes importants (Cyr 1998; Breisner 2001). Ce grand potentiel de broutage des daphnies a un effet important sur la succession saisonnière du phytoplancton lacustre (Soranno et al. 1993; Kasprzak et al. 1999). Au début de l'été, la diminution de la biomasse algale provoquée par le broutage intense des daphnies crée une phase des eaux claires dans la zone pélagique des lacs qui se traduit par une augmentation significative de la transparence de l'eau (Lampert 1988). Le rôle primordial des daphnies pour le développement de la phase des eaux claires a été confirmé dans de nombreuses études (révisé par Lampert 1988). De plus, des études en milieu naturel et des expériences en enceintes limniques ont démontré l'importance des daphnies pour le transfert de l'énergie des producteurs primaires aux niveaux trophiques plus élevés (Carpenter et Kitchell 1993; Benndorf 1995). Ainsi, les écosystèmes lacustres incluant une majorité de daphnies dans la communauté zooplanctonique sont plus sujets aux cascades tropiques en réponse aux changements dans l'abondance des ressources algales ou des prédateurs planctonophages (Leibold 1989; Carpenter et Kitchell 1993; Elser et al. 2000).

1.2 Hétérogénéité de la zone pélagique lacustre

La dynamique du zooplancton des lacs tempérés dépend de l'hétérogénéité spatiale et temporelle des conditions abiotiques et biotiques dans la zone pélagique. Elle est principalement gouvernée par la température de l'eau, l'accessibilité à la nourriture et la compétition pour la nourriture, ainsi que par la prédation des poissons et des invertébrés (Threlkeld 1987). Parmi les facteurs temporels abiotiques, on retrouve la température, la lumière et la qualité physico-chimique de l'eau (calcium, nutriments) alors que les principaux facteurs temporels biotiques sont les ressources algales, la compétition et la prédation. Par exemple, les contraintes temporelles dues au cycle saisonnier de la température et de la photopériode influent sur l'alternance entre la production d'œufs parthénogénétiques et d'œufs de durée (éphippium) (Pijanowska et Stolpe 1996; Hairston et al. 2000). L'intensité lumineuse, tout comme l'anoxie, modifient le comportement migratoire journalier (Ringelberg 1999; Lass et al. 2000) et la profondeur de résidence des crustacés (de Meester et al. 1999). La quantité et la qualité des ressources consommées affectent le taux de croissance et la reproduction (Urabe et Sterner 2001; Boersma et al. 2001; Hülsmann 2001) tandis que les prédateurs contrôlent surtout la taille à maturité et la densité des populations (Stibor et Navarra 2000; Hanazato et al. 2001; Mikulski 2001; Gliwicz 2001; Stibor 2002), la production d'œufs de durée (éphippium) chez les daphnies (Slusarczyk 1995) ainsi que les comportements migratoires journaliers (Lampert 1993a; Angeli et al. 1995a et b; Masson et al. 2001).

Dans la zone pélagique des lacs profonds de la région boréale, il s'établit durant l'été une stratification des masses d'eau créant une hétérogénéité spatiale verticale de la colonne d'eau. Les trois couches d'eau correspondent à l'épilimnion, une zone d'eau chaude bien mélangée et bien éclairée en surface, au métalimnion, une zone associée à un fort gradient thermique et chimique au niveau de la thermocline et à l'hypolimnion, une zone d'eau froide peu éclairée en profondeur (Wetzel 2001). Le principal facteur physique ayant une action déterminante sur la dynamique du zooplancton est la température de l'eau qui diminue en fonction de la profondeur. La stratification thermique agit et contrôle les processus métaboliques, telle que la croissance et la durée de développement puisque les organismes zooplanctoniques sont poïkilothermes (Lair 1995). Un individu peut survivre sous le seuil optimal de température mais ne peut se reproduire (Vijverberg 1980). Des températures élevées permettent un développement embryonnaire plus rapide mais la disponibilité de la nourriture, sa quantité et sa qualité, jouent également un rôle primordial (Müller-Navarra et Lampert 1996). Une résidence dans l'épilimnion en eau chaude et bien oxygénée est favorable à la croissance et la reproduction, des paramètres clés qui déterminent le taux de natalité des populations zooplanctoniques.

La production algale n'est pas uniforme dans la colonne d'eau. En général, elle est plus forte dans l'épilimnion puisque c'est la zone de surface qui est la plus éclairée et qui reçoit les apports en phosphore et azote du bassin versant. Toutefois, il peut se former des pics de chlorophylle en profondeur au niveau du métalimnion ou de la zone supérieure de l'hypolimnion dans les lacs oligo-mésotrophes ayant une forte transparence (Pick et al. 1984). Ces pics profonds de biomasse algale peuvent être utilisés par les daphnies qui peuvent migrer de la zone métalimnétique où elles se tiennent en journée à la zone épilimnétique durant la nuit. La distribution des algues peut influencer de façon importante la distribution des crustacés planctoniques, et en particulier des daphnies (Pilati et Wurtsbaugh 2003). Toutefois, plusieurs autres facteurs peuvent aussi modifier la dynamique de distribution verticale des daphnies. Le gradient de température joue un rôle déterminant (Winder et al. 2003) ainsi que le niveau d'oxygénation de l'eau. La concentration minimale en oxygène requise pour la survie des communautés zooplanctoniques est de 1 $mg.L^{-1}$. L'anoxie dans l'hypolimnion de certains lacs peut donc forcer les daphnies à rester dans l'épilimnion toute la journée et ce, même en présence de poissons planctonophages (Lass et al. 2000; Santos-Magalhaes 2005). Cependant, les daphnies peuvent fréquenter temporairement l'hypolimnion anoxique des lacs grâce à des adaptations métaboliques de production d'hémoglobine (Weider et Lampert 1985).

L'anoxie des eaux profondes restreint également la distribution spatiale des poissons planctonophages. Les zones profondes des lacs sont donc des zones de refuge potentiel pour le zooplancton vis-à-vis de la prédation par les poissons planctonophages (Wright et Shapiro 1990).

L'épilimnion est considéré comme la zone idéale qui favorise la croissance et la reproduction du zooplancton. Les eaux superficielles chaudes et la grande biomasse algale favorisent la croissance et la reproduction des crustacés planctoniques. Par contre, la grande luminosité de cette zone augmente la visibilité des proies zooplanctoniques et par conséquent le risque qu'elles soient attaquées par des prédateurs chassant à vue. En zone profonde dans le metalimnion et l'hypolimnion, la température et l'oxygénation plus faibles limitent la croissance et la reproduction du zooplancton mais la faible luminosité et l'anoxie diminue le risque de prédation. Pour assurer leur survie en limitant les risques de prédation tout en maximisant leur croissance et leur reproduction (fitness), les crustacés zooplanctoniques, en particulier les daphnies, doivent choisir durant le jour la profondeur de résidence idéale qui représente le meilleur compromis. Par contre, ce compromis n'est plus en vigueur la nuit puisque le risque de prédation est faible dû à l'absence de lumière et les crustacés peuvent alors choisir la zone de surface qui assure les meilleures conditions de croissance. En conséquence, les crustacés, et en particulier les daphnies, ont adopté un comportement migratoire journalier (DVM : diel vertical migration) qui comporte un mouvement ascendant durant la nuit afin de profiter de la chaleur et de l'abondance de nourriture en surface et un mouvement descendant durant le jour pour se protéger de la prédation en profondeur (Lampert 1989; Ringelberg 1999; Lass et al. 2000). L'intensité lumineuse influence l'amplitude de la migration verticale (Ringelberg 1999), mais la réponse varie selon le niveau de satiété des daphnies. L'amplitude de migration des individus affamés est beaucoup plus faible que celle des individus bien nourris, peu importe la présence ou l'absence de prédateurs (Van Gool et Ringelberg 1998). En conditions expérimentales, seules les daphnies bien nourries en présence de kairomones de poissons ont répondu positivement à l'augmentation de l'intensité de lumière en nageant vers le fond de la colonne d'eau (Van Gool et Ringelberg 1998; Ringelberg 1999). Toutefois, le comportement migratoire implique un coût métabolique qui limite la croissance et la reproduction. Loose et Dawidowicz (1994) ont trouvé que le coût principal de la migration journalière est la réduction du taux d'accroissement (r) de la population due aux températures froides des couches profondes des lacs stratifiés peu importe la quantité de nourriture (Dawidowicz et Loose 1992). Pour les individus migrants, la rareté de la nourriture en zone profonde couplée à sa faible qualité sont désavantageux comparé aux individus non-migrants qui sont situés dans les couches superficielles et bénéficient de bonnes conditions. De façon générale, les prédateurs ont un impact direct sur la dynamique des populations, la profondeur de résidence et les patrons de migration des crustacés zooplanctoniques. Toutefois, il y a encore peu d'études qui ont examiné les effets complexes des prédateurs sur la dynamique des populations de crustacés planctoniques en milieu naturel, sujets aux variations temporelles et spatiales d'ordre naturel et aux perturbations anthropiques.

1.3 Prédation préférentielle

La prédation est un agent important de la sélection naturelle sur les communautés de zooplancton (Brooks et Dodson 1965). L'été est une phase intensive de prédation par les poissons et les invertébrés planctonophages et les populations de crustacés zooplanctoniques ont développé des stratégies pour contrer la prédation. Par le biais des cascades trophiques, la présence de poissons planctonophages dans un lac peut complètement changer la communauté, la dynamique et la structure en taille du zooplancton (Brook et Dodson 1965). Dans certains lacs du Connecticut, seulement les petites espèces comme les rotifères et les bosminidés étaient présentes dans les lacs ayant de fortes densités poissons planctonophages (Aloses) alors que seules les espèces de grande taille (> à 1mm) comme les daphnies étaient présentes dans les lacs exempts de prédateurs planctonophages (Brook et Dodson 1965). Ce phénomène est maintenant reconnu comme étant la prédation sélective en fonction de la taille 'size-selective predation'.

Les communautés de zooplancton sont donc façonnées en fonction de la présence ou de l'absence de prédateurs. Les poissons planctonophages et les invertébrés prédateurs (larves de *Chaoborus* et de *Leptodora kindtii*) sont les principaux types de prédateurs de zooplancton en milieu pélagique. Les poissons sont des prédateurs chassant à vue sélectionnant les proies les plus visibles et les plus profitables au niveau énergétique, donc préférablement des individus d'une taille supérieure à 1mm. Apparemment, les proies ayant une taille inférieure à 1 mm sont trop petites pour être détectées visuellement et n'offrent pas un grand gain énergétique. Il s'ensuit que les petits individus de zooplancton deviennent dominants en présence de poissons planctonophages, alors que dans les lacs sans poissons, les larves de *Chaoborus* deviennent les prédateurs zooplanctoniques les plus importants, car elles sont elles-mêmes des proies les plus recherchées par les poissons planctonophages (Lampert et Sommer 1997). Les larves de *Chaoborus* migrent aussi verticalement dans la colonne d'eau (Leibold 1990) afin d'éviter la prédation des poissons (Pinel-Alloul 1995) tout comme les daphnies. Les prédateurs invertébrés utilisent des signaux mécaniques pour détecter les vibrations produites par les mouvements natatoires de leurs proies. Les individus de taille inférieure à 1.3 mm (Pastorok 1981; Krylov 1992; Riesssen 1999) sont les proies les plus sélectionnés par les invertébrés prédateurs, ce qui entraîne une dominance des espèces ou individus de grande taille dans la communauté zooplanctonique. La variation saisonnière dans le type de prédateurs ainsi que la distribution verticale de ces prédateurs forcent le zooplancton à s'adapter à différentes pressions de prédation (Stibor et Lampert 2000).

La pression exercée par les poissons planctonophages varie au cours de l'été avec le recrutement larvaire et la croissance des jeunes poissons de l'année au printemps. Ceux-ci ont un métabolisme élevé et atteignent des densités élevées au début de l'été alors que la température de l'eau est en hausse, ce qui entraîne une forte consommation de proies planctoniques. Plusieurs études en laboratoire ont montré qu'en choisissant un régime composé de zooplancton, les jeunes poissons de l'année augmentaient leur survie et croissance (Hansen et Wahl 1981; Mills et Forney 1983; Mayer et Wahl 1997; Graeb et al. 2004). Une diète composée en majorité de cladocères constitue un choix ayant un potentiel énergétique plus élevé qu'une diète composée de petits copépodes (Graeb et al. 2004). Certaines espèces de poissons sont planctonophages facultatives et changent leur régime alimentaire à l'âge adulte en effectuant une transition vers un régime benthonophage puis un régime piscivore réduisant ainsi la pression exercée sur les communautés zooplanctoniques au cours de l'été. C'est le cas des perchaudes, des crapets et des menés. Pour contrer la prédation intense au printemps, les daphnies développent des défenses anti-prédatrices en présence des kairomones des prédateurs. Le type de prédateurs (poissons planctonophages ou invertébrés) déclenche des défenses spécifiques. Ces défenses résultent en une modification des traits morphologiques, démographiques et comportementaux communément appelé plasticité phénotypique (voir aussi Pourriot 1995 et Lass et Spaak 2003, pour une revue).

1.4 Plasticité phénotypique des daphnies

La plasticité phénotypique est un mécanisme qui contribue au maintien des populations quand les conditions environnementales fluctuent dans le temps et dans l'espace. La production de défenses est une réponse phénotypique due à un agent de sélection biotique qui peut varier spécifiquement (Stibor et Lampert 2000). Plusieurs études en laboratoire ont démontré l'influence des facteurs abiotiques et biotiques sur la plasticité phénotypique des traits morphologiques, démographiques et comportementaux des daphnies (Lass et Spaak 2003). La production de défenses anti-prédatrices a été observée et mesurée à l'aide d'expériences en laboratoire en employant des kairomones de poissons (substance spécifique provenant d'un prédateur : Larsson et Dodson 1993). Par contre, en nature, les relations entre la pression de prédation et les défenses anti-prédatrices produites par les daphnies ont été peu évaluées à cause des effets confondants des variables environnementales.

L'évolution des traits de vie des daphnies en réponse à la prédation dépend principalement de cinq facteurs. Premièrement, elle dépend des contraintes liées à l'hétérogénéité spatiale et temporelle de l'environnement dans lequel les populations évoluent. Concrètement, l'impact saisonnier des prédateurs dans les lacs tempérés se révèle bref et intense à cause du recrutement printanier des jeunes poissons de l'année, suivi d'une forte mortalité et du changement ontogénique de leur diète alimentaire (Vijverberg et al. 1990; Hülsmann et al. 1999; Mehner 2000). Dans les lacs stratifiés, s'ajoute à ces variations saisonnières de la prédation, l'hétérogénéité verticale des conditions physiques et chimiques et la présence de refuge pour le zooplancton en eau profonde (Wright et Shapiro 1990). Deuxièmement, plusieurs des mécanismes de défenses sont initiés seulement après la détection de kairomones spécifiques provenant des prédateurs vertébrés et invertébrés présents dans le milieu (Parejko et Dodson 1991; Larsson et Dodson 1993; Tollrian et Dodson 1999; Stibor 2002; Lass et Spaak 2003). Troisièmement, comme les daphnies peuvent coexister avec plusieurs espèces de prédateurs au cours de leur vie (Brancelj et Blejec 1994), elles doivent s'adapter en conséquence et développer des mécanismes de défense contre la prédation de différents types de prédateurs à tous les stades de leur vie (juvéniles, adultes) (Dodson 1989). Quatrièmement, les mécanismes de défense sont produits uniquement en présence de prédateurs. L'absence de prédateurs dans le milieu ne nécessitant pas la formation de défenses entraîne par le fait même la réduction des coûts associés à leur production (Dawidowicz and Loose 1994). Les crustacés zooplanctoniques peuvent alors allouer leur énergie à la croissance et la reproduction. En définitive, la modification d'un trait de vie ou d'un comportement doit avoir un impact positif sur le fitness d'un individu en milieu naturel puisque la formation d'une défense mal adaptée, et davantage le maintien de cette défense, se révèlera extrêmement désavantageux pour la survie des populations.

Chez la plupart des espèces de daphnies, différentes stratégies (morphologiques, comportementales ou démographiques) ont été développées afin de contrer la prédation (Lynch 1980, Pourriot 1995; Tollrian et Dodson 1999; Lass et Spaak 2003). Les défenses anti-prédatrices développées chez les daphnies sont propres à chaque espèce et répondent aux types de prédateurs présents (Tableau 1-I). En général, les poissons planctonophages induisent des défenses qui vont diminuer la visibilité des proies alors que les prédateurs invertébrés vont induire des défenses qui vont limiter l'ingestion des proies. Par exemple, les défenses morphologiques développées par les daphnies pour contrer la prédation par les poissons planctonophages sont la réduction de la taille et du capuchon céphalique. Par contre, l'élongation de l'épine dorsale reste un trait efficace pour empêcher la manipulation lors de la consommation. Une réduction de la taille et de l'âge à la première reproduction sont deux traits démographiques employés également pour contrer la pression de prédation des poissons (Tableau 1-I). De plus, la présence de poissons planctonophages dans le milieu induit des défenses comportementales comme la sélection de la profondeur optimale de résidence, les migrations verticale ou horizontale diurne et les distributions en agrégats (Tableau 1-I). À l'opposé, les kairomones de prédateurs invertébrés induisent la formation de défenses morphologiques comme l'augmentation de la taille des daphnies (longueur et largeur) ainsi que la formation de protubérance dorsale, le développement du capuchon céphalique, l'augmentation de l'épine dorsale (Tableau 1-I). Les défenses démographiques contrant la prédation par les invertébrés sont une augmentation de la taille et de l'âge à la première reproduction puisque les individus de grande taille sont moins susceptibles d'être attaqués et ingérés (Tableau 1-I).

Tableau 1-I : Défenses morphologiques, démographiques et comportementales chez différentes espèces de daphnies produites par différents prédateurs.

Proies	Prédateurs	Traits morphologiques	Références
Daphnia ambigua	*Lepomis* (poisson)	Capuchon céphalique réduit chez l'adulte Élongation de l'épine caudale	Dodson 1989
D. galeata mendotae	*Chaoborus* (inv.)	Augmentation du capuchon céphalique	Dodson 1988
D. galeata mendotae	*Lepomis* (poisson)	Réduction du capuchon céphalique	Dodson 1988
D. lumholtzi	Bluegill (poisson)	Augmentation du capuchon céphalique	Kolar & Walh 1998
D. pulex	*Chaoborus* (inv.)	Élargissement corporel, protubérance dorsale	Tollrian 1993
D. pulex	*Chaoborus* (inv.)	Protubérance dorsale	Sell 2000
D. pulex	*Lepomis* (poisson)	Élongation de l'épine chez l'adulte	Dodson 1989
D. pulicaria	*Chaoborus* (inv.)	Élongation de l'épine chez l'adulte	Dodson 1989
D. pulicaria	Lepomis (poisson)	Élongation de l'épine chez l'adulte	Dodson 1989
D. rosea	*Chaoborus* (inv.)	Élongation de l'épine	Sell 2000
Proies	**Prédateurs**	**Traits démographiques**	**Références**
D. hyalina	*Leuciscus* (poisson)	Petite taille à PR jeune âge PR Augmentation du nombre d'oeufs de petite taille	Stibor 1992
D. magna	*Alburnus* (poisson)	Production éphippium	Slusarczyk 1995
D. pulex	*Chaoborus* (inv.)	Vieil âge PR Augmentation du nombre d'oeufs	Spitze 1992
Proies	**Prédateurs**	**Traits de comportement**	**Références**
D. galeata mendotae	*Micropterus* (poisson)	MHJ	White 1998
D. galeata mendotae	poisson	MVJ	Lampert 1993
D. magna	*Abramis* (poisson)	Échappement	Pijanowska 1997

PR : première reproduction MHJ : migration horizontale journalière

MVJ : migration verticale journalière

1.5 Impact des perturbations anthropiques

Une grande fraction de la surface de la terre est convertie par les humains en territoires utilisés soit pour l'agriculture ou le développement résidentiel (Vitousek et al. 1997). Les lacs sont une partie intégrante du territoire pouvant être considérés comme des îles au milieu du paysage terrestre. Les changements anthropiques provoquent des modifications parfois dramatiques dans les écosystèmes aquatiques. Les perturbations des écosystèmes lacustres résultent des interactions entre les perturbations à l'intérieur d'un lac dites locales (activités récréatives, pêche sportive) et les perturbations du territoire au niveau des bassins versants dites régionales. Par exemple, le développement des bassins versant des lacs en zones agricoles, urbaines ou résidentielles perturbe la biodiversité aquatique à l'intérieur de ces lacs en changeant la composition et la richesse spécifique du zooplancton (Dodson et al. 2005).

Dans la région boréale tempérée, les lacs dits vierges sont de plus en plus rares à cause de la croissance des populations riveraines. Cette croissance entraîne le développement d'habitations sur le pourtour des lacs, la construction de routes ainsi que le déboisement d'une partie du bassin versant. Ces perturbations à l'échelle des bassins versants et au niveau des rives peuvent altérer les composantes physiques, chimiques et biologiques des lacs. L'évaluation des effets des perturbations anthropiques sur les écosystèmes lacustres a fait l'objet d'études seulement depuis deux décennies alors que l'évaluation des effets des facteurs naturels d'ordre géologique, géographique et trophique a été plus approfondie. Plusieurs études effectuées sur des lacs vierges ont démontré l'impact des caractéristiques morphologiques du bassin versant et de la position topographique des lacs dans le paysage (Kratz et al. 1997) sur la qualité des eaux et les communautés planctoniques. Par exemple, un grand ratio de drainage, un bassin versant en pente faible et un grand pourcentage de marécages sont tous des variables du bassin versant qui influencent la chimie de l'eau en augmentant les apports en nutriments et en matière organique. Ceci a comme conséquences d'accroître la couleur de l'eau et la biomasse algale (Rasmussen et al. 1989; D'Arcy et Carignan 1997). Les perturbations anthropiques du bassin versant et des rives des lacs ont un effet additif sur les apports en nutriments et les communautés planctoniques. En effet, plusieurs études comparatives ont montré que dans les lacs perturbés de la région tempérée, c'est l'enrichissement en éléments nutritifs, principalement en phosphore (P) et en azote (A), qui affecte la communauté pélagique en augmentant la biomasse algale (Dillon et Rigler 1974; Knoll et al. 2003). Cet enrichissement en nutriments et en biomasse algale est généralement connu sous le terme d'eutrophisation (Schindler 1997; Knoll et al. 2003; Dodson et al. 2005). Parmi les conséquences néfastes dénotées à l'eutrophisation des lacs, il y a la floraison de fleurs d'eau (cyanobactéries) qui ont la capacité de produire des toxines (Carmichael 1992).

Le zooplancton est un système idéal pour faire le suivi des effets des changements naturels et des perturbations anthropiques dans les lacs tempérés (Dodson et al. 2005). Les organismes zooplanctoniques sont reconnus comme étant de bons indicateurs de l'état trophique d'un lac au niveau régional (Stemberger et Lazorchak 1994; Stemberger et al. 2001) et continental (Pinto-Coelho et al. 2005). Toutefois, compte tenu de la position d'impasse trophique du zooplancton entre les compartiments ascendants et descendants, les effets des perturbations anthropiques du bassin versant sur la communauté zooplanctonique résultent d'interactions complexes directes et indirectes (Dodson et al. 2005). Dans les lacs tempérés, l'enrichissement en phosphore augmente la biomasse des crustacés zooplanctonique (Yan 1986) et change la structure en taille et la composition de la communauté zooplanctonique (Pace 1986; Stemberger et Lazorchak 1994). La biomasse et la structure de la communauté des crustacés zooplanctoniques changent en fonction du statut trophique du lac (Yan 1986; Pace 1986; Pinto-Coelho et al. 2005). Les petits cladocères et les copépodes cyclopoïdes sont plus abondants dans les lacs et les réservoirs eutrophes alors que les calanoïdes sont plus abondants dans les lacs oligotrophes. De plus, les copépodes calanoïdes montrent une plus grande sensibilité au perturbations du bassin versant et des rives que les rotifères et les copépodes cyclopoïdes (Stemberger et al. 2001). Le zooplancton peut aussi être affecté par des perturbations majeures du bassin versant des lacs de la zone boréale à la suite de feux de forêt ou de coupes forestières. Dans l'est du Canada, les coupes forestières sont associées à une augmentation du carbone organique dissous et de la couleur de l'eau ainsi à qu'une diminution de la biomasse des copépodes calanoïdes. Quant aux feux de forêt, ils entraînent l'augmentation de la biomasse des rotifères et de copépodes cyclopoïdes (Patoine et al. 2000; 2002). Comparativement à ces études sur les effets de perturbations majeures par l'agriculture et la déforestation, très peu d'études ont évalué le potentiel des crustacés planctoniques comme indicateur des effets des perturbations anthropiques occasionnées par le développement résidentiel des zones riveraines des lacs de la région boréale ayant encore un faible niveau trophique. Dans quelle mesure, le développement résidentiel récent des lacs tempérés nordiques en zone périurbaine affecte la biomasse, la structure en taille et la composition de la communauté zooplanctonique est une question de très grand intérêt. En particulier, les écologistes doivent comparer l'influence des effets anthropiques aux effets des facteurs naturels déjà connus (Dodson et al. 2005). Le lien entre l'utilisation du bassin versant et la communauté zooplanctonique, et les effets sur les cascades trophiques en zone pélagique, peut avoir des implications importantes pour la gestion et l'aménagement des lacs (McQueen et al. 1986; Carpenter et Kitchell 1993). Ainsi le développement résidentiel des rives d'un lac en augmentant les apports de nutriments accélèrera les processus ascendants (bottom-up) de prolifération des algues et diminuera la transparence de l'eau (Figure 1.3). Ces modifications à la baisse du réseau pélagique peuvent se répercuter indirectement au niveau de la communauté zooplanctonique. De plus, ce même développement résidentiel est responsable d'une augmentation de la pêche sportive qui pourra modifier les interactions trophiques descendantes (top-down) et changer la biomasse, la structure en taille et la composition du zooplancton (Figure 1.3).

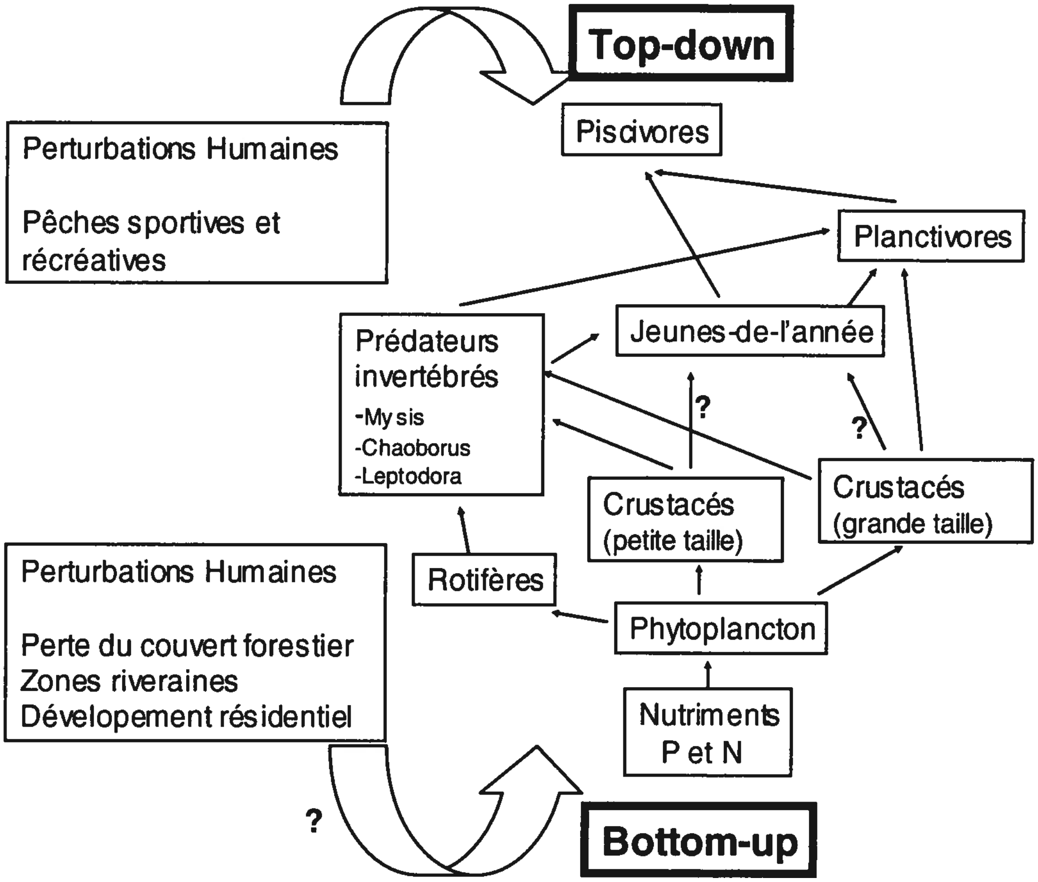

Figure 1.3 : Effets des perturbations anthropiques sur les interactions trophiques en cascade dans un réseau pélagique simplifié.

1.6 Objectifs et hypothèses de recherche

Le thème général de la thèse est l'évaluation des effets des facteurs naturels et des perturbations anthropiques sur un maillon essentiel du réseau trophique pélagique en milieu lacustre : le zooplancton. La recherche traite essentiellement des crustacés planctoniques et en particulier des populations de daphnies.

Le premier volet de la recherche traite de l'adaptation phénotypique des populations de daphnies à un facteur naturel : la prédation des vertébrés et invertébrés. Nous avons étudié la capacité de différentes populations de daphnies à s'adapter à la prédation sélective exercée par les jeunes perchaudes de l'année (*Perca flavescens*) et les invertébrés (*Chaoborus*) dans le lac Brome, un lac méso-eutrophe de la région des Cantons de l'Est. Cette étude a été réalisée en milieu naturel ce qui implique que les daphnies étaient exposées aux changements estivaux de plusieurs variables environnementales non contrôlées, alors que la plupart des études antérieures avaient été faites en conditions expérimentales contrôlées.

Dans le premier article (Chapitre 2), nous avons étudié la plasticité phénotypique des daphnies i.e. les changements dans les traits démographiques et comportementaux des deux espèces de daphnies qui cohabitent dans le lac Brome. Ces deux espèces ont des tailles différentes; *D. pulicaria* est une espèce de grande taille (1.4-2 mm pour les adultes) alors que *D. galeata mendotae* est de plus petite taille (1-1.5 mm pour les adultes). Cette première étude traite essentiellement des effets de prédation sélective des jeunes perchaudes de l'année sur les deux espèces de daphnies. Les objectifs spécifiques étaient de 1) démontrer la sélection préférentielle des jeunes perchaudes de l'année pour l'espèce de grande taille, *D. pulicaria*, 2) observer la présence de plasticité phénotypique dans les traits démographiques et comportementaux des deux espèces de daphnies en présence de prédateurs visuels, 3) déterminer si une sélection préférentielle par les jeunes perchaudes de l'année sur l'espèce de daphnie grande taille, *D. pulicaria*, induisait des réponses anti-prédatrices plus prononcées que chez l'espèce de plus petite taille *D. g.mendotae* et 4) évaluer la valorisation de certains traits anti-prédateurs tels que les traits comportementaux au dépend des traits démographiques. *Nous voulions tester l'hypothèse selon laquelle la soudaine présence de jeunes perchaudes au printemps affectait les traits démographiques et comportementaux des deux espèces de daphnies de façon spécifique en réponse au comportement sélectif de prédation des jeunes perchaudes de l'année.*

Dans un deuxième article (Chapitre 3), nous avons examiné les autres stratégies anti-prédatrices, soit les défenses morphologiques développées par les deux espèces de daphnies en présence des prédateurs vertébrés (jeunes perchaudes de l'année) et invertébrés (Chaoboridés). Les réponses morphologiques sont en général produites dans le but d'interférer dans la capture et la manipulation lors de l'ingestion par les prédateurs. Nous avons évalué 1) les réponses morphologiques des deux espèces de daphnies face à la prédation sélective des poissons et des invertébrés, 2) si la profondeur de résidence des daphnies dans la colonne d'eau influençait ces réponses morphologiques et 3) si ces réponses semblaient variées au cours de l'été en fonction des changements dans le niveau de pression de prédation exercée par les poissons et les invertébrés. *L'hypothèse générale est que les deux espèces de daphnies réagissent différemment et développent des défenses morphologiques spécifiques selon leur vulnérabilité vis-à-vis des différents types de prédateurs.*

Le deuxième volet de la recherche traite des effets du développement résidentiel récent autour des lacs de la zone tempérée boréale du sud du Québec sur la communauté des crustacés planctoniques et les assemblages d'espèces de daphnies. Cette étude est la première à prendre en considération des perturbations relativement faibles reliées au développement résidentiel récent des lacs de villégiature en zone périurbaine alors que les études antérieures s'intéressaient plutôt à des perturbations majeures telles que l'agriculture et le déboisement par les feux de forêts ou les coupes forestières. Nous avons étudié les effets de l'urbanisation du bassin versant et des rives sur la biomasse, la distribution spatiale verticale et la structure des communautés de crustacés planctoniques et les assemblages de daphnies dans les lacs de la région des Laurentides. La population des Laurentides a augmenté de 78% depuis les années 1970 (Statistique Canada). Ce phénomène est principalement causé par la transformation de chalets en résidences permanentes suite à la retraite des 'baby-boomers'. Le développement résidentiel entraîne le déboisement des rives, la construction de nouvelles résidences et de routes et l'aménagement de terrains autour des lacs. Ces perturbations sont responsables d'un apport supplémentaire en sels minéraux (déglaçage des routes l'hiver) et en nutriments (engrais pour le gazon). Cette urbanisation récente devrait avoir des effets directs et indirects sur les crustacés pélagiques via l'enrichissement des eaux en sels minéraux et en nutriments et l'augmentation dans la biomasse algale. Ces effets devraient se traduire par une augmentation de la biomasse des crustacés et par des changements dans la structure et la distribution spatiale des crustacés zooplanctoniques et des espèces de daphnies.

Dans le troisième article (Chapitre 4), nous avons comparé les communautés de crustacés zooplanctoniques et les assemblages d'espèces de daphnies dans 13 lacs de la région des Laurentides distribués le long d'un gradient de développement résidentiel et de création de zones ouvertes par perturbation du couvert forestier. Nous avons utilisé pour la première fois en milieu lacustre le concept d'effet en cascade des perturbations du territoire (LCC concept : land-cover cascade concept; Burcher et al. 2007) pour déterminer les effets directs et indirects du développement résidentiel et des perturbations du territoire sur les communautés de crustacés zooplanctoniques et les espèces de daphnies. Premièrement, nous avons déterminé les variations dans la biomasse totale des crustacés, de 7 groupes fonctionnels et des espèces de daphnies en fonction de l'intensité du développement résidentiel et des perturbations du couvert forestier. Ensuite nous avons décrit l'intensité et le sens de la cascade d'effets du développement résidentiel et de la perte de couvert forestier sur les communautés zooplanctoniques (groupes fonctionnels de crustacés et espèces de daphnies) via les effets sur les nutriments et la biomasse algale. *L'hypothèse générale à tester est qu'il existe une relation entre les perturbations anthropiques dues au développement résidentiel et à la perte de couvert forestier et les groupes fonctionnels de crustacés planctoniques ou les espèces de daphnies présentes dans un lac en voie d'urbanisation.*

Enfin, dans un quatrième article (Chapitre 5), nous avons évalué les effets de l'hétérogénéité verticale des lacs (stratification des masses d'eau) et du niveau de perturbation anthropique sur la profondeur moyenne de résidence et les patrons de migration journalière des groupes fonctionnels de crustacés et des espèces de daphnies dans 8 lacs des Laurentides. Nous avons évalué 1) la profondeur moyenne de résidence des groupes fonctionnels de crustacés et des espèces de daphnies dans la zone pélagique, 2) si les biomasses des crustacés et des daphnies dans les zones épilimnétique, métalimnétique et hypolimnétique variaient entre le jour et la nuit et 3) les effets des variables environnementales naturelles et anthropiques sur la distribution spatiale des groupes fonctionnels de crustacés et des espèces de daphnies en utilisant une nouvelle méthode statistique d'arbre de régressions multiples. *L'hypothèse principale était de tester quelles variables naturelles structurant l'hétérogénéité spatiale de la colonne d'eau et quelles variables de perturbation étaient reliées à la sélection de la profondeur de résidence et aux patrons migratoires journaliers des différents groupes fonctionnels de crustacés et des espèces de daphnies.*

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Chapitre 2

Alternative antipredator responses of two coexisting *Daphnia* species to negative size selection by YOY perch

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2.1 Abstract

Our study showed, in nature, that two coexisting *Daphnia* adopted alternative life-history and behavioural strategies to cope with negative size-selection predation by gape-limited YOY perch. We evaluated the phenotypic plasticity in life history and behavioural traits of two coexisting *Daphnia* species, *D. pulicaria* and *D. galeata mendotae*, in response to seasonal changes in predation by YOY yellow perch (*Perca flavescens*) in a mesotrophic lake. We expected that the large-sized *D. pulicaria*, the most likely subjected to size-selective predation by YOY perch, will show stronger antipredator responses than the small-sized *D. galeata mendotae*. To test this hypothesis, we examined changes in life history and behavioural traits in juveniles and adults of both species during four YOY fish predation periods that were selected based on the presence of YOY perch in the pelagic zone and the relative abundance of *Daphnia* prey in their gut contents. Our study supports the scenario of negative size-selective predation by gape-limited YOY perch on both *Daphnia* species. The electivity index indicated that no daphnids with a body length > 1.75 mm were predated by YOY yellow perch. Coexisting *Daphnia* exhibited phenotypic plasticity in their antipredator defenses based on their vulnerability to seasonal changes in size-selective predation of YOY perch. Juvenile *Daphnia* were the targeted prey and they responded by a decreased body length. Behavioural defenses were the dominant strategy used by both adult *Daphnia* species to withstand high predation. A decreased size at maturity was not employed by *Daphnia*, except at the very end of the predation period. Behavioural defenses are short-term strategy adopted to avoid predation. Both antipredator defenses became unnecessary expenses and were no longer sustained after the predation period.

Keywords: life history traits, behavioural traits, coexisting *Daphnia*, YOY perch

2.2 Introduction

The phenotypic plasticity of life history or behavioural defenses developed by *Daphnia* species in response to risk of predation by planktivorous fish has already been extensively investigated under laboratory conditions (Boersma *et al.*, 1998; de Meester *et al.*, 1999; Tollrian and Dodson, 1999; Lass and Spaak, 2003). Visually hunting fish tend to select energetically more rewarding conspicuous large-sized *Daphnia* over smaller ones (Brooks and Dodson, 1965; Riessen, 1999; Tollrian and Dodson, 1999). Therefore, changes in life history traits, especially decreasing size and age at maturity associated with lower investment in growth and higher reproductive effort (Stibor, 1992) can increase fitness of *Daphnia* populations under positive size-selection by planktivorous fish. Another way of avoiding fish predation by *Daphnia* is to develop behavioural defenses such as depth selection and diel vertical migration (Lampert, 1993; de Meester *et al.*, 1999). Inhabiting the colder and darker deep strata of the water column during daytime allows *Daphnia* to decrease the risk of predation by visually hunting planktivorous fish (Lampert, 1993).

Fish predation pressure varies in a predictable way during summer season with the spring recruitment of new-hatched fish (young-of-the-year; YOY) and their ontogenic changes. Prey selection changes during their growth, prey organisms may develop multiple alternative defenses depending on their vulnerability (Tollrian and Dodson, 1999). The relative importance of these alternative antipredator defenses for *Daphnia* populations facing YOY fish predation in nature has been less studied (Sakwínska and Dawidowicz, 2005). Nonetheless, it is now recognized that both life history strategies and depth selection behaviour are mutually-adjusted alternative ways for *Daphnia* to cope with fish predation (de Meester and Weider, 1999; Sakwínska and Dawidowicz, 2005). However, most of evidences comes from experimental studies (de Meester *et al.*, 1995; Winder *et al.*, 2004; Hülsmann *et al.*, 2004), and there are still few studies considering the relative importance of life history and behavioural antipredator defenses for *Daphnia* populations in lakes where factors other than predation, such as food quantity and quality, and temperature gradients can blur the expected inducible responses (Sakwínska and Dawidowicz, 2005). Furthermore, studies examining how these antipredator strategies are employed by coexisting *Daphnia* having different size and predator vulnerability have still been limited to enclosure experiments (Bernot *et al.*, 2004).

The present study investigates in nature how both life history and behavioural defensive strategies are associated in two coexisting *Daphnia* species of different size facing seasonal changes in planktivory by YOY yellow perch (*Perca flavescens*). The coexisting species are the large-sized *Daphnia pulicaria* (2 mm) and its smaller congener *D. galeata mendotae* (1.4 mm) inhabiting a mesotrophic lake. In early summer, YOY perch feed mainly on zooplankton before switching to benthic prey and this seasonal pattern is generally associated with a drastic decline in *Daphnia* densities (Mills and Forney, 1983; Persson, 1986; Roseman *et al.*, 1996; Johnson and Kitchell, 1996). Therefore, a question exists if daphnids were temporarily vulnerable to negative size-selective predation by new-hatched YOY perch which are limited by their gape dimension to eating small-sized prey (Hülsmann *et al.*, 2004)? Our main hypothesis is that the coexisting *Daphnia* species will show phenotypic plasticity in their antipredator defenses and adopt different life history and behavioural strategies to cope with changing YOY perch size-selective predation. Positive size selection by large YOY perch would induce a stronger response in terms of life history and behavioural defenses in the large *D. pulicaria* than in the small *D. galeata mendotae*. Negative size selection by small YOY perch would rather affect life history and behavioural traits of the small *D. galeata mendotae*. To test these hypotheses, we compared the antipredator life history and behavioural strategies developed during the summer season by juveniles and adults of the two *Daphnia* species in relation to their different size and vulnerability to YOY perch predation.

2.3 Method

2.3.1 Study site and field sampling

Lake Brome is a large (14 km^2), dimictic lake of glacial origin located in the Eastern Townships region, south-east of Montréal, Québec, Canada (45°14'N, 72°30'W). Mean and maximum depths are 5.9 and 12.2 m, respectively. The lake is normally ice-free from early

April through late November. The lake is mesotrophic with maximum concentrations of 19 $\mu g \cdot L^{-1}$ for total phosphorus and 8 $\mu g \cdot L^{-1}$ for chlorophyll *a*.

Sampling was carried out every 4-10 days from May through August 2002 at 3 sampling stations, situated 200 meters apart at the deepest site (12 m) of the lake using GPS navigation. All measurements and water sampling were done during the day (12h00-17h00). Water temperature and oxygen profiles were measured with an YSI-54A temperature-oxygen meter at 1 m intervals. Vertical profiles of light intensity were also measured at 1 m intervals with a LiCor-1000 quantum meter, and water transparency was recorded with a Secchi disk. An integrated water sample was collected within the euphotic zone (above 1% surface light irradiance: 0-9 m) using weighted Tygon tubing fitted with a one-way foot valve. Chlorophyll *a* depth profiles were measured with a bbe Moldaenke FluoroProbe (Beutler *et al.*, 2002). In addition, 250 ml water subsamples were collected and preserved in 1% acid Lugol solution for phytoplankton identification.

To analyse the crustacean zooplankton community and *Daphnia* traits, zooplankton samples were collected during daytime with a plankton net (28 cm diameter, 150 μm mesh size) by vertical hauls in the water column (0-12 m) at each sampling station. The mesh size used in this study was small enough to collect most crustacean species, especially juvenile and adult daphnids, while filtering small rotifers and algae. To examine *Daphnia* behavioural traits, additional zooplankton samples were collected at six depths (1, 3, 5, 7, 9, 11 m) during day (12h00-17h00) and night (22h00-00h00) with a Schindler-Patalas sampler (12 L) fitted with a 150 μm mesh size net. A total volume of 24 L was filtered at every depth. Zooplankton samples were fixed in the field in 4% sugar buffered-formalin solution (Haney and Hall, 1973).

YOY yellow perch (*Perca flavescens*) were collected in the pelagic zone every week from 23 May until 29 July. A large Bongo net (0.25 m^2 area, 6 m length, and 1 mm mesh size) was trawled in the center of the lake along 200 m transects at 1, 3 and 5 m depths two hours after sunset (between 20h00 and 22h00 depending on sunset time). The collected fish were identified, counted, measured and their gape width was estimated based on their body length using Schael et al. (1991) regression. We counted the total number of

YOY perch captured at each sampling date to evaluate seasonal changes in their density (ind.m-3) during the survey. When fish were caught, at least 30 YOY fish specimens were fixed in methanol-formaldehyde solution immediately after fishing and kept for further analysis of their gut content.

2.3.2 Plankton analyses

Phytoplankton samples were analysed only at four dates corresponding to the fish predation periods (see *YOY planktivory analysis* below) using an inverted microscope (Utermöhl method) to evaluate the density (10^6 cells·L^{-1}) of major taxonomic groups and dominant species. A sub-sample (5 or 10 ml) of each zooplankton sample collected with the plankton net in the water column was analysed under a dissecting microscope using a Ward counting wheel to determine the crustacean community composition. We estimated the density (ind·L^{-1}) of main cladoceran and copepod taxa (including the two *Daphnia* species) based on the relative percentage of the total volume of the sample analyzed and the volume of lake water filtered. Morphometric traits of the two *Daphnia* populations (*D. pulicaria* and *D. galeata mendotae*) were examined on around 50 daphnids in each zooplankton sample collected with the plankton net. The animals were examined at 100X magnification with a dissecting microscope (Leica MZ12) and measurements were taken with an image analyser (Image Pro Plus). Body length was defined as the length between the top of the compound eye and the base of the tail spine, body width was defined as the largest distance between a ventral and a dorsal horizontal line (Tollrian, 1994). Size at maturity (SAM) was evaluated according to Stibor and Lampert (1993). The clutch size was estimated by counting the number of eggs per gravid parthenogenetic female. We also recorded the presence of ephippium in gravid *Daphnia* in each sample. In zooplankton samples collected at discrete depths with the Schindler-Patalas sampler, we identified and counted juvenile and adult of the two *Daphnia* species to estimate their weighted mean depth (WMD) during day and night, and the amplitude of their diel vertical migration (DVM).

$$\text{WMD} = \Sigma\,(N_i * d_i)/\,\Sigma\,N_i$$

where N_i = number of *Daphnia* at the depth i, and d_i = depth i when i = 1, 3, 5, 7, 9, 11 m. The amplitude of the DVM was estimated as the difference between WMDs of the day and night samples.

2.3.3 YOY planktivory analysis

The summer survey was divided in 4 YOY fish periods according to the presence/absence of YOY perch in the pelagic zone of the lake and the abundance of *Daphnia* prey in their gut contents: the before predation period (BP), the low-predation period (LP), the high-predation period (HP), and the after-predation period (AP). The BP period (27 April to 31 May) corresponds to the absence of fish larvae in the pelagic zone of the lake as no YOY fish were caught in the Bongo net until the end of May. The LP period (1 to 16 June) corresponds to the presence of YOY fish which were caught in high numbers (3-6 ind.m^{-3}) in the pelagic zone; however, they did not significantly feed on *Daphnia* but mainly on *Bosmina* sp. and small calanoid copepods. The HP period (17 June to 15 July) represents the period of lower abundance in YOY fish but of important predation pressure on both *Daphnia* species which were the dominant prey in the gut contents during most of the period. The period AP (15 July to 19 August) is the after-predation period when YOY fish were not caught anymore in the pelagic zone. We analyzed the entire length of the gut content of YOY perch collected on each sampling date during the LP and HP periods. We identified and counted all prey organisms including crustacean zooplankton species, detached eggs of copepods, and other invertebrates. All *D. pulicaria* and *D. galeata mendotae* observed in gut contents of YOY perch from 16 June to 15 July were counted and measured. The percentage of different prey items was calculated based on numbers of each prey item in the gut contents relative to the total number of prey. We compared the size distribution of *Daphnia* collected in the lake and *Daphnia* found in the gut contents of YOY perch. Size classes ranged from 0.75 to 2.25 mm with an increment of 0.25 mm. YOY perch feeding selectivity relative of other *Daphnia* species was estimated using the electivity index E_i (Ivley, 1961) based on the proportion of each *Daphnia* size class in the gut content (r_i) and in the lake (p_i):

$$E_i = (r_i - pi) / (r_i + p_i)$$

2.3.4 Statistical analyses

Repeated-measured ANOVAs were used to test for differences in the mean body length of adult and juvenile of each *Daphnia* species. The mean SAM and the mean clutch size of each *Daphnia* species were also analysed with repeated-measured ANOVAs to test for differences along the summer survey. Data were normally distributed according to Kolmogorov-Smirnov tests ($P > 0.05$) (Lilliefors) (Sokal and Rolf, 1995). Differences among the 4 YOY fish periods in WMD during day and night for the juvenile and adult of each *Daphnia* species were analysed using Kruskal-Wallis tests (Zar, 1999). The amplitude of the DVM pattern was estimated during the high-predation period (HP) based on differences in WMD during day and night. We tested if DVM amplitude was significant during the HP period using paired *t*-tests for differences between day and night WMD in juveniles and adults of both species. All computations were run with Systat 8 (Wilkinson, 1999).

2.4 Results

2.4.1 Limnological conditions and plankton community composition

Following ice-melt, spring water mixing in May maintained an isothermal water column, which gradually warmed from 10°C in April to 15°C in early June (Fig. 2.1A). Thermal stratification developed during June and the lake was stratified from mid-June until the end of the survey. Water temperature in the epilimnion increased from 10°C in spring to 24°C in late summer, while hypolimnetic waters remained at 15-17°C. Lake Brome was well oxygenated (11 $mg \cdot L^{-1}$) over the entire water column in early May and in the epilimnion (> 9 $mg \cdot L^{-1}$) during summer (Fig. 2.1B). Oxygen concentration in the hypolimnion began to decrease in June below 9 m depth and remained anoxic throughout the end of summer (< 1 $mg \cdot L^{-1}$) after 10 July. Secchi disk depth was consistently around 3 m, and the euphotic depth remained around 9 m throughout summer.

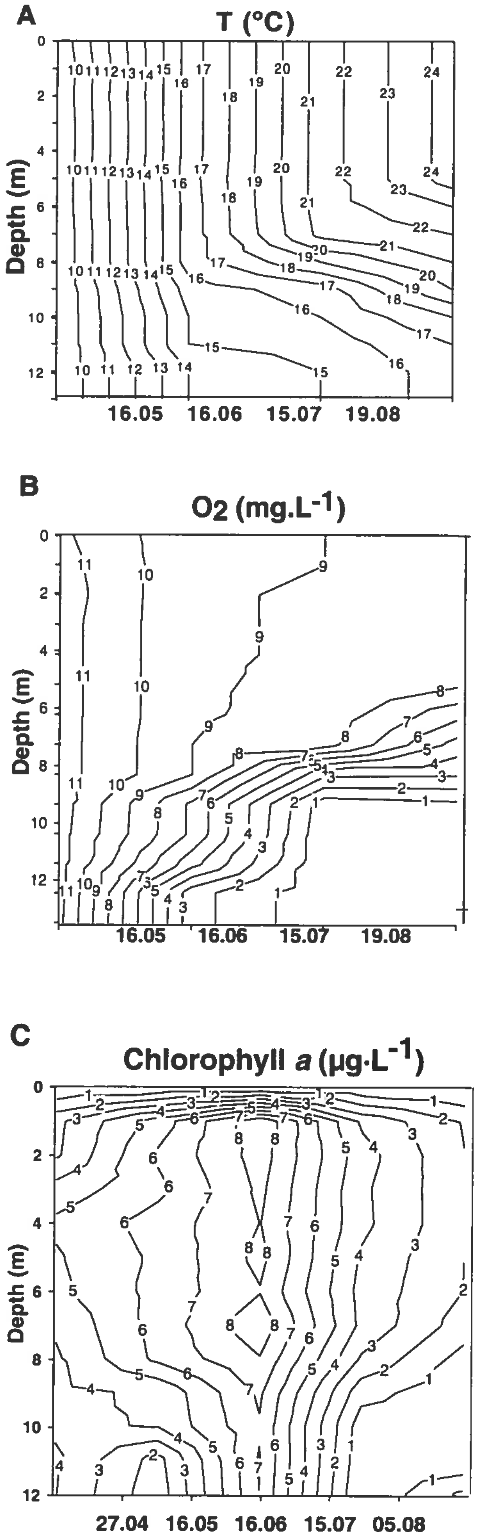


Figure 2.1: Contour plots of water temperature (°C) (A), oxygen concentrations (mg·L-1) (B) and total chlorophyll a biomass (µg·L-1) (C) based on weekly observations during summer 2002.

In general, total chlorophyll *a* concentrations were always low in surface waters (0-1 m: < 5 $\mu g \cdot L^{-1}$), and reached a maximum of 8 $\mu g \cdot L^{-1}$ in the epilimnion on 16 June (Fig. 2.1C). Thereafter, chlorophyll *a* concentrations decreased throughout the summer until a minimum of 2-3 $\mu g \cdot L^{-1}$ was reached in August. Phytoplankton density was the highest in early summer around 2.63 10^6 $cell \cdot L^{-1}$ during the BP period and 1.46 10^6 $cell \cdot L^{-1}$ during the LP period. Chrysophytes (*Dinobryon divergens* and *Mallomonas pumilio canaensis*) and large diatoms (*Asterionella formosa* and *Melosira ambigua*) composed almost 100% of the phytoplankton community in spring (Fig. 2.2). Later in summer, densities of phytoplankton decreased to around 0.39 10^6 $cell \cdot L^{-1}$ and 0.55 10^6 $cell \cdot L^{-1}$ during the HP and AP periods, respectively (Fig. 2.2). The phytoplankton community was dominated by filamentous cyanobacteria (83-97 % of total density) such as *Anabaena flos-aquae*, *Anabaena spiroides* and *Aphanizomenon gracile*, and the small diatom *Cyclotella glomerata* represented only 16 and 3 % of total phytoplankton abundance, respectively (Fig. 2.2).

In spring, during the before predation period (BP), zooplankton densities reached around 700 and 400 $ind \cdot L^{-1}$ and the crustacean community was dominated by calanoid and cyclopoid copepods (Fig. 2.2). Among the cladocerans, 3 dominant taxa were present at low density: *Bosmina* sp., *D. pulicaria* and *D. galeata mendotae*. At the beginning of the low-predation period (LP), zooplankton abundance was still high (around 700- 800 ind. L-1), and the community dominated by copepods. However, *D. pulicaria* density increased up to 170 $ind \cdot L^{-1}$, and the density of *D. galeata mendotae* reached 85 $ind \cdot L^{-1}$ on 1 June. The density of total zooplankton and both *Daphnia* species decreased drastically at the end of the LP period. During the high-predation period (HP), zooplankton density varied between 300 to 500 $ind.L^{-1}$, and *D pulicaria* accounted for a higher proportion of the community. At the end of the HP period, *D. pulicaria* abundance decreased to a minimum of 20 $ind \cdot L^{-1}$ and *D. galeata mendotae* dropped to less than 5 $ind \cdot L^{-1}$, suggesting that both *Daphnia* species were affected by YOY perch predation (Fig. 2.2). In the after-predation period (AP), the density of *D. pulicaria* stayed low at 10 $ind \cdot L^{-1}$. In contrast, the density of *D. galeata mendotae* greatly increased and reached a maximum of 105 $ind \cdot L^{-1}$ on 19 August. At one date during the after-predation period (AP), *Bosmina* was the dominant cladoceran (Fig. 2.2).

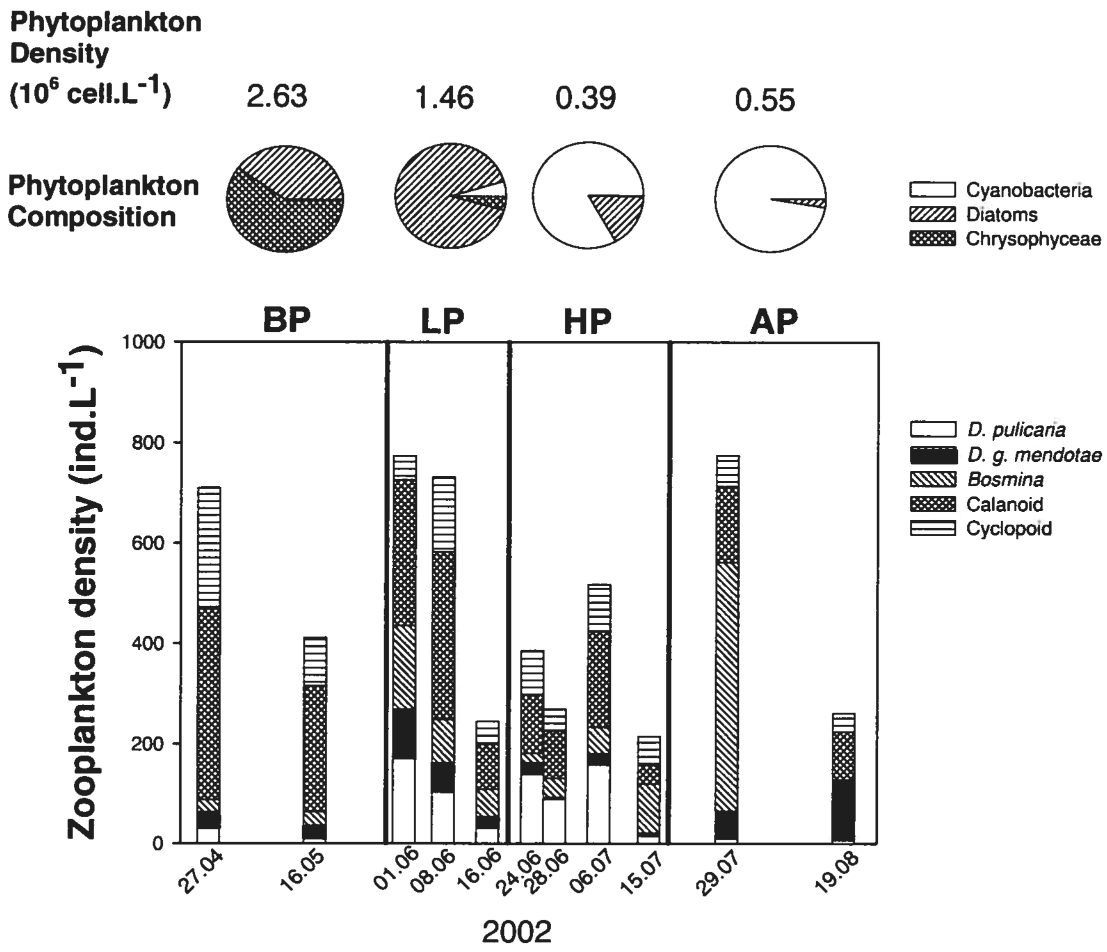


Figure 2.2: Phytoplankton density (cell.L-1) and composition during each YOY fish period and changes during summer in zooplankton density (ind.L-1) and composition. BP: before-predation period, LP: low predation period, HP: high-predation period, AP: After-predation period, as defined based on the presence/absence of YOY perch in the pelagic zone of the lake and the importance of *Daphnia* prey in their gut contents.

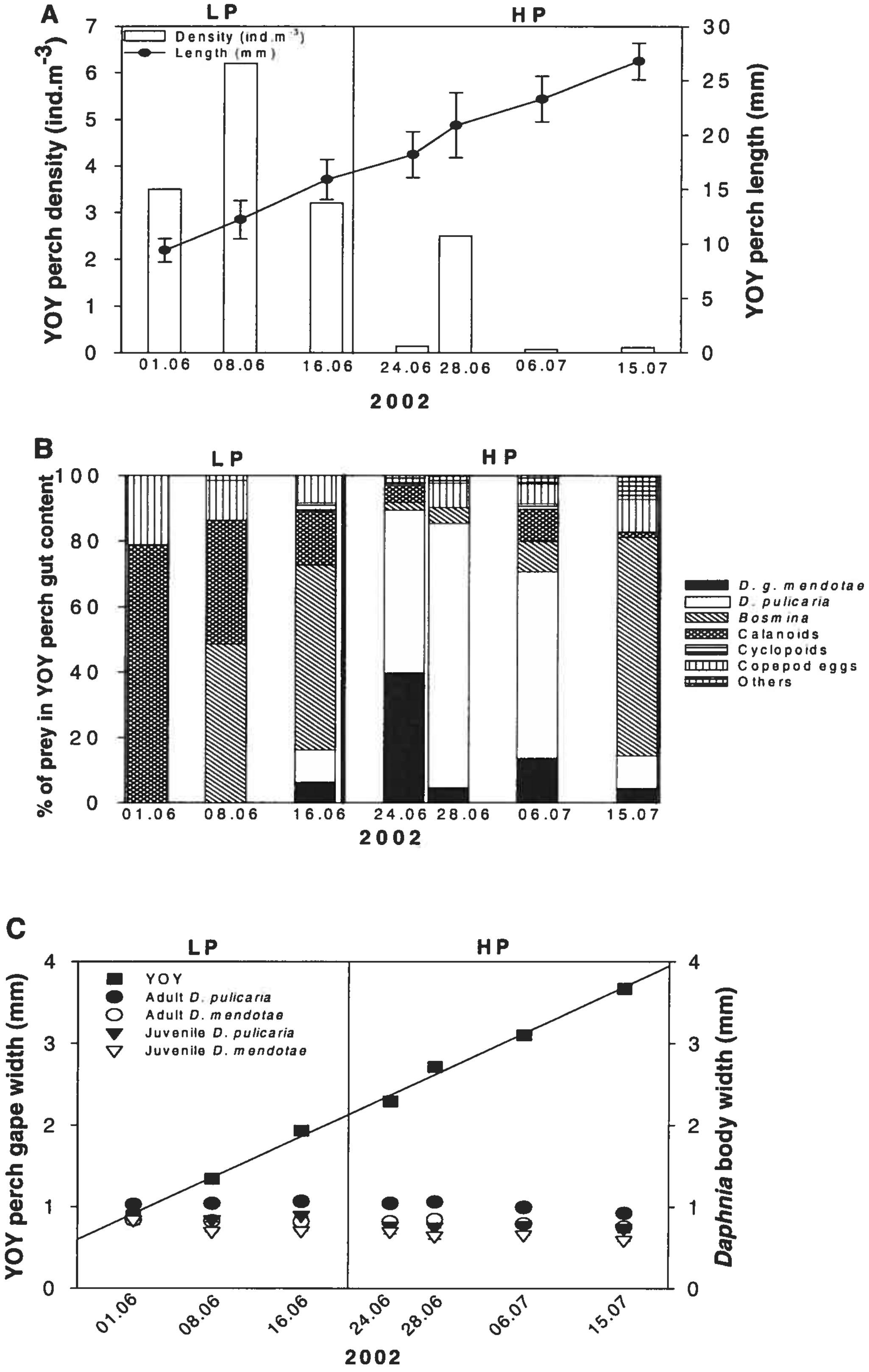
2.4.2 Seasonal changes in YOY fish planktivory

YOY perch (*Perca flavescens*) was the dominant species captured during the survey; YOY yellow perch represented 99% of the samples. As stated above, the BP period was defined by absence of perch larvae in the pelagic zone. During the LP and HP periods, their density varied between 0.25 and 6 ind·m^{-3} (Fig. 2.3A). New-hatched YOY perch had a mean length of 8 mm, and by the end of the HP period, they reached in average 27 mm in total length

(Fig. 2.3A). The highest densities (3-6 ind.m^{-3}) were observed when YOY fish were smaller than 15 mm. Lower densities (< 3 ind.m^{-3}) were observed when YOY fish reached lengths greater than 15 mm. The low density on 24 June could be explained by the period of full moon when fish avoid the pelagic zone because moonlight makes them more vulnerable to their predators (Gliwicz, 1986; Gaudreau and Boisclair, 2000). During the AP period after mid-July, we did not collect any more YOY yellow perch in the pelagic zone; this was also confirmed by hydroacoustic data of the water column (Ślusarczyk et al., in prep.). Either the sampling was inefficient for catching larger YOY perch which, by having greater swimming capacity, could escape the large Bongo net, or larger YOY perch moved to the littoral zone of the lake to escape piscivorous fish (Okun *et al.*, 2005).

Gut content analysis showed important seasonal changes in the diet of YOY fish during their summer growth in the pelagic zone (Fig. 2.3B). For the first two weeks of June, the diet of new-hatched YOY perch (< 15 mm) was mainly composed of calanoid copepods and eggs, and of the small cladoceran *Bosmina*; their gape width was too small to capture daphnids (Fig. 2.3C). When YOY perch reached a length of 15 mm with a gape width larger than 2 mm in mid-June, they began to feed on *Daphnia*, selecting a small proportion of both the small-sized *D. galeata mendotae* and the large-sized *D. pulicaria*. The large-sized *D. pulicaria* became the predominant item in the diet of YOY perch later at the end of June and the beginning of July when YOY perch measured between 15 and 27 mm. On 15 July, both *Daphnia* species were rarely found in the gut content of larger YOY perch which fed again on *Bosmina* and copepods.

Figure 2.3: (A). Density (ind·m^{-3}) and mean length (mm) of YOY perch (B). Relative abundance (%) of zooplankton prey items in their gut content. Error bars on mean values correspond to the standard deviation. Data are presented only for the LP (low-predation) and HP (high-predation) periods when YOY fish were present and caught in the pelagic zone of the lake. No YOY perch were caught with the Bongo net during the BP (before-predation) and AP (after-predation) periods. (C). YOY perch gape width (mm) and D. pulicaria and D. galeata mendotae adults and juveniles body width (mm) during the LP and HP periods.


A
LP
HP
Density (ind.m⁻³)
Length (mm)
YOY perch density (ind.m⁻³)
YOY perch length (mm)
0
1
2
3
4
5
6
7
0
5
10
15
20
25
30
01.06
08.06
16.06
24.06
28.06
06.07
15.07
2002
B
LP
HP
% of prey in YOY perch gut content
0
20
40
60
80
100
01.06
08.06
16.06
24.06
28.06
06.07
15.07
2002
D. g. mendotae
D. pulicaria
Bosmina
Calanoids
Cyclopoids
Copepod eggs
Others
C
LP
HP
YOY
Adult D. pulicaria
Adult D. mendotae
Juvenile D. pulicaria
Juvenile D. mendotae
YOY perch gape width (mm)
Daphnia body width (mm)
0
1
2
3
4
01.06
08.06
16.06
24.06
28.06
06.07
15.07
2002

The selectivity index indicated that YOY fish are limited by their small gape to the smaller zooplankton because they started by feeding on the very small juveniles (0.75 mm) of both *Daphnia* species on 16 June when they were smaller than 15 mm (Fig. 2.4). Moreover, they only fed on *Daphnia* prey with a maximum size of 1.5 mm in July when they reached larger length (15-27 mm), although larger *Daphnia* (1.5 - 2.5 mm) were present in the lake. Ivlev's selectivity index values indicated that small juveniles (0.75-1 mm) of both *Daphnia* species were the only *Daphnia* prey selected by very small YOY perch larvae (< 15 mm) on 16 June, while *Daphnia* of medium size (1-1.5 mm) were selected later in June and in July when YOY fish grew to greater length (> 15 mm) (Table I). *Daphnia* prey of size greater than 1.75 mm were never found in the gut contents of YOY perch caught in the pelagic zone during the survey (Table 2-I).

2.4.3 Life history traits

The mean body length of *D. pulicaria* was always larger than that of *D. galeata mendotae* in both adults and juveniles (Fig. 2.5). For both *Daphnia* species, repeated-measured ANOVAs indicated significant changes in body length of adults and juveniles among dates during the summer survey (Table 2-II). For adults of *D. pulicaria*, there was a significant tendency for a smaller mean body length at the very end of the high-predation period (HP) on 15 July (Fig. 2.5). The mean body length of juveniles of *D. pulicaria* was smaller during the entire HP period (Fig. 2.5). The mean body length of *D. galeata mendotae* was least at the end of the high-predation period (HP) in both adults and juveniles. The decrease in body length for *D. galeata mendotae* at the end of the HP period was less pronounced than for *D. pulicaria* (Fig. 2.5).

Table 2-I: Ivlev's selectivity index of YOY perch for *D. pulicaria* and *D. galeata mendotae* of different size classes (mm) (-1 highly avoided, 1 preferred). Calculations based on the size distributions of each *Daphnia* species in the lake and in the YOY gut contents during the LP and HP periods.

Daphnia pulicaria					
Size structure (mm)	16 June	24 June	28. June	06 July	15 July
0.75	0.77	0.30	0.28	0.44	-0.30
1	-0.67	-0.12	0.18	-0.11	0.52
1.25	-0.98	0.49	0.42	0.26	-0.11
1.5	-1	0.40	-0.01	-0.49	-0.76
1.75	-1	-0.90	-0.86	-0.49	
2	-1	-1	-1		
2.25	-1	-1	-1		
2.5		-1			
Daphnia galeata mendotae					
0.75	0.77	0.66	0.22	-0.18	-1
1	-0.99	0.47	0.73	0.37	0.78
1.25	-0.99	-0.77	-1	0.68	-1
1.5	-1	-0.81	-1		
1.75			-1		
2					
2.25					
2.5					

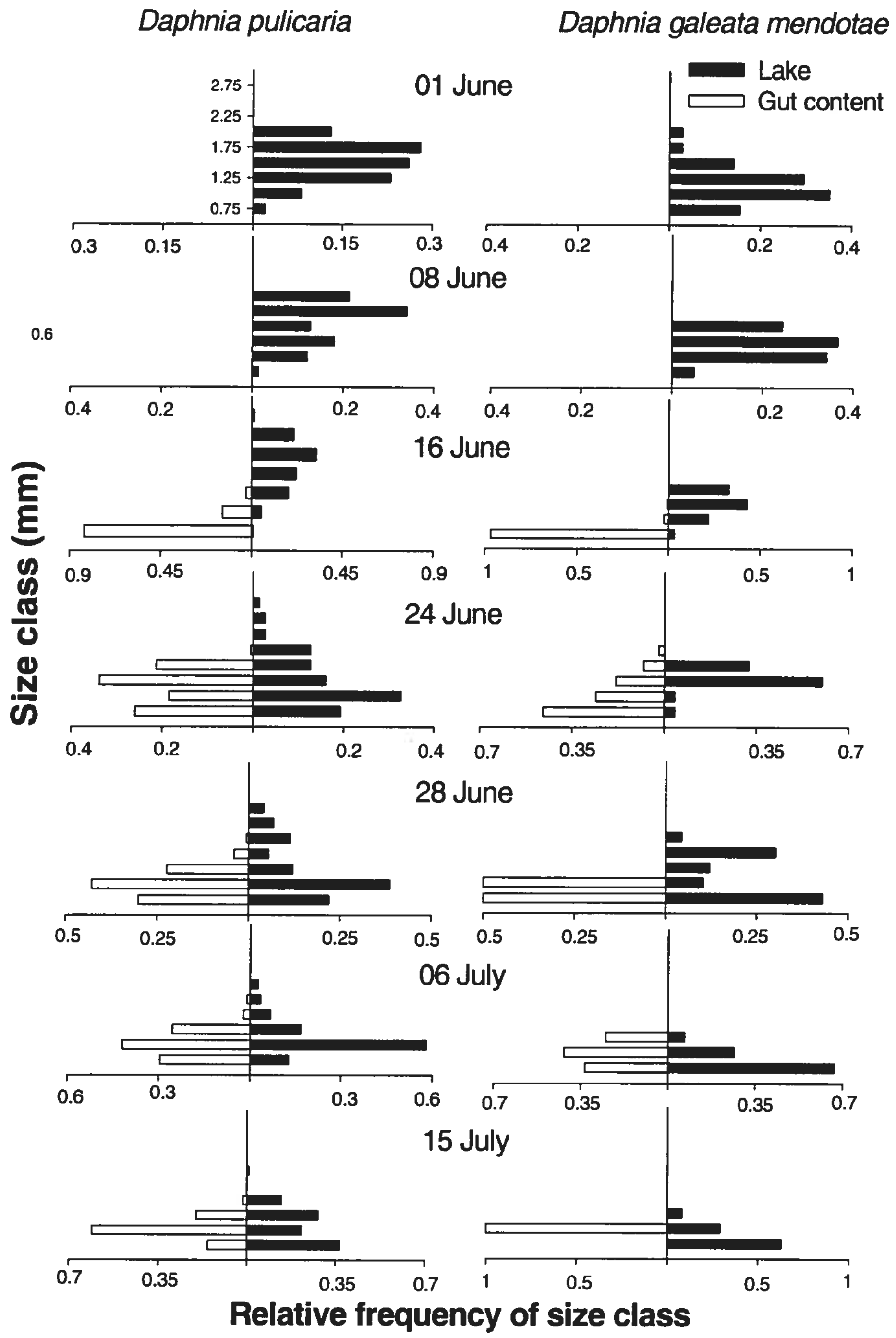
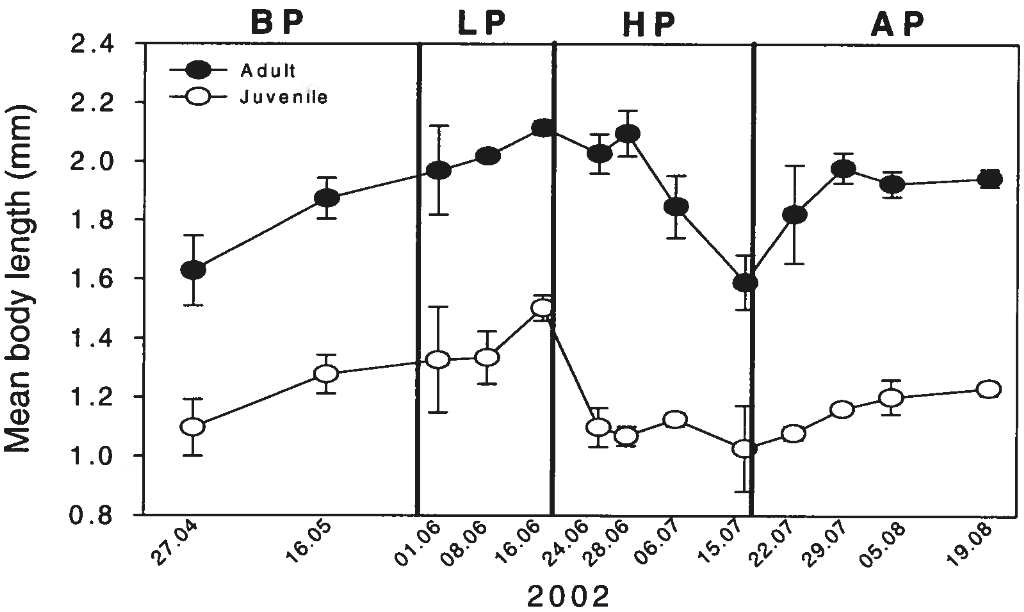


Figure 2.4: Size distributions of D. pulicaria and D. galeata mendotae found in YOY perch gut contents (white) and in zooplankton samples collected in the lake (black) from 1 June to 15 July. Size classes were established with an increment of 0.25 mm on the total range of size of *Daphnia* observed in our study.

Daphnia pulicaria



Daphnia galeata mendotae

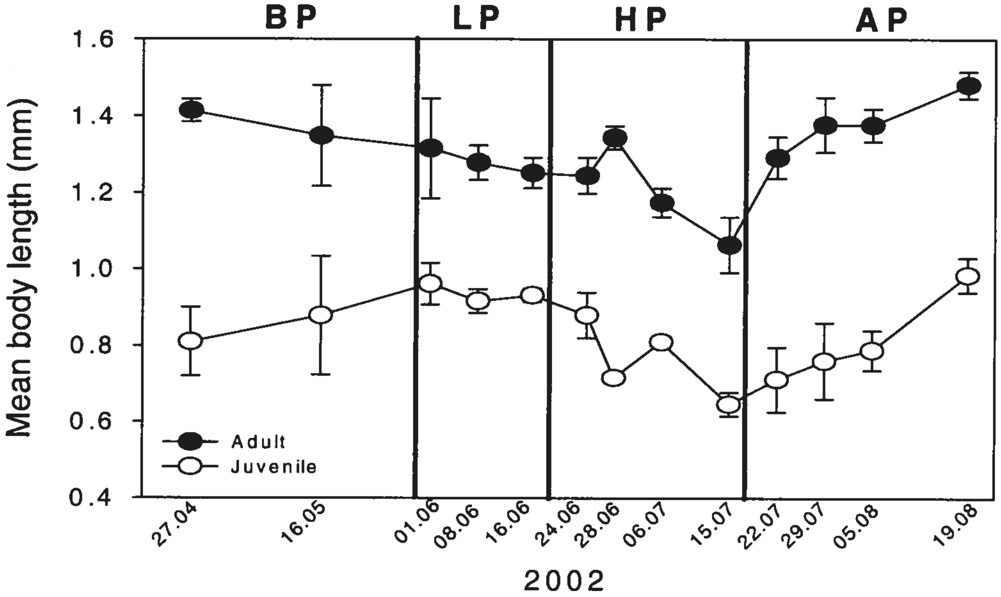


Figure 2.5: Variation in the mean body length (mm) of adults and juveniles of D. pulicaria (top panel) and D. galeata mendotae (bottom panel) during the YOY fish periods (BP, LP, HP, AP) in summer 2002. Error bars on mean values correspond to the standard deviation.

Table 2-II: Repeated-measured ANOVA testing for the differences among dates during the summer period in the body length of *D. pulicaria* and *D. galeata mendotae*, respectively for the juveniles and adults, and the size at maturity (SAM) and clutch size of adults.

Life history traits		Df	MS	*F*	*P*
Daphnia pulicaria					
Adults	Body length	12.24	0.077	9.561	< 0.001
	SAM	12.24	0.0082	10.125	< 0.001
	Clutch size	11.22	5.147	15.747	< 0.001
Juveniles	Body length	12.24	0.056	7.731	< 0.001
Daphnia galeata mendotae					
Adults	Body length	12.24	0.035	7.272	< 0.001
	SAM	12.24	0.027	16.116	< 0.001
	Clutch size	11.22	9.751	6.422	< 0.001
Juveniles	Body length	12.24	0.033	6.498	< 0.001

The size at maturity (SAM) changed significantly during the summer survey (Table 2-II). SAM was the smallest at the very end of the high-predation period (HP) on 15 July for both species (Fig. 2.6). *D. pulicaria* showed the strongest reduction in SAM (1.75 to 1.35 mm), whereas the response of *D. galeata mendotae* was weaker (1.2 to 1 mm).

Clutch size of *D. pulicaria* and *D. galeata mendotae* varied significantly among dates during the survey (Table 2-II). It was the highest during the BP period when YOY perch were not yet present in the pelagic zone of the lake (Fig. 2.6). During the other periods (LP, HP, AP), *D. pulicaria* clutch size decreased to values around or lower than 2 eggs per female. *D. galeata mendotae* clutch size declined as low as 1.5 eggs per gravid female at the end of the LP period, then increased during the HP period to 2.5 eggs, and reached values around 4 eggs during the AP period (Fig. 2.6). Only, the large-sized *D. pulicaria* produced ephippia during the LP and HP periods. The first ephippium was recorded on 1 June and resting egg production was an active phenomenon until 15 July.

2.4.4 Behavioural traits

Day and night WMD and DVM amplitude of *D. pulicaria* and *D. galeata mendotae* were determined for juveniles and adults separately (Fig. 2.7). Daytime WMD of adults of both species changed significantly between the YOY fish periods (Table 2-III), being clearly deeper during the HP period (Fig. 2.7). In contrast, night time WMD of adults of both species did not change significantly between the periods. The WMD of the juveniles of *D. pulicaria* was deeper during the HP period both during day and night whereas WMD of juvenile *D. galeata mendotae* did not change significantly during the HP period (Table 2-III).

In spring (BP period) and at the beginning of the LP period, the WMD of juveniles and adults of both species were located at the mean depth of the lake (6 m); observations indicated that *Daphnia* were distributed uniformly throughout the water column. During the HP period, both *Daphnia* species stayed deeper; WMD ranged from 9 to 11 m in daytime and remained around 8 m at night. After the predation period (AP), although an upward increase in the WMD of juveniles and adults of both *Daphnia* was observed during the day and night, the WMD of the large-sized *D. pulicaria* still stayed deeper (6-9 m) while the small-sized *D. galeata mendotae* were located at shallower depths (4-6 m) (Fig. 2.7).

During the HP period, DVM amplitude of adult *D. pulicaria* and *D. galeata mendotae* reached 3m and was marginally significant (Fig. 2.7; Table 2-III). Adult daphnids resided deeper in the water column during the day. DVM amplitude of juveniles of *D. pulicaria* and *D. galeata mendotae* was not significant even though WMD was deeper during day time at the beginning of the HP period (Fig. 2.7; Table 2-III).

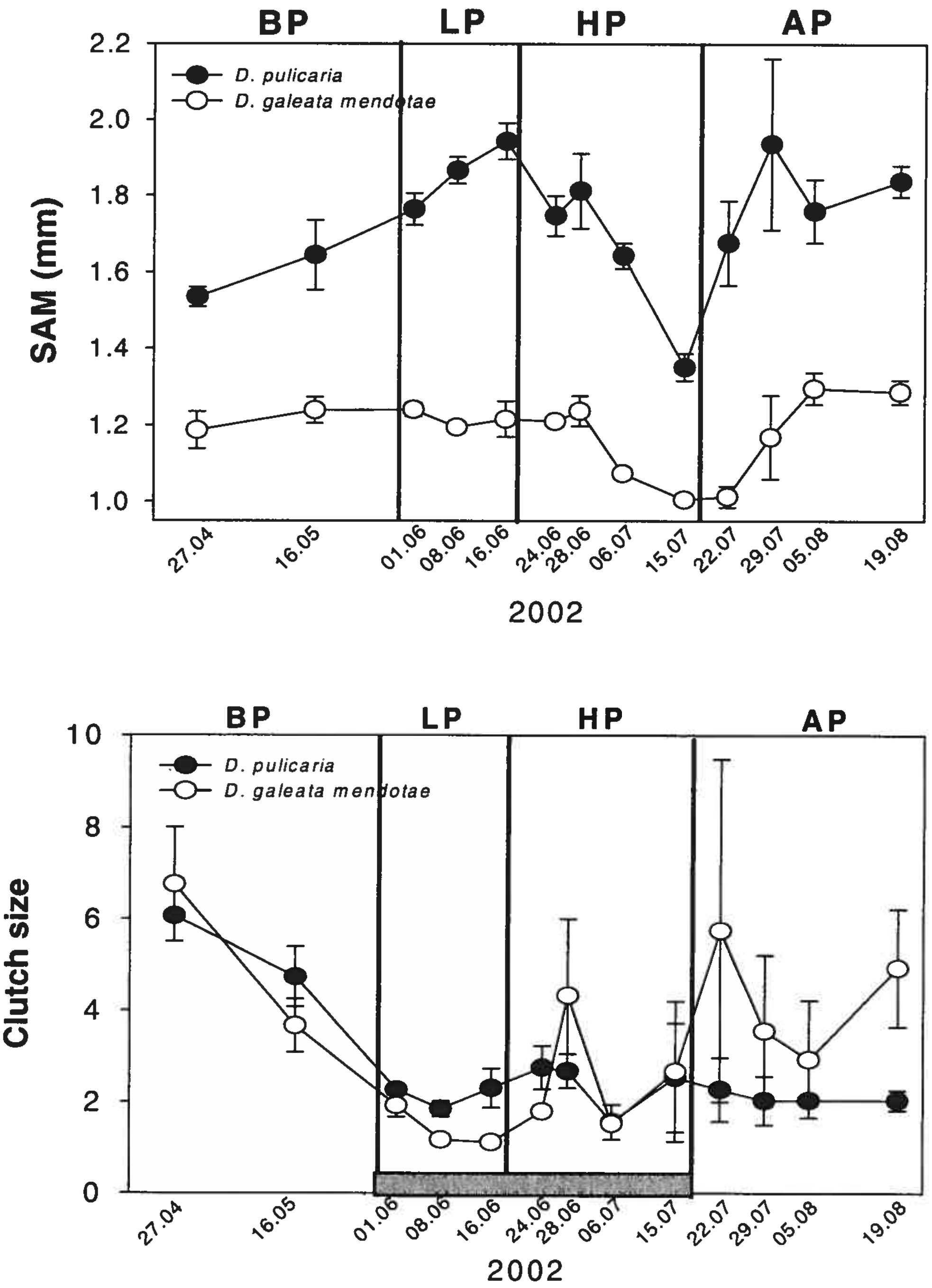


Figure 2.6: Variation in the size at maturity (SAM: mm) (top panel) and in clutch size (nb. of eggs per gravid parthenogenetic female) (bottom panel) of D. pulicaria and D. galeata mendotae during the YOY fish periods (BP, LP, HP, AP) in summer 2002. Shading area in the bottom panel corresponds to period of ephippium production by D. pulicaria. Error bars on mean values correspond to the standard deviation.

Table 2-III: Results of Kruskal-Wallis tests for differences among the 4 YOY fish periods (BP, LP, HP, AP) in the weighted mean depth (WMD) at day and night of juveniles and adults of *D. pulicaria* and *D. galeata mendotae*. Results of paired t-tests for differences between day and night in the WMD of juveniles and adults of *D. pulicaria* and *D. galeata mendotae* during the HP period only.

WMD		WMD among fish periods Kruskall-Wallis test			WMD among day and night Paired *t*-test		
		k	*H*	*P*	df	*T*	*P*
Daphnia pulicaria							
Adults	Day	3	10.693	0.014			
	Night	3	6.085	0.108	4	2.642	0.057
Juveniles	Day	3	10.693	0.014			
	Night	3	10.588	0.014	4	0.057	0.958
Daphnia galeata mendotae							
Adults	Day	3	7.84	0.049			
	Night	3	4.553	0.208	4	2.893	0.044
Juveniles	Day	3	7.593	0.055			
	Night	3	6.505	0.089	4	2.19	0.094

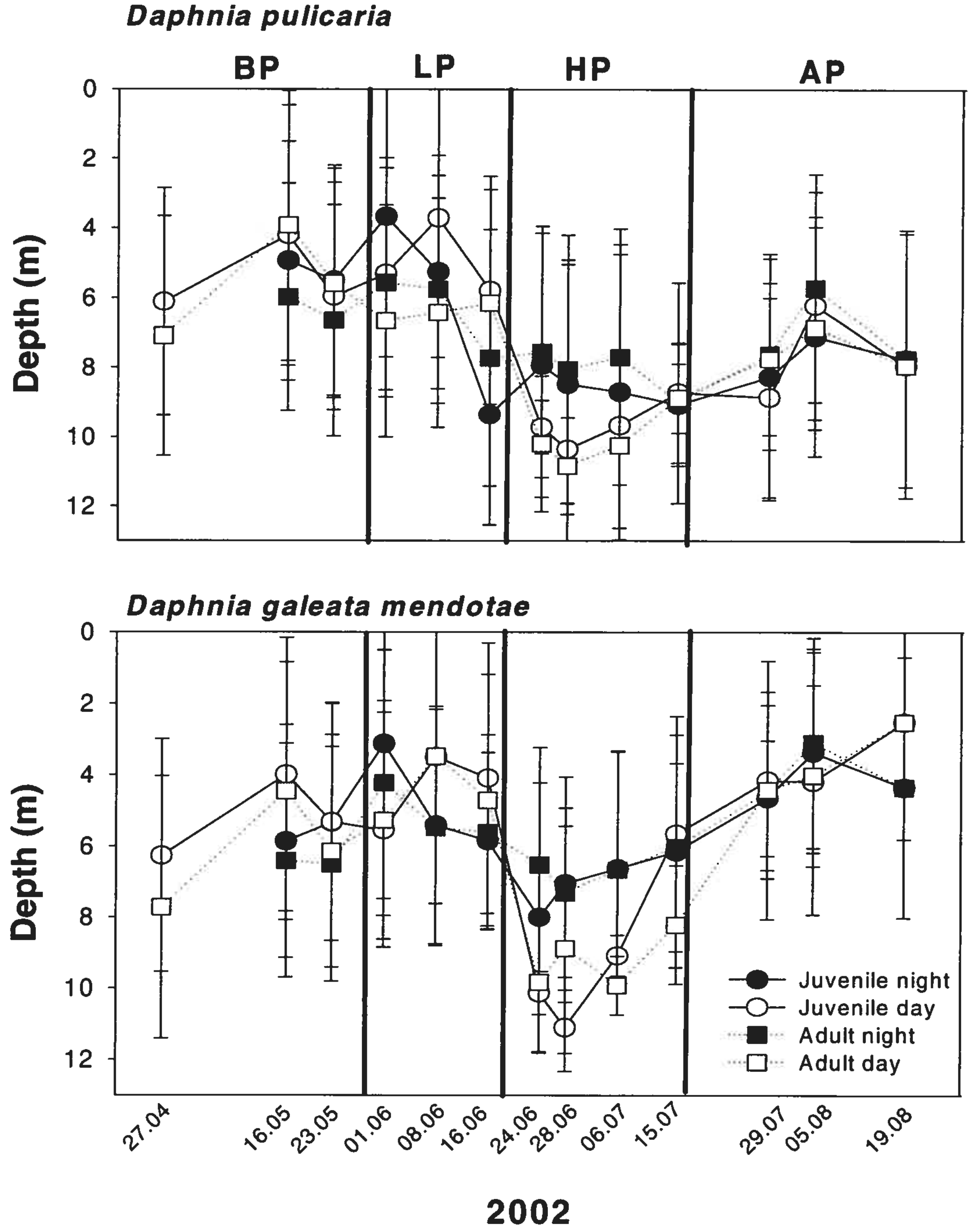


Figure 2.7: Variation of the mean residence depth (WMD) of juveniles (circles) and adults (squares) of D. pulicaria (top panel) and D. galeata mendotae (bottom panel) at day (white symbols) and night (black symbols) during the YOY fish periods (BP, LP, HP, AP) in summer 2002. Error bars on mean values correspond to the standard deviation.

2.5 Discussion

Our field study shows important seasonal changes in size-selective predation of YOY perch associated with phenotypic plasticity in life history and behavioural traits of the two coexisting *Daphnia* species. Even though the impact of small YOY perch cannot be dissociated from the potential impact of larger planktivorous fish known to occur during summer in Lake Brome (Masson *et al.*, 2004), YOY perch was the main visually hunting predator of *Daphnia* captured in the pelagic zone during our survey (Pierce *et al.* 1994). Generally, young fish of all species combined numerically dominates over larger planktivorous fish by several orders of magnitude after their hatching at spring (Wagner *et al.*, 2004) and they are among the most important vertebrate zooplanktivores in lakes (Hülsmann *et al.*, 2004).

Our study supports the alternative hypothesis of negative size-selective predation by small YOY perch, as observed by Hülsmann *et al.* (Hülsmann *et al.* 2004). Gape-limited feeding and negative-size selection are predatory strategies already observed for YOY of yellow perch and Eurasian perch in previous field studies (Hansen and Wahl, 1981; Mayer and Wahl, 1997; Mehner *et al.*, 1998; Graeb *et al.*, 2004) and laboratory experiments (Hülsmann *et al.* 2004). An interesting result is that small YOY perch (< 15 mm), restricted by their gape width, can not prey on large body length and width of *Daphnia* species. Medium-size YOY perch (15-20 mm) and larger YOY perch (20-25 mm) showed negative size-selection on *Daphnia* species, selecting prey of size less than 1.5 mm, even though larger *D. pulicaria* prey were available in the lake. Such a threshold in the maximum size of *Daphnia* prey ingested by gape-limited YOY perch could also be attributed to a population-density threshold operating at both the individual and population levels (Gliwicz, 2001). Individuals selected by planktivorous fish tend to be more conspicuous not only in terms of their body size but also in terms of their abundance in the field (Gliwicz, 2001). In our study, a population-density threshold could explain foraging switch of YOY perch from *D. galeata mendotae* to *D. pulicaria* in late June and from *D. pulicaria* to *Bosmina* sp. in late July. On 15 July, *Bosmina* was the selected prey of large YOY fish (27 mm) probably because its population was the most abundant even though its body size was two times smaller than the daphnids which were in low numbers. The seasonal changes in size-selective feeding of YOY perch influence the succession pattern of coexisting *Daphnia* species in Lake Brome. Because larger YOY perch shifted their diet towards the slightly larger *D. pulicaria* during the HP period, *D. galeata mendotae* was released from predation pressure and could reach again high abundance after the fish predation period. In contrast, the heavily predated *D. pulicaria* produced diapausing eggs as the ultimate response to survive during the high predation period, and did not recover after the high predation period (Slusarczyk *et al.* 2005).

Common antipredator responses to positive size selection may be maladaptive responses to gape-limited predators which feed on small or medium-size prey (Hülsmann *et al.*, 2004). In Lake Brome, the strong decrease in the body length of adults for both *Daphnia* species at the end of the high-predation (HP) period could have been caused by selective elimination of large bodied *Daphnia* by visually feeding fish or by the simultaneous maturation of smaller juveniles into small body size adult. However, the absence of large *D. pulicaria* prey in gut contents of YOY perch (no *Daphnia* prey > 2 mm) and their selective feeding on smaller specimens (with 1 mm *Daphnia* most eagerly eaten by the YOY perch) indicate negative size-selective predation of perch fingerlings. Clearly, the body size reduction of juveniles at the end of the HP period can be seen as disadvantageous when facing gape-limited YOY perch that selectivity fed on them, but may be a consequence of selective predation on the larger juveniles by growing YOY perch. Interactive effects of fish predation and algal food limitation may also explain seasonal changes in *Daphnia* body length (Ghadouani *et al.*, 2003, 2006; Hülsmann *et al.*, 2004). However, the food limitation interference is likely of low influence in Lake Brome because body size of both juveniles and adults of each species increased again as soon as YOY perch predation pressure is released while cyanobacteria were still dominant. Ślusarczyk *et al.* (Ślusarczyk; Warsaw University & Pinel-Alloul, Gélinas, Université de Montréal) measured the lipid content and the weight-length relationship parameters (intercept and slope) of *D. pulicaria* and none of these indices suggested a potential food limitation.

The decrease in size at maturity (SAM) is another life history response to counteract positive size-selective predation by fish (Boersma *et al.*, 1998; Riessen, 1999). However, the adaptive significance of a decreased SAM in *Daphnia* populations facing gape-limited predation by YOY fish has recently been questioned under experimental conditions (Hülsmann *et al.*, 2004). Our study indicates that SAM was relatively constant except at the very end of the HP period where a significant short-term reduction was observed in both *Daphnia*. A lack of variation in SAM life history trait in response to gape-limited predation has already been reported in enclosure experiments and laboratory studies for *D. galeata* (Hülsmann and Mehner, 1997), *D. magna* (Mikulski, 2000) and *D. pulicaria* (Bernot *et al.*, 2004). Hülsmann *et al.* (2004) suggested that under field conditions, a lack of response in SAM under negative size-selective predation early in the summer is advantageous for *Daphnia* survival later in the season under positive size-selective predation by older planktivorous fish. Again, the short-term reduction of SAM observed for both species may be due to the maturation of small juveniles. Interestingly, SAM increased markedly in the AP period. Mikulski *et al.* (2005) showed that removing fish-chemical signal can induce *Daphnia* to withdraw from life history changes and mature at a larger size. In our study, the phenomenon of the SAM increase when YOY fish disappeared from the pelagic zone after 15 July could be explained by this mechanism.

Both *Daphnia* species had smaller clutch sizes during the LP and HP periods. Reducing clutch size may be beneficial for *Daphnia* fitness by reducing prey visibility (Pearre, 2003). The reduction in clutch size was also associated with a shift in algal food resource from edible (Chrysophytes and diatoms) to inedible (cyanobacteria) algal food during the HP period. Another alternative explanation could be that *Daphnia* decreased the energy allocated to fecundity to allow the production of other inducible defenses such as morphological defenses as a way to increase their long-term fitness, as reported by Boersma *et al.* (1998) for clones of *D. magna* and for the two coexisting *Daphnia* species in Lake Brome (Gélinas *et al.*, 2007). Seasonal variation in clutch size of the small *D. galeata mendotae* also supports the hypothesis of negative-size selective predation by the gape-limited YOY perch. As predation pressure on the small species declined during the HP period, its clutch size tended to increase and reached its highest value at the beginning of the AP period. As already mentioned, the large-sized *D. pulicaria* adopted another life history response by producing ephippia while maintaining small clutch size in parthenogenetic individuals. In enclosure experiments with gape-limited small larval walleye (8-mm standard length), coexisting *D. pulicaria* and *D. galeata mendotae* exhibited similar shifts in life history traits (Bernot *et al.*, 2004), as observed in Lake Brome. It appears that the tendency to produce ephippia in spring is a characteristic associated with the large species most likely to be eliminated later in summer, as reported by Threlkeld (1979).

Deep-water habitat selection and DVM are well-known behavioural strategies used by *Daphnia* to escape positive size-selective predation by visually-hunting fish (Mills and Forney, 1983; Lampert, 1993; Ringelberg *et al.*, 1997; de Meester *et al.*, 1999). Our study indicates that a behavioural response is strongly induced in *Daphnia* populations by the small YOY perch also. Intense predation by YOY yellow perch > 15 mm during the HP period activated DVM behaviour and forced the juveniles and adults of both *Daphnia* species to seek refuge in daytime in deeper and darker waters. Similar behavioural strategy was developed by *Daphnia hyalina x galeata* facing predation by YOY of Eurasian perch of size > 15 mm (Ringelberg *et al.*, 1997; Van Gool and Ringelberg, 2002). One interesting point is that the two coexisting *Daphnia* species displayed similar habitat selection strategies while facing YOY predation: they both selected deeper habitat with lower light level. This result is contrary to what is usually observed, the large-sized *D. pulicaria* tend to select deeper habitat than the small-sized *D. galeata mendotae* as observed in a large indoor enclosure experiment (de Meester *et al.*, 1995) and in field studies (Threlkeld, 1979; Leibold and Tessier, 1991, 1998; Tessier and Leibold 1997). Possible explanations could include a large bin width allowing movement within the bins. Thus, one species could have a mean depth only slightly below the other, and it might have been difficult to detect the difference between their depth preference or the two species did not migrate at exactly the same time and so reached their maximum depths at different times (Pearre 2003). DVM behaviour is the predominant strategy adopted by the adults, whereas the juveniles did not show significant DVM behaviour. Habitat segregation of the two coexisting *Daphnia* was reinforced by the thermal stratification and the lack of oxygen in the hypolimnion. The less visible *D. galeata mendotae* was distributed in shallow waters while the more conspicuous *D. pulicaria* stayed at the level of the thermocline avoiding both the warm epilimnetic waters (temperature > 22 °C) and the anoxic waters ($O_2 < 1$ mg.L^{-1}). Similar habitat segregation has been reported for the same *Daphnia* species coexisting in a hypereutrophic lake (Threlkeld, 1979). By staying in the upper water column at the end of the summer, *D. galeata mendotae* benefited from optimal environmental conditions as shown by higher reproduction and abundance compared to *D. pulicaria*. In a hypereutrophic lake, the light would be rapidly attenuated, so plankters would not need to go far from the surface to find refuge (Pearre, 2003).

This study, as do other experimental and field studies (Ringelberg *et al.*, 1997; Boersma *et al.* 1998; Lass and Spaak, 2003) provides strong evidence that refuge behaviour (deeper WMD and DVM) and life history responses (smaller body length, clutch size and SAM) are alternative prominent antipredator defenses against YOY fish (Sakwinska and Dawidowicz 2005). Our field study indicated that deep habitat selection may be the dominant defense used by the adults of both *Daphnia* species to withstand high negative size-selective predation by small YOY yellow perch. Nonetheless, on 15 July, this response (WMD) was replaced by a decreased SAM, demonstrating the uncoupling of traits within Lake Brome in two coexisting species. Our study also supports the conclusions of Vos *et al.* (2002) who showed using an individual-based modelling approach, that diel vertical migration (DVM) confers a much stronger protection against YOY fish predation than a decreased size at first reproduction (SFR). They found that the coupling of DVM behaviour with a decreased SFR was the best scenario to sustain *Daphnia*. The alternative use of DVM behaviour alone was almost as efficient as the coupling of behavioural and life history defenses. In contrast, using only life history strategy was the worst scenario with a decline in *Daphnia* populations four times higher. Different phenotypic plasticity in antipredator traits in coexisting prey are considered beneficial in sustaining biodiversity and ecosystem function and in decoupling potential trophic cascades in freshwater pelagic ecosystems (Leibold and Tessier, 1998; Bernot *et al.*, 2004).

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Chapitre 3

Formation of morphological defences in response to YOY perch and invertebrate predation in two *Daphnia* species coexisting in a mesotrophic lake

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3.1 Abstract

This study examined the formation of morphological defences by two coexisting *Daphnia* species, the large-sized *D. pulicaria* (2 mm) and the small-sized *D. galeata mendotae* (1.4 mm), in response to the presence of young-of-the-year (YOY) yellow perch (*Perca flavescens*) and invertebrate predators (*Chaoborus*, *Leptodora*) during summer in a mesotrophic lake. We hypothesized that due to differential size-selective predation risk by YOY fish and invertebrates, the large-sized and the small-sized *Daphnia* species would show different morphological responses to predation threats. We followed changes in two morphological traits (relative length of the tail spine in *D. pulicaria* and of the helmet in *D. g. mendotae*) among different periods during summer according to YOY fish and invertebrate predation. We defined four YOY fish predation periods based on the presence of YOY perch in the pelagic zone of the lake and the relative abundance of *Daphnia* prey in their gut contents, and two invertebrate predation periods based on exclusive or mutual occurrence of the invertebrate predators. The large-sized (*D. pulicaria)* and the small-sized (*D.g. mendotae*) species showed different morphological responses to YOY fish and invertebrate predators, respectively. The tail spine ratio of the juveniles and adults of *D. pulicaria* did not change in response to YOY fish predation or to invertebrate predation. A gradual increase in the helmet ratio was observed in the small-sized *D. mendotae* over the summer period. This change was related to the co-occurrence of the invertebrate predators (*Chaoborus* and *Leptodora*) and to YOY fish predation. The warmer temperature cannot be accounted for helmet elongation since it was constant across depths, and not related with the co-occurrence of *D .mendotae* and YOY perch.

Keywords: Tail spine ratio, *D. pulicaria,* helmet ratio, *D. galeata mendotae*, YOY yellow perch, *Chaoborus, Leptodora*

3.2 Introduction

Evolution has forged an assortment of phenotypic adaptations in plankton to deal with different types of predators through changes in prey morphology, behaviour and life history (Lass & Spaak, 2003; Riessen & Young, 2005). Planktonic crustaceans in freshwater habitats commonly face predation by multiple predators. Fish and invertebrate predators may occur simultaneously but usually their relative densities vary in space and time, allowing the coexistence of many planktonic species of different sizes (Weber & Declerck, 1997; González & Tessier, 1997).

Predation risk posed by fish and invertebrate predators depends of the occurrence of each predator, their size-selective feeding and competitive interactions. It is generally assumed that visual-hunting planktivorous fish tend to select large-sized zooplankton (Brooks & Dodson, 1965; Lazarro, 1987), while invertebrate predators feed on small and medium-sized zooplankton (Pastorok, 1981; Pourriot, 1995; Pinel-Alloul, 1995a). However, prey selection varies greatly along the summer season. Young-of-the-year (YOY) planktivorous fish change their prey selection with ontogenesis from negative size-selective feeding by gape-limited YOY fish larvae at spring to positive size-selective feeding by larger YOY fish later in summer (Hansen & Wahl, 1981; Mills & Forney, 1983; Mayer & Wahl, 1997; Wagner et al., 2004; Hülsmann et al. 2004). *Chaoborus* larvae generally select small and medium-sized cladocerans (Dodson, 1974; Pastorok, 1981; Havel & Dodson, 1985; Krylov, 1992), and *Leptodora kindtii* is recognized as an efficient predator of small zooplankton (McNaught et al., 2004). As planktonic invertebrates are also preyed upon by fish, their predation pressure on smaller zooplankton can be alleviated when YOY fish are present, as shown experimentally (González & Tessier, 1997). According to the local adaptation hypothesis (Stibor & Lampert, 2000), *Daphnia* should show stronger antipredator responses to the predominant predator. However, multiple predators can induce phenotypic plasticity in antipredator responses of *Daphnia* coexisting in nature due to the seasonal changes in predator dominance, size-selective feeding, and predator-prey interactions (Riessen, 1999; Tollrian & Dodson, 1999).

Among morphological defences, elongation of the tail spine or the helmet and the development of a neck tooth are common strategies developed by *Daphnia* in response to info-chemicals (kairomones) released by planktivorous fish and invertebrates (reviewed in Larsson & Dodson, 1993; Lass & Spaak, 2003). Induction of morphological defences in *Daphnia* populations by either fish or invertebrate predators is well studied under experimental conditions (Spaak & Boersma, 1997; Kolar & Walh, 1998; Sell, 2000) but more rarely in field studies (Havel & Dodson 1985; Lindholm, 2002). Several experimental studies showed that *Daphnia* respond to fish kairomones by increasing tail spine length (Tollrian, 1994; Spaak & Boersma, 1997), whereas elongation of the helmet or formation of a neck tooth are common responses of *Daphnia* to invertebrate predators (mainly *Chaoborus*) (Tollrian, 1993; Brancelj et al., 1996; Sell, 2000). However, evidence of phenotypic plasticity in morphological defences in coexisting *Daphnia* populations facing multiple predators in natural environments is still missing.

In the present study, we examined the formation of morphological defences by two coexisting *Daphnia* species, the large-sized *D. pulicaria* (2 mm) and the small-sized *D. mendotae* (1.4 mm), in response to the presence of YOY yellow perch (*Perca flavescens*) and invertebrate predators (*Chaoborus punctipennis*, *Leptodora kindtii*) during summer in a mesotrophic lake. The main goal was to investigate temporal and spatial variation in two morphological traits (relative length of the tail spine in *D. pulicaria* and of the helmet in *D. mendotae*) according to changes in YOY fish and invertebrate predation pressure. We hypothesized that due to differential predation risk exerted by YOY perch and invertebrate predators, the small and large-sized species would develop different morphological traits. Predation risks posed by YOY perch would trigger a stronger response in the large-sized *D. pulicaria*, whereas predation risks posed by invertebrate predators, mainly *Chaoborus*, would influence the small-sized *D. mendotae*.

3.3 Methods

3.3.1 Study site and field sampling

Lake Brome is a large (14 km^2) mesotrophic lake of glacial origin situated in the Eastern Townships region, south-east of Montréal, Québec (45°14'N, 72°30'W). Mean and maximum depths are 5.9 and 12.2 m, respectively. The lake is normally ice-free from early April through late November, and thermal stratification developed from early June till late August. Epilimnion extended to 7 m depth, the metalimnion ranged from 7 to 9 m depth, and the hypolimnion was below 9 m. Water temperature in the epilimnion increased from 10°C in spring to 24°C in late summer, while remaining at 15-17°C in the hypolimnion. Total phosphorus and chlorophyll *a* concentrations reached 19 $\mu g.L^{-1}$ and 8 $\mu g.L^{-1}$, respectively. During summer, Secchi water transparency was consistently around 3 m and the euphotic depth (1% of surface light) remained around 9 m. Lake Brome was well oxygenated (> 9 $mg.L^{-1}$) in the epilimnion while the hypolimnion became anoxic (< 1 $mg.L^{-1}$) below 9 m depth after mid-July (Gélinas et al., 2007, in press).

Zooplankton was collected during the day (12h00-17h00) every week from May to August 2002 by vertical hauls (0-12 m) at the deepest site in the pelagic zone with a plankton net (14 cm diameter, 150 µm mesh size). The mesh size was small enough to collect all crustacean species, especially juvenile and adult daphnids, while filtering small rotifers and algae. In addition, zooplankton samples were also collected at six depths (1, 3, 5, 7, 9, 11 m) with a Schindler-Patalas trap (12 L) fitted with a net of 150 µm mesh size. A total volume of 24 L was filtered at every depth. Depth-discrete zooplankton sampling was carried out during summer at four dates corresponding to the different periods of YOY fish and invertebrate predation (for details see the *Analysis of YOY perch and invertebrate planktivory* section below). Zooplankton samples were fixed in the field in 4% sugar buffered-formalin solution for further analysis in the laboratory.

Sampling of YOY fish and invertebrate predators was carried out in the pelagic zone, at every week from 23 May until 29 July, 2002. Invertebrate predators we collected during night time (22h00-00h00) by vertical hauls (0-11m) using a large plankton net (0.25 m^2, 1 mm mesh size). YOY fish were caught with a large Bongo net (0.25 m^2 area, 7 m length, 2 mm mesh size) trawled in the center of the lake along 200m transects at 1, 3 and 5 m depths two hours after sunset (between 20h00 and 22h00). Captured YOY fish, mainly yellow perch, were counted and measured before being fixed in methanol-formaldehyde solution. Density of YOY fish and invertebrates (ind.m^{-3}) was evaluated at each sampling date. We analyzed the gut contents of 30 individuals of YOY perch collected on each sampling date, by identifying and counting all planktonic prey (*Bosmina*, *Daphnia* species, cyclopoid and calanoid copepods and eggs).

3.3.2 Analysis of *Daphnia* morphological traits

Analysis of morphological traits was done on both juvenile and adult instars of *D. pulicaria* and *D. mendotae* collected from vertical hauls and at discrete depths in the pelagic zone of the lake. We analysed *Daphnia* morphological traits only on a biweekly interval on zooplankton samples collected with the plankton net). Adult and juvenile status for *Daphnia* individuals was established based on the estimation of the size at maturity of each species (SAM) (Stibor & Lampert, 1993). Individuals smaller than the SAM were categorized as juveniles while the ones larger as adults. Around 100 specimens of each species from vertical haul samples and 50 specimens of each species from the discrete-depth samples were randomly selected and measured. The animals were examined at 100X magnification with a dissecting microscope (Leica MZ12) and measured with an image analyser (Image-Pro Plus). The body length from the top of the eye to the base of the tail spine was measured on each species. For *D. pulicaria*, we measured the tail spine length from the base to the tip, and we estimated the tail spine elongation based on the ratio of the tail spine length to the body length (so-called tail spine ratio). For *D. mendotae*, the helmet length was measured from the tip of the helmet to the top of the eye, and we estimated the helmet elongation based on the ratio of the helmet length to the body length (so-called helmet ratio).

3.3.3 Analysis of YOY perch and invertebrate planktivory

According to the single or conjoint occurrence of invertebrate predators in the pelagic zone, the summer survey was divided into two periods. The C period corresponded to the month of June when *Chaoborus punctipennis* was the single invertebrate predator in high abundance. The LC period corresponded to the months of July and August when both

Chaoborus punctipennis and *Leptodora kindtii* were co-dominant but less abundant (Fig. 3.1).

According to the presence/absence of YOY perch in the pelagic zone of the lake and the importance of *Daphnia* prey in their gut contents, the summer was divided into four YOY fish periods: the before-predation period (B), the low-predation period (LP), the high-predation period (HP), and the after-predation period (A) (Fig. 3.2). The B period (27 April to 31 May) corresponded to the absence of YOY fish in the pelagic zone of the lake as no fish were caught in the Bongo net until the end of May. The LP period (1 to 16 June) corresponded to the presence of YOY fish in high density (up to 7 ind.m^{-3}) in the pelagic zone, however, not yet feeding on *Daphnia* but mainly on *Bosmina* sp. and small calanoid copepods (Fig. 3.2). The HP period (17 June to 15 July) represented the period of low abundance but of high predation by YOY fish on both *Daphnia* species (Fig. 3.2). The period A (15 July to 19 August) was the after-predation period when YOY fish were not longer captured in the pelagic zone.

3.3.4 Statistical analysis

Repeated-measured ANOVAs (RM-ANOVAs) were used to test the difference in the mean values of morphological defences in adults and juveniles of each *Daphnia* species (tail spine ratio of *D. pulicaria*; helmet ratio of *D .mendotae*) between the two invertebrate predation periods, and between the four YOY fish periods. RM-ANOVA was also used to test the effects of depths on the body length and morphological defences of each *Daphnia* species. For *D. mendotae*, the 11-m depth was removed from the analysis since no *D. mendotae* were found at that depth during the last two YOY fish periods. Data were checked for normality in distribution with a Kolmogorov-Smirnov test (Lilliefors) (Sokal & Roff, 1995). All computations were run using Systat 8.

3.4 Results

3.4.1 Invertebrate and YOY perch planktivory

The dominant invertebrate predator was *Chaoborus punctipennis*, whose larvae were present at night in the water column throughout summer (Fig. 3.1). Its abundance increased during the C period until a maximum density above 100 ind·m^{-3} at the end of June. During the LC period, *Chaoborus* density decreased and ranged from 10 to 60 ind.m^{-3}, and the carnivorous Cladocera *Leptodora kindtii* appeared in the water column at densities under 50 ind·m^{-3} (Fig. 3.1).

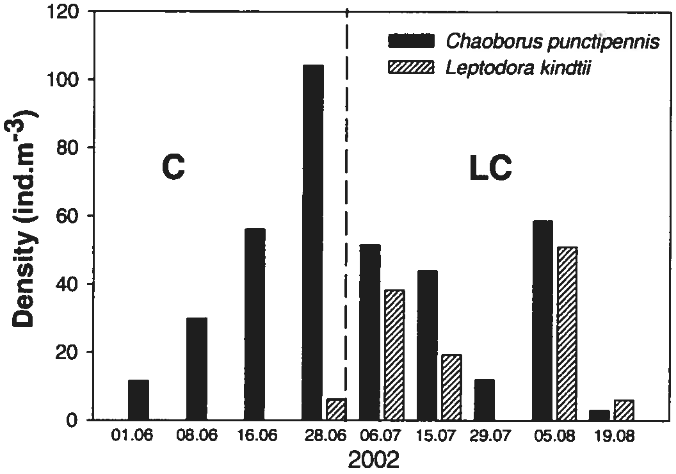

Figure 3.1: Variations in Chaoborus larvae and Leptodora kindtii densities (ind·m^{-3}) over the summer 2002 in Lake Brome with the distinction between the Chaoborus predation period (C) and the combined Chaoborus and Leptodora predation period (LC).

Before 1 June (period B) no YOY fish were caught with the Bongo net in the pelagic zone of the lake. During the LP period, new-hatched yellow perch of small size (8-15 mm) appeared in the pelagic zone at the beginning of June and aggregated at 2-m depth with a maximum density of 7 ind·m^{-3} (Fig. 3.2A). During the HP period, YOY perch having size > 15 mm stayed in surface waters but their density decreased from 4 to 1 ind·m^{-3} during the last two weeks of June. YOY perch measuring around 27 mm avoided surface waters and were only caught at 5 m depth from the end of June until mid-July (Fig. 3.2A). After 15 July (period A), no more YOY perch were caught in the pelagic zone of the lake. Gut content analysis showed that during the LP period, new-hatched yellow perch fed on small calanoids, eggs of copepods, and on the small cladoceran *Bosmina* (Fig. 3.2B). *Daphnia* species became the preferred food item of YOY perch > 15 mm during the HP period (Fig. 3.2B). Both *D. mendotae* and *D. pulicaria* were found in the YOY gut content.

D. pulicaria was the predominant item in the diet of larger YOY perch (20-27 mm) (Fig 3.2B).

3.4.2 Variation in morphological defences among YOY fish and invertebrate predation periods

The mean values of body length of the juveniles and adults of *D. pulicaria* were always greater than those of the juveniles and the adults of *D. mendotae* in each of the YOY fish periods (Table 3-I). The morphological defences were more pronounced in the juvenile instars than in the adults for both *Daphnia* species. The tail spine ratio of *D. pulicaria* and the helmet ratio of *D. mendotae* were always greater in the juveniles than in the adults (Table 3-I). RM-ANOVAs testing for differences among the YOY fish periods did not demonstrate any significant change in the tail spine ratio of both the juveniles and adults of *D. pulicaria* ($F_{3,3} = 1.749$, $P = 0.329$; $F_{3,3} = 0.228$, $P = 0.872$). In average, the tail spine ratios of the juveniles and adults of *D. pulicaria* were relatively similar along the YOY fish periods (Table 3-1). In contrast, the helmet ratios of the juveniles and adults of *D. mendotae* were significantly different between the YOY fish periods ($F_{3,3} = 112.3$, $P < 0.001$; $F_{3,3} = 15.0$, $P = 0.026$). In average, the helmet ratios steadily increased along the YOY fish periods (Table 3-I).

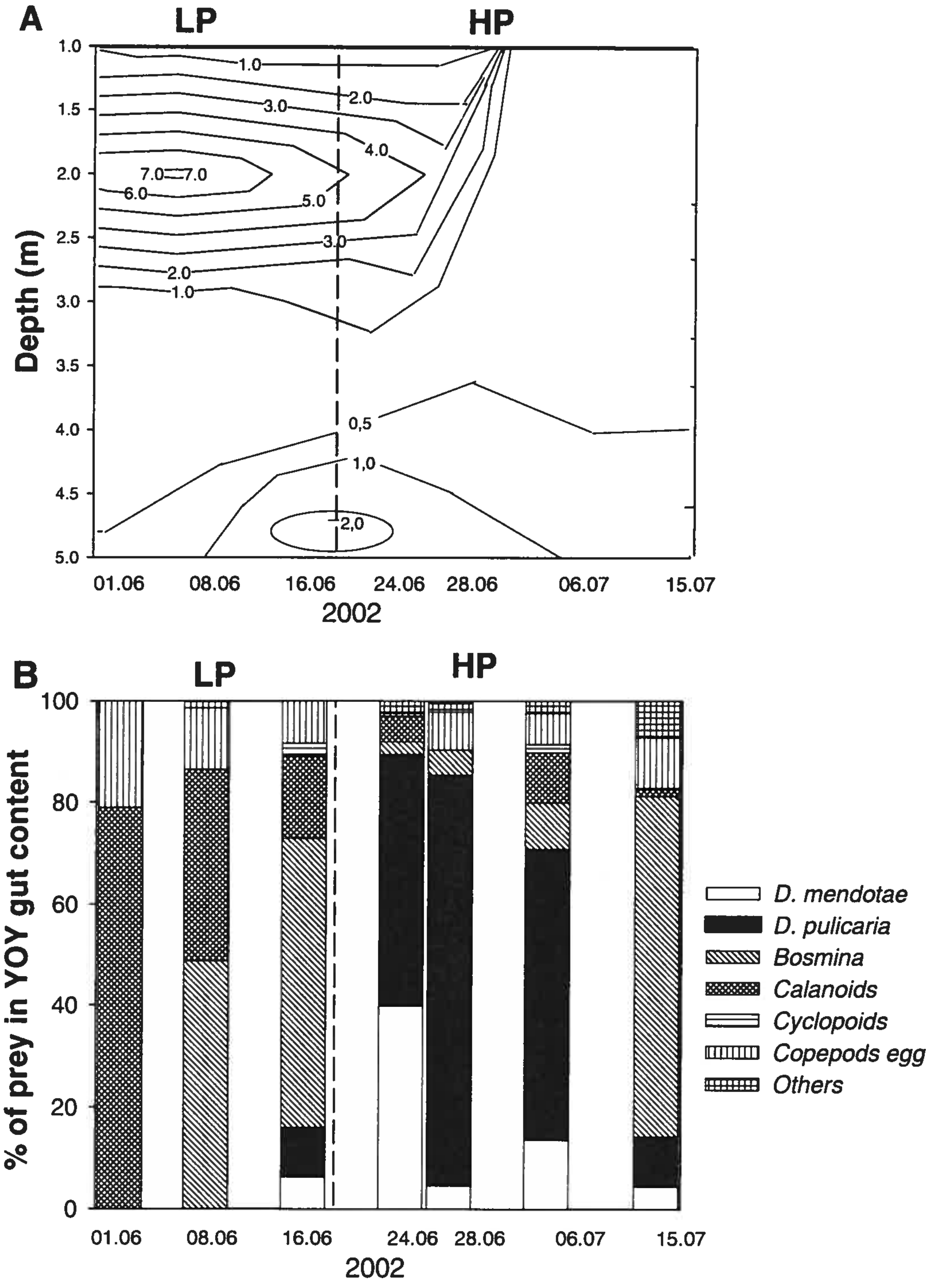

Figure 3.2: Contour plot of the YOY yellow perch density according to depth (A) and seasonal changes in the percentage of different zooplankton prey in YOY gut content (B) in Lake Brome during two YOY fish predation periods (LP, HP) in summer 2002. The periods B (before-predation) and A (after predation) are not shown because no YOY perch were captured in the pelagic zone.

The mean body lengths of the juveniles and adults of *D. pulicaria* were similar during the two invertebrate periods (Table 3-II). As seen before, morphological defences of both *Daphnia* species were relatively more pronounced in the juvenile instars than in the adults (Table 3-II). RM-ANOVAs did not indicate significant difference in the tail spine ratio of the juveniles and adults of *D. pulicaria* between the invertebrate periods (C vs LC) ($F_{1,3}$ = 0.216, P = 0.674; $F_{1,3}$ = 0.406, P = 0.569). In contrast, the helmet ratios of the juveniles and adults of *D. mendotae* were significantly different between the C and LC invertebrate periods ($F_{1,3}$ = 309.6, $P < 0.001$; $F_{1,3}$ = 36.0, P = 0.009). The helmet ratios in the juveniles and adults of *D. mendotae* were 1.7 and 1.5 fold higher during the LC period when both invertebrate predators co-occurred (Table 3-II).

3.4.3 Variation in morphological defences between depths

We examined the changes in body length and in morphological defences of each *Daphnia* species (juveniles and adults pooled) at different depths using mean values during the four YOY fish periods. Depth variation in the mean body length and tail spine ratio of *D. pulicaria* (Fig. 3.3) tended to indicate that during the HP period the smallest individuals with the longest tail spine were situated at 5-m depth, whereas the largest individuals with the shortest tail spine were located at 11-m depth (Fig. 3.3). However, RM-ANOVAs did not indicate significant differences among depths neither for the mean body length nor the mean tail spine ratio of *D. pulicaria* ($F_{5,15}$ = 1.489, P = 0.251; $F_{5,15}$ = 2.279 P = 0.099). The body length of *D. mendotae* seemed slightly smaller during the HP, especially closer to the surface, while the helmet ratio increased drastically along the YOY fish periods (Fig. 3.4). However, no significant difference among depths was found neither for the mean body length nor the mean helmet ratio of *D. mendotae* ($F_{4,12}$ = 1.471, P = 0.272; $F_{4,12}$ = 0.914, P = 0.487).

Table 3-I: Mean values for the body length (mm) and the morphological defences of *Daphnia pulicaria* and *Daphnia mendotae* in juveniles and adults during the 4 YOY periods (B, LP, HP, A). Standard deviations are in brackets.

	Traits	B	LP	HP	A
D. pulicaria					
Juveniles	Body length	0.973 (0.317)	1.206 (0.257)	0.842 (0.166)	1.26 (0.45)
	Tail spine ratio	0.471 (0.101)	0.431 (0.075)	0.492 (0.068)	0.413 (0.096)
Adults	Body length	1.992 (0.211)	1.881 (0.177)	1.732 (0.383)	1.722 (0.337)
	Tail spine ratio	0.317 (0.059)	0.308 (0.055)	0.350 (0.076)	0.356 (0.100)
D. mendotae					
Juveniles	Body length	0.776 (0.179)	0.869 (0.12)	0.635 (0.138)	0.835 (0.205)
	Helmet ratio	0.138 (0.035)	0.163 (0.036)	0.217 (0.039)	0.246 (0.038)
Adults	Body length	1.292 (0.157)	1.249 (0.176)	1.228 (0.221)	1.319 (0.283)
	Helmet ratio	0.098 (0.025)	0.145 (0.046)	0.178 (0.038)	0.215 (0.031)

Table 3-II: Mean values for the body length (mm) and the morphological defences of *Daphnia pulicaria* and *Daphnia mendotae* in juveniles and adults during the 2 invertebrate predation periods (C, LC). Standard deviations are in brackets.

	Traits	C	LC
D. pulicaria			
Juveniles	Body length	1.086 (0.311)	1.030 (0.386)
	Tail spine ratio	0.452 (0.091)	0.457 (0.091)
Adults	Body length	1.910 (0.193)	1.732 (0.380)
	Tail spine ratio	0.310 (0.056)	0.350 (0.077)
D. mendotae			
Juveniles	Body length	0.818 (0.161)	0.722 (0.203)
	Helmet ratio	0.149 (0.037)	0.230 (0.041)
Adults	Body length	1.275 (0.166)	1.276 (0.209)
	Helmet ratio	0.116 (0.042)	0.198 (0.039)

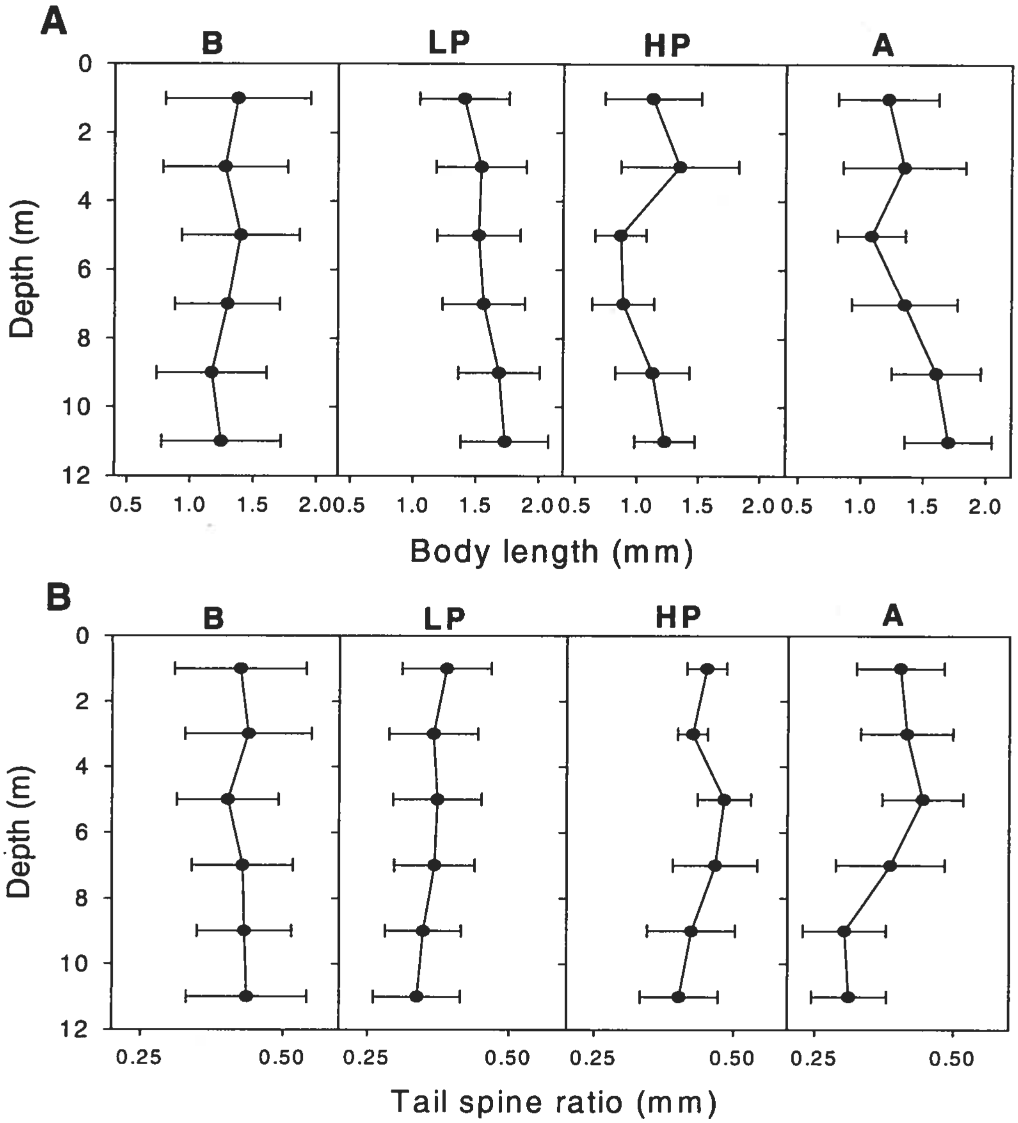

Figure 3.3: Variation in the body length (mm) (±SD) (A) and the tail spine ratio (B) of D. pulicaria across depths during the four YOY fish periods (B, LP, HP, A).

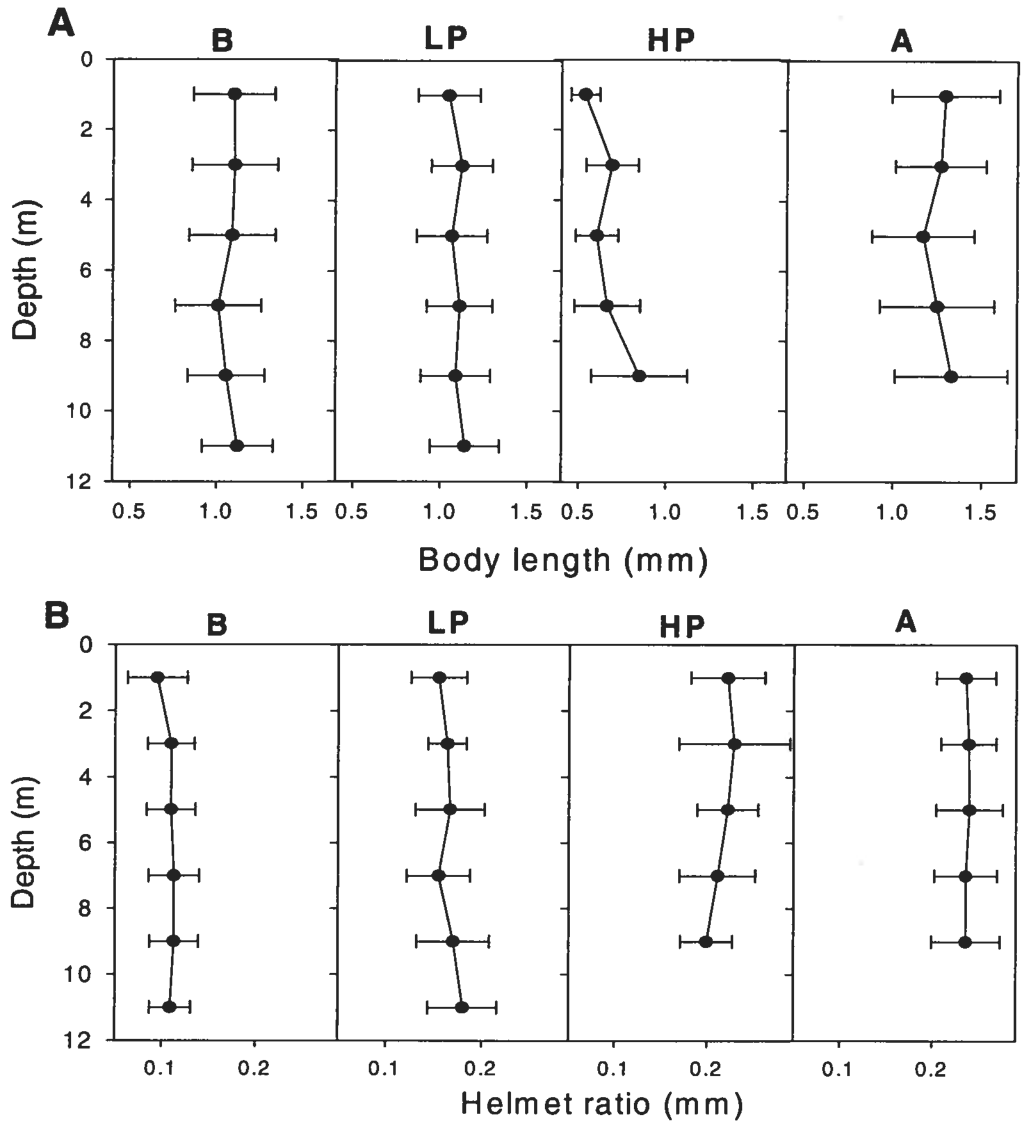

Figure 3.4: Variation in the body length (mm) (±SD) (A) and helmet ratio (B) of D. mendotae across depths during the four YOY fish periods (B, LP, HP, A).

3.5 Discussion

3.5.1 Relative importance of YOY perch and invertebrate predation

In Lake Brome, *Daphnia* populations faced important seasonal changes in predation pressure by the three predators (YOY perch, *Chaoborus*, *Leptodora*) inhabiting the pelagic zone during summer. In spring (first 2 weeks of June), predation pressure was weak because the new-hatched YOY perch were gape-limited and did not feed on *Daphnia*, and the density of *Chaoborus* was also low. It is only during a short period of 1 month (16 June - 15 July) that the three predators were exerting predation pressure on both coexisting *Daphnia*. Following 15 July, YOY perch disappeared from the water column, whereas invertebrate predators remained relatively abundant. One interesting point in our study is that both YOY fish and invertebrate predators exerted negative-size selection on *Daphnia* during the spring and early summer. Recent laboratory experiment (Hülsmann et al., 2004) and field studies (Mehner et al., 1998; Graeb et al., 2004) showed that small YOY perch (< 25-30 mm) were gape-limited predators. We also found in a companion study conducted in Lake Brome that gape-limited YOY perch from 8 to 27 mm selected *Daphnia* smaller than 1.75 mm (Gélinas et al., 2007, in press). Invertebrate predators are known to exert negative size-selection on daphnids (Pinel-Alloul, 1995a, 1995b). *Chaoborus* larvae generally select *Daphnia* smaller than 1.3 mm (Dodson, 1974; Pastorok, 1981; Havel & Dodson, 1985; Krylov, 1992; Brett, 1992), and *Leptodora kindtii* is recognized as an efficient predator of small zooplankton due to its transparency (McNaught et al., 2004).

In this study, to some extent, YOY perch might be considered the dominant predator in Lake Brome in early summer (mid-June to mid-July) since *Daphnia* were their preferred food. Indeed, the density of both *Daphnia* drastically declined at the end of the high-predation period (HP) of YOY perch (Gélinas et al., 2007). However, the co-occurrence of the three common predators might have resulted in complex interactions due to YOY fish predation on the two invertebrate predators. In general, large planktivorous fish with positive size-selective feeding exhibit a strong preference for *Chaoborus* larvae (Pinel-Alloul, 1995a, 1995b). Although *Chaoborus* were present in high numbers in the water column at the end of June no *Chaoborus* larvae were found in the gut contents of the small YOY perch. However, some individuals of *Leptodora kindtii* were ingested by the YOY perch. Thus, the presence of invertebrate predators did not mediate or reduce the risk that gape-limited YOY perch (8-27 mm) posed to the *Daphnia* population, at least until mid-July. In another study, Makino et al., (2001) also found that the sudden emergence of chironomids did not alleviate fish predation pressure on daphnids. Later in summer, when gape-limitation was offset, large YOY perch > 30 mm might have preyed on invertebrate predators. However, the possible interaction among fish and invertebrate predators during late summer remains unknown because we did not capture larger YOY perch after mid-July in Lake Brome. Based on previous studies, we suggest that two main factors could have limited YOY fish predation on the two invertebrate predators occurring in Lake Brome in late summer: the inverse diel vertical migration of Chaoborids (Soranno et al., 1993), and the transparency of the cladoceran predator (McNaught et al., 2004). Therefore, in Lake Brome, the presence of simultaneous predators with similar prey-size selectivity might force coexisting *Daphnia* species to develop morphological defences against their greatest predators, namely YOY perch for the large *D. pulicaria*, and the invertebrate predators for the small *D. mendotae*.

3.5.2 Tail spine elongation in *D. pulicaria*

Neither gape-limited predation exerted by YOY perch or the presence of invertebrate predators in high abundance induced morphological defences in *D. pulicaria*. The large-sized *D. pulicaria* did not respond to predation threats by increasing its tail spine ratio during the high predation (HP) period of gape-limited YOY perch or during the C period when *Chaoborus* were present in high abundance during night in the pelagic zone. No response to invertebrate predator was expected because of the large size of *D. pulicaria*; however, the lack of response to YOY fish predation was unexpected. Dodson (1989) found that *D. pulicaria* tail spine ratio increased in adults subjected to positive size-selective predation, but not in juveniles. In our study, in accordance with the negative size-selective predation exerted by YOY perch in early summer, we were expecting to observe a relatively longer tail spine during the high YOY fish predation period in the juveniles of *D. pulicaria*. Our results demonstrated only that the tail spine ratio was always relatively larger in juveniles than in adults. In Lake Brome, as YOY perch were gape-limited, they selected preferentially the juveniles of *D. pulicaria* < 1 mm (Gélinas et al., 2007). We can only assume that YOY fish selection of smaller-sized daphnids may have greatly increased predation pressure on juveniles, in turn forcing them to develop relatively longer tail spine than the adults. However, we were not able to demonstrate higher tail spine ratio during the high predation (HP) period, although the maximum mean value of tail spine ratio was observed during the HP period for the juvenile.

Our study did not indicate that the induction of morphological defences by *D. pulicaria* varied among depths. However, as both *D. pulicaria* and large YOY perch colonised the oxygenated 5-m metalimnetic water layer during the HP period, *D. pulicaria* had higher tail spine ratio and smaller body size. In contrast, *D. pulicaria* inhabiting deep water layers (9-11 m) not colonized by YOY fish, probably due to the low oxygen concentration (< 1 mg·L^{-1}), had larger body size and smaller tail spine ratio. Similar decrease in tail spine ratio with depth was reported by Spaak & Boersma (1997) for *Daphnia galeata* facing predation by roach, perch and *Chaoborus flavicans*.

3.5.3 Helmet elongation in *D. mendotae*

In Lake Brome, helmet elongation in adults and juveniles of *D. mendotae* during summer was related to seasonal changes in both YOY perch and invertebrate predation. This result is similar to the field study of Lindholm (2002) that showed induction of cyclomorphosis (increase in relative helmet and tail spine length) in *Daphnia leavis* facing predation by Cichlid fish of large size (40-53 mm length) in a tropical floodplain. In Lake Brome, the formation of a longer helmet was probably triggered in early summer during the low predation YOY fish period when *D. mendotae* faced predation by the gape-limited YOY perch of small size (8-27 mm). This antipredator defence was fully developed later in summer, when YOY perch vanished from the pelagic zone while invertebrate predators were still abundant. Relatively high abundance of both *Chaoborus* and *Leptodora* at the beginning of August may have enhanced the occurrence of longer helmet in the small *D. mendotae*. Under experimental conditions, Brett (1992) showed that the *Chaoborus* predation led to an increased incidence of helmets in small-sized *Daphnia* relatively to both the fish treatment and the predator-free control. Brancelj et al. (1996) also reported higher frequency of cornered head in small-bodied *D. hyalina* (0.9-1.3 mm) in the presence of a high density of *Chaoborus* larvae under field and experimental conditions. In addition, it has been suggested that increasing water temperature during summer, above a threshold value of 25-28°C, may induce helmet elongation in *D. cuccullata* and *D. lumholtzi*, (Lampert & Wolf, 1986; Yurista, 2000). However, the constant elongation in the helmet of *D. mendotae* over summer seems unlikely to be attributed to the increasing water temperature in the epilimnion, because the elongation of the helmet was consistent throughout the water column without any effect of depth. In Lake Brome, *D. mendotae* experienced a wide range of temperature seasonally and vertically within the water column. As the lake was thermally stratified, the difference of 7°C in temperature between water surface (20-24°C) and deeper layers (15-17°C) did not induce a decrease in the helmet ratio of *D. mendotae* with depth.

Our study showed that a full understanding of the development of predator-specific morphological defences in coexisting different-sized *Daphnia* require several environmental cues from fish and invertebrate predators. *Daphnia* species coexisting in Lake Brome showed phenotypic plasticity in morphological antipredator strategy when facing predation by both YOY perch and invertebrate predators. Only the small-sized *D. mendotae* developed morphological defences to cope with negative size-selective predation by both YOY fish and invertebrate predators. The large-sized *D. pulicaria* did not respond to YOY fish predation by increasing its tail spine probably because of its lower vulnerability to predation by gape-limited YOY fish and invertebrate predators, and of its ability to do diel migration and stay deeper in the water column (Gélinas et al., 2007, in press), and produce resting eggs (Ślusarczyk et al., 2005).

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Chapitre 4

Relating crustacean zooplankton community in nutrient-poor Canadian shield lakes to residential development and land-cover disturbance

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4.1 *Abstract*

We applied the land-cover cascade (LCC) concept to evaluate whether human disturbance affects crustacean community in 13 still nutrient-poor lakes of the Laurentian region representing a gradient of residential development (RD) and land-cover disturbance (LCD) at the watershed and sub-watershed (within riparian strips of increasing width) scales. Residential development was estimated as the number of dwellings per km^2 and land cover disturbance as the percentage of open area. Studied lakes distributed along two independent gradients: a disturbance gradient associated to TP enrichment and a gradient of water transparency and lake depth. Recent urbanization of watersheds in the Laurentian region induced nutrient enrichment (TP and TN), and indirectly affected crustacean zooplankton community. Crustacean zooplankton responded mainly to large scale disturbances within the watershed. TP was the best predictor of changes in crustacean zooplankton biomass and was a key intermediate element in the cascades linking the disturbance stimuli to increasing biomass of crustacean zooplankton. Crustacean community structure also changed along the disturbance gradient. The biomass of total crustaceans, some cladocerans (*Bosmina*, *CerioDaphnia*, and *Diaphanosoma*) and small *Daphnia* (*D. g.mendotae*, *D. ambigua*) increased in relation to TP enrichment, while the biomass of calanoid and large *Daphnia* (*D. pulicaria*, *D. catawba*) decreased. Both changes in water transparency, lake depth and nutrient enrichment associated to the disturbance gradient are important drivers of crustacean community structure. However, these factors explained only 30 % of variance in crustacean functional groups. Land-cover cascade (LCC) models linking disturbance stimuli to crustacean functional groups and *Daphnia* species also explained less than half of the total variance, suggesting that other drivers such as planktivory may also control crustacean zooplankton community in nutrient-poor Canadian shield lakes. Our study has several implications for management and biomonitoring of Canadian shield lakes facing increasing residential and recreational development.

4.2 Résumé

On a utilisé le concept du « land-cover cascade » (LCC) pour évaluer si les perturbations humaines affectent la communauté de crustacés planctoniques dans 13 lacs des Laurentides, représentant un gradient de développement résidentiel (residential development : RD) et de déboisement (land-cover disturbance : LCD) à l'échelle du bassin versant ou dans des zone riveraines de largeur croissante. Le développement résidentiel a été estimé par le nombre de résidence par m^2 et le déboisement par le pourcentage de zones ouvertes. Les lakes se distribuaient selon deux gradients environnementaux indépendants: un gradient de perturbation associé à un enrichissement en phosphore et un gradient de transparence et de profondeur des lacs. L'urbanisation récente des lacs de Laurentides s'est traduite par un enrichissement en nutriments (phosphore, azote), et indirectement par des changements dans la communauté des crustacés planctoniques, qui répondait surtout au niveau de perturbation à l'échelle du bassin versant. Le phosphore était le meilleur indicateur de la biomasse totale des crustacés et jouait un rôle intermédiaire essentiel dans les cascades reliant les perturbations aux hausses de la biomasse des crustacés zooplanctoniques. La structure des communautés de crustacés variait aussi le long du gradient de perturbation. La biomasse totale des crustacés, celles des cladocères (*Bosmina*, *CerioDaphnia*, *Diaphanosoma*) et des petites *Daphnia* (*D. g.mendotae*, *D. ambigua*) augmentaient en fonction de l'enrichissement en phosphore tandis que celles des calanoïdes et des grandes *Daphnia* (*D. pulicaria*, *D. catawba*) diminuaient. À la fois, le gradient de transparence et de profondeur et le gradient de perturbation et d'enrichissement en phosphore représentaient d'importants facteurs de contrôle de la structure des crustacés planctoniques. Toutefois, ils n'expliquaient que 30% de la variance totale. Les modèles de cascade (LCC) reliant les perturbations aux groupes fonctionnels de crustacés et aux espèces de *Daphnia* expliquaient aussi moins de la moitié de la variance totale, ce qui suggère que d'autres facteurs comme la pression de prédation des poissons planctivores pourraient aussi avoir un rôle important dans le contrôle de la structure des communautés de crustacés. Notre étude a des implications pour la gestion et le suivi écologique des lacs de la zone boréale faisant face à un développement résidentiel et récréatif croissant.

4.3 Introduction

Identifying the effects of residential and land-cover disturbances within lake shores and watersheds on aquatic biota is crucial for the development of an ecological framework coupling land and water, as well as for ecosystem management and conservation. The land-cover cascade (LCC) concept was recently introduced as an organized approach to quantify the transfer of land-cover disturbance effects to stream biota (Burcher et al. 2007). It suggests important indirect links between land-use disturbances and stream community responses. The LCC concept has not been applied to detect land-cover disturbance effects on lacustrine biota yet. The concept LCC will, with pathways, define the mechanisms responsible for changes in the biota by identifying key intermediate components. Previous studies that related shore and watershed land use to lake abiotic and biotic features focused on water nutrient enrichment and changes in microbial food web and plankton communities (Dodson et al. 2005; Hoffmann and Dodson 2005; Galbraith and Burns 2006; Burns and Galbraith 2007). In north temperate lakes, nutrient enrichment due to watershed and lakeshore land use increases phytoplankton biomass (Dillon and Rigler 1974; Knoll et al. 2003) and alters zooplankton richness and community structure (Pace 1986; Stemberger and Lazorchak 1994; Dodson et al. 2005). However, none of these studies adopted the LCC concept to evaluate both direct and indirect effects of anthropogenic disturbances on lake zooplankton communities.

Zooplankton communities provide an ideal system for studying the effects of anthropogenic land use (Dodson et al. 2005). They are considered good indicators for lake regional monitoring (Stemberger et al. 2001). Crustacean zooplankton biomass and community structure change with lake trophic status at regional and continental scales, and total phosphorus has been shown to be the better predictor compared to chlorophyll *a* biomass (Yan 1986; Pace 1986; Dodson et al. 2005; Pinto-Coelho et al. 2005; Finlay et al. 2007). Zooplankton organisms are sensitive to important watershed disturbances by agriculture (Stemberger and Lazorchak 1994; Dodson et al. 2005; Dodson et al. 2007), forest logging and wildfires (Patoine et al. 2000, 2002). However, studies relating changes in zooplankton community to weak land-cover disturbances by residential development and forest clearing on shores and watersheds of relatively pristine Canadian shield lakes are still limited.

The current study is a first attempt to detect the influence of recent residential development and land-cover disturbance on crustacean zooplankton in nutrient-poor Canadian shield lakes. Here, we employed the LCC approach (Burcher et al. 2007) to examine how crustacean zooplankton biomass and community structure varied in 13 lakes along a gradient of residential development and land-cover disturbance. We hypothesised that the effects of residential development and land cover clearing in still nutrient-poor lakes may indirectly affect crustacean zooplankton biomass and community structure through intermediate increases in nutrients and algal biomass. We examined effects of anthropogenic disturbances on crustacean zooplankton at the watershed and sub-watershed (within riparian strips of increasing width) scales. We compared the relative influence of variables associated with: 1) residential development and land-cover disturbances, 2) associated changes in water chemistry and algal biomass, and 3) natural variation in lake and watershed morphometry. We expected that crustacean zooplankton biomass will increase along the gradient of residential and land-cover disturbances and that crustacean biomass increase will be more directly related to nutrient enrichment (total phosphorus) than to increasing algal biomass, as previously observed in other studies (Yan et al. 1986; Pinto-Coelho et al. 2005; Findlay et al. 2007). Because nutrient concentrations and algal biomass tend to be higher in Canadian shield Shield lakes having high drainage ratio and flat watershed (D'arcy and Carignan 1997), we also considered that zooplankton response to disturbances will vary with morphometry of lakes and watersheds. Furthermore, we examined the effects of residential and land-cover disturbances on crustacean community structure based on the assemblages of functional groups and key species such as *Daphnia.* Understanding the effects of anthropogenic disturbances on crustacean herbivores may be crucial for predicting the responses of nutrient-poor Canadian shield lakes facing recent residential development, where cladocerans and especially *Daphnia* can control water clarity and algal biomass (Mazumder 1994; Mazumder and Havens 1998; Stemberger and Miller 2003).

4.4 Materials and methods

4.4.1 Study sites

Sampling was conducted in 13 lakes of the Laurentian region, north of Montréal (Canada) within a 65 km radius from the "Station de Biologie des Laurentides" (SBL: 45°59'N, 73°60'W). The Laurentian region supports one of the most important demographic developments in the province of Quebec since the seventies with a 98% rise of its residential population, while agricultural and industrial activities remain negligible (Laurin 2000; Institut de la Statistique du Québec). The Laurentian region is of glacial origin (Wisconsin glaciation: 18 000 years ago, Martignole 1975), and characterised by a continental climate with a mean annual temperature of 4°C and mean annual precipitation between 1100 and 1400 mm (25-40% as snow) (Savage 2001). The bedrock is composed predominantly of granitic and gneiss rocks and the landscape defined by hilltops and valleys. Forest cover is composed of yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloïders*), and black spruce (*Picea mariana*) (Savage 2001). All lakes contained planktivorous fish (minnows, pumpkinseed sunfish, rock bass: D. Boisclair, pers. com) but were stocked at some point (records start in 1944) with piscivorous fish, mostly brook trout (*Salvelinus fontinalis*), rainbow trout (*Onchorynchus mykiss*) and walleye (*Stizostedion vitreum*) (MAPAC, 2003). Lakes were chosen to represent the typical natural span in lake and watershed morphometry, water chemistry and trophic status occurring in the Laurentian region, while ranging along a gradient in residential development and land-cover disturbances (Tables 1-3).

4.4.2 Morphometry of lakes and watersheds and disturbance gradients

Morphometric characteristics of watersheds (area and slope) and lakes (area, volume, maximum and mean depth) were measured (MapInfo, V 6.5) from numerical topographic and bathymetric maps (Lambert 2006; Lambert et al. 2007). From these variables, we calculated several morphological indices for watersheds (drainage ratio relative to lake area or volume) and lakes (relative depth). To evaluate anthropogenic disturbance by residential development (RD) and land-cover disturbance (LCD), we estimated the density of dwellings (per km^2) and the percentage of open area on orthorectified aerial photographs (1:30 000 and 1:10 000) acquired in 2002 and 2004 (MapInfo V 6.5) (Lambert 2006). Because residential development in the Laurentian region is usually concentrated around lake shores, we measured dwelling density at sub-watershed scales (within riparian strips of increasing width: 50 m, 100 m, 150 m, 200m, 250, 500m, 1000m) and for the whole watershed (Table 3). Land cover disturbance was estimated as the percentage of open area for the near shore (50 m) and for the whole watershed. Open areas represented previously forested zones cleared for buildings, roads, parking lots, and lawns; a golf course and ski down hill trails were also included in the case of two lakes.

4.4.3 Water sampling and analysis

Sampling was carried out in June, July, and August 2003 at the location of maximum depth in each lake to reflect responses of pelagic ecosystems. Temperature, oxygen concentration, and pH were measured at 1 m intervals through the water column with a Hydrolab Surveyor® 4, and light intensity with a photometer Licor 1000. Secchi depth transparency was measured and the euphotic zone (EZ) was estimated as the depth of 1% of surface light irradiance. Euphotic depth-integrated water samples were collected with weighted Tygon™ tubing fitted with a one-way foot valve. Water samples were transferred into two 1-L polypropylene containers, a dark one for chlorophyll *a* (Chl. *a*) analysis and a clear one for chemical analysis of total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), dissolved organic carbon (DOC) and pH. In the laboratory, Chl. *a* water samples were filtered on GF/C Whatman filters (1.2 µm pore size) and the filters were kept frozen until analysis. Chl. *a* pigments were extracted in cold 95% ethanol for 24h and measured before and after acidification at 665nm and 750 nm (Spectronic Genesys 5 spectrophotometer) (Nusch 1980). TP and TDP concentrations were determined on 50 ml of unfiltered and filtered (Gelman type glass-fiber filters: 0.45 µm pore size) water samples, respectively. TP and TDP samples were analysed as orthophosphate after persulfate digestion in an autoclave (Stainton et al. 1977). TN was analysed with a LACHAT Continuous Flow Quick-Chem 8000 and DOC with a Shimadzu ASI-5000A.

4.4.4 Zooplankton sampling and analysis

Zooplankton was sampled from the deepest site in each lake with vertical hauls from 1 m above the sediments to the surface using a conical plankton net (12 cm mouth-diameter and 153 μm mesh size). Samples were preserved in buffered 4 % sucrose-formalin after narcotisation in carbonated water. Taxonomic identification, counting and size measurements were done on 10 ml sub-samples withdrawn from the entire concentrated sample gently mixed before handling, using a large pipette. Zooplankton sub-samples were placed into a grooved Plexiglas Ward counting cell (10 ml capacity) under a dissecting microscope (Leica MZ20) connected to an image analyser (Image Pro Plus) enabling direct sizing of organisms. Copepod nauplii and rotifers were excluded from the analysis because the 153 μm mesh size plankton net did not adequately collect nauplii stages and small rotifers; it only collected the large rotifer *Asplanchna* and the species with spines like *Keratella* and *Kellicottia*. Body length of cladocerans was measured from the top of the head to the base of the tail spine. Copepods were measured from the top of the head to the end of the caudal ramus. Generally, a minimum of 20 individuals were measured for each crustacean functional group and a minimum of 100 individuals for each *Daphnia* species, or all individuals present in the entire sample if these minimum numbers could not be achieved after searching the 10-ml sub-sample. To estimate the biomass of taxa, body lengths were converted to dry weights using published regression models (Malley et al. 1989) for each crustacean functional group or *Daphnia* species (see below).

Crustaceans were classified into functional groups according to their feeding mode and body size. The utilisation of functional groups implied that they play a similar role in the ecosystem (Stemberger and Lazorchak 1994). Cladocerans were divided in different feeding groups: the filter-feeders, the filter- and grasping-feeders, and the raptorial-feeders. First, large cladocerans as *Daphnia, CerioDaphnia, Diaphanosoma* and *Holopedium* were considered as filter-feeders because they can filter a broad range of particles of which the maximum size usually increases with herbivore body length (Chow-Fraser and Knoechel 1985; Knoechel and Holtby 1986). Small cladocerans such as *Bosmina* use distinct modes of feeding by combining filter- and grasping-feeding on bacteria, small algae, and flagellates (DeMott and Kerfoot 1982; Vanderploeg 1990). Copepod filtration rates are less efficient than cladocerans of similar size and they select large particles (Peters and Downing 1984). Copepods were divided in two feeding groups: the calanoids that collect a variety of small and large particles using passive and active mechanisms (Vanderploeg 1990) and the cyclopoids which are raptorial omnivores and effective predators but also feed on algae (Adrian and Frost 1993). Therefore, according to their feeding behaviour and body size, crustaceans were separated into seven functional groups and species: calanoids, cyclopoids, *Daphnia*, *CerioDaphnia*, *Holopedium*, *Diaphanosoma* and *Bosmina*. In addition, *Daphnia* species were considered separately since competition between species of different sizes occurs in nature and grazer-resource interactions vary among species (Kreutzer and Lampert 1999; Tessier et al. 2001).

4.4.5 Statistical analyses

We used univariate and multivariate statistical analyses to evaluate the response of crustacean zooplankton to residential development (RD) and land cover disturbance (LCD) keeping in account the associated changes in water chemistry and natural variation in morphometry of lakes and watersheds.

To reduce and extract the important variables from the set of natural and disturbance explanatory factors, principal component analysis (PCA) was performed on all environmental variables including watershed and lake morphometry (Table 4-I), water quality (Table 4-II) and disturbance (Table 4-III) variables. All PCA's were performed using CANOCO (ter Braak, 1988, 1990). Repeated-measures ANOVA was performed on the total biomass of crustaceans, each crustacean functional group and *Daphnia* species to test for differences among sampling months. As we did not find important variation during summer, simple linear regression models based on summer mean values served to identify underlying bivariate relationships between disturbance factors, water quality, algal biomass, and biomass of total crustaceans and of each functional group. Data were normally distributed ($P > 0.05$: Kolmogorov-Smirnov test), and all univariate statistical analyses were done using Systat 8.

As the land-cover cascade (LCC) concept implies that land-cover disturbance and biota interact indirectly through one or several intermediate elements or links (Burcher et al. 2007), we built a conceptual LCC design (Fig. 4.1) to address direct and indirect relationships between disturbance factors and crustacean zooplankton communities, based on main explanatory factors detected using bivariate regressions. We tested how residential and land-cover disturbance at the watershed scale might be propagated to zooplankton biota through nutrient and algal enrichment and influenced by watershed morphometry using path analysis (Shipley 2000). We arranged conceivable paths to test if our data fit hypothesized LCC paths among disturbance factors and biomass of total crustaceans, functional groups and *Daphnia* species. Model fit was determined primarily by mean squared error approximation (RMSEA) where a significant RMSEA ($P > 0.05$) indicated no significant difference between the data and our LCC model. Path analyses were designed in Systat (Wilkinson 1999). In addition, path coefficients were calculated; they correspond to bivariate correlation coefficients and quantify the strength and direction of the relationships between the disturbance factors, TP and Chl. *a* enrichment, watershed morphometry (drainage ratio and slope) and the zooplankton responses, overall, describing the existence of cascades.

Redundancy analyses (RDA) were performed to assess changes in crustacean zooplankton community structure and *Daphnia* species assemblages in response to the main disturbance gradients and natural variation in lacustrine environments from the PCA analysis (Legendre and Legendre 1998). Hellinger's transformations were applied to zooplankton biomass data (Legendre and Gallagher 2001). The significant explanatory variables were chosen via forward selection and tested with a permutation Monte-Carlo test using 999 permutations; only variables with $P < 0.05$ were included in the model. Adjusted r^2 were calculated (Legendre and Legendre 1998). By utilizing all samples from the summer survey (June, July and August), the RDA encompassed both spatial (among lake) and temporal variation (among month) in crustacean community composition and *Daphnia* species assemblages. The partitioning of the variation was calculated from partial RDA analysis to correctly assess the proper amount of variation explained independently by each set of explanatory factors i.e. disturbances (Table 4-III), water quality (Table 4-II) and morphometry (Table 4-I). All RDA's were performed using CANOCO (ter Braak, 1988, 1990).

4.5 Results

4.5.1 Lake environments and disturbance gradients

Although the studied lakes were located in lacustrine environments of similar origin and geology, they showed important variation in their morphometry, water quality and anthropogenic disturbances (Tables 4-I, 4-II and 4-III). They were generally of small area but different in terms of and volume, watershed area and slope, and drainage ratio relative to lake area or volume (Table 4.I). According to trophic classification (OCDE 1982), the lakes were all oligotrophic except three lakes (René, Rond and Connelly) which reached mesotrophic state with mean summer nutrient concentrations exceeding 10 $\mu g \cdot L^{-1}$ for total phosphorus (TP), and 340 $\mu g \cdot L^{-1}$ for total nitrogen (TN), and Chl. *a* concentration higher than 3.8 $\mu g \cdot L^{-1}$ (Table 4-II). The lakes covered a wide range in Secchi transparency, euphotic depth, and dissolved organic carbon (DOC) concentrations. Most of the lakes were circumneutral or slightly acidic, except two lakes (Morency, Rond) surrounded by important recreational infrastructures and roads which were slightly alkaline (Table 4-II). Gradients in residential development and land-cover disturbance ranged from 0 to 340 dwellings/km^2 and from 0 to 53% of forest cleared (open area) at the scale of the watershed. The intensity of the disturbance was the highest nearshore within the 50 m or 100 m riparian strips with maxima of 686 dwellings/km^2 and 86 % of open area in the 50 m riparian zone (Table 4-III).

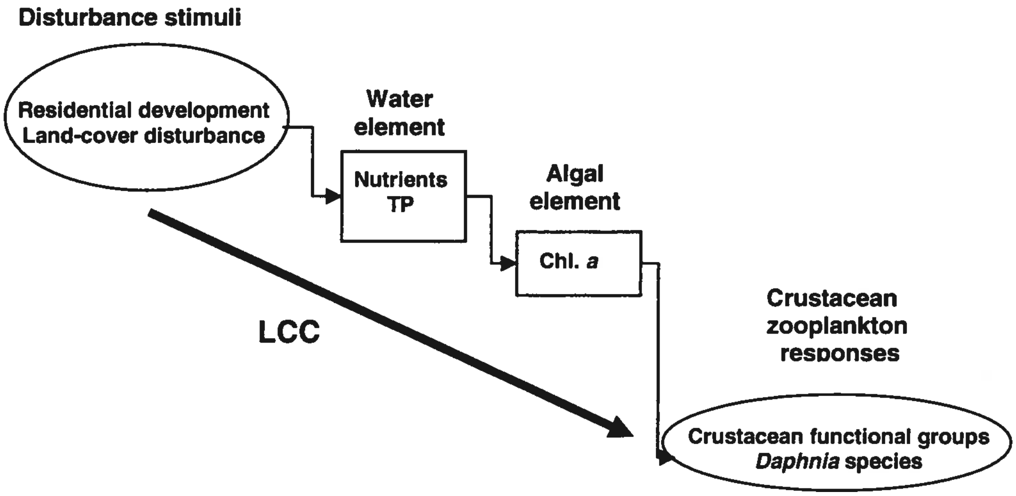


Figure 4.1: Conceptual land-cover cascade (LCC) model linking land-cover disturbance to crustacean zooplankton responses via intermediate chemical and algal elements. Text inside each box describes the principal variables included as explanatory variables within each element. Path arrows represent mechanistic cause-effect-cause links between disturbance stimuli, elements and crustacean zooplankton responses.

Table 4-I: Watershed and lake morphometric characteristics with the calculated morphological indices for the 13 studied lakes.

Lakes		Watershed area	Watershed mean slope	Drainage ratio /lake area	Drainage ration/lake volume	Lake area	Lake Volume	Lake max. depth	Lake mean depth	Lake relative depth
		(km²)	(%)			(km²)	(m^3)	(m)	(m)	
	Code	WA	slope	Rd	Rdv	LA	volume	Zmax	Zmean	Zrel
Cabane	Cab	2.45	7.5	8.8	1.34	0.25	1 836 000	20.8	7.3	3.13
Croche	Cro	0.84	13	3.7	0.96	0.18	877 000	12.9	4.9	2.69
Violon	Vio	4.41	9.2	10.5	1.33	0.38	3 325 000	22.6	8.9	2.63
Blanche	Bla	3.94	8.2	8.6	0.86	0.41	4 590 000	26	11.7	3.59
du Nord	Nord	13.94	12.5	15.1	2.53	0.87	5 514 000	20.6	6.4	1.74
Gervais	Ger	8.65	6.2	8	0.37	0.97	23 526 000	60	24.4	5.41
Connelly	Con	24.36	6.2	18.6	2.55	1.24	9 561 000	20.8	7.7	1.65
Morency	Mor	2.33	14.6	8	1.04	0.26	2 246 000	20.3	8.7	3.53
Purvis	Pur	0.6	10.6	2.2	0.42	0.19	1 446 000	19.7	7.8	4
Truite	Tru	4.23	5.9	7.3	0.89	0.51	4 783 000	21.6	9.3	2.67
Tracy	Tra	0.24	8.3	1.9	0.36	0.08	676 000	22.9	8.1	7.03
Renée	Ren	0.2	10.1	2.1	0.73	0.07	296 000	9.7	4.2	3.23
Rond	Ron	1.5	7.5	8	1.24	0.17	1 206 000	15.9	7.2	3.45

Table 4-II: Water chemistry, phytoplankton chlorophyll a biomass, Secchi transparency and euphotic depth for the 13 studied lakes. Values represent means ± standard of summer 2003.

Lake	Chl a (µg·L-1)	TP (µg·L-1)	TPD (µg·L-1)	TN (µg·L-1)	pH	DOC (mg·L-1)	Secchi (m)	EZ (m)
Cab	3.0 ± 0.7	8.2 ± 2.1	2.6 ± 0.3	259.8 ± 20.6	6.2	3.6 ± 0.0	3.3 ± 0.3	7.1 ± 0.7
Cro	1.2 ± 0.9	5.0 ± 0.3	2.0 ± 0.3	256.9 ± 23.1	6.2	4.1 ± 0.3	4.0 ± 0.2	6.8 ± 0.2
Vio	1.2 ± 0.1	5.7 ± 1.3	3.1 ± 1.4	215.1 ± 16.1	6.6	3.5 ± 0.3	5.3 ± 1.0	7.5 ± 0.5
Bla	2.6 ± 0.9	4.9 ± 0.3	1.7 ± 0.5	258.0 ± 10.9	6.4	2.8 ± 0.1	5.3 ± 0.1	11.8 ± 1.1
Nord	1.5 ± 0.9	9.9 ± 2.1	3.4 ± 0.7	329.2 ± 40.1	6.7	6.2 ± 0.3	3.2 ± 0.2	5.6 ± 0.2
Ger	0.7 ± 0.4	4.6 ± 0.6	1.7 ± 0.2	190.4 ± 12.8	7	2.7 ± 0.2	7.7 ± 0.5	12.3 ± 3.7
Con	4.4 ± 4.4	8.0 ± 0.4	3.0 ± 0.5	340.0 ± 38.6	7.4	4.6 ± 0.03	3.5 ± 0.7	7 ± 0.5
Mor	2.3 ± 0.8	10.4 ± 0.8	2.9 ± 0.4	313.6 ± 3.3	7.8	3.3 ± 0.2	4.7 ± 1.0	8.8 ± 0.2
Pur	2.7 ± 1.4	10.3 ± 1.9	3.8 ± 0.7	272.7 ± 13.7	7.2	3.1 ± 0.1	6.2 ± 1.5	12 ± 1.3
Tru	1.7 ± 1.2	6.5 ± 1.7	2.0 ± 0.4	290.5 ± 18.5	7.7	3.0 ± 0.1	5.2 ± 1.1	11 ± 0.8
Tra	1.3 ± 1.1	6.2 ± 0.4	2.5 ± 0.2	266.5 ± 87.2	7	2.9 ± 0.2	5.3 ± 1.7	11.1 ± 1.2
Ren	3.8 ± 1.7	14.2 ± 2.1	4.5 ± 1.3	485.6 ± 67.2	6.1	4.2 ± 0.1	4.0 ± 1.8	8.6 ± 2.4
Ron	4.6 ± 5.8	13.0 ± 4.8	4.0 ± 0.6	384.6 ± 140	8.1	3.6 ± 0.2	5.5 ±1.3	10.1 ± 2.5

Table 4-III. Residential development and land-cover disturbance within different wide riparian strips and the whole watershed (W) for the 13 studied lakes.

	Residential development (number of dwelling /km^2)								Land-cover disturbance (% of open area)	
	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	W	50 m	W
Code	**RD50**	**RD100**	**RD150**	**RD200**	**RD250**	**RD500**	**RD1000**	**RCDW**	**LCD50**	**LCDW**
Cab	0	0	0	0	0	0	0	0	0	0
Cro	5	3	2	2	2	2	2	2	0	0
Vio	8	13	9	7	5	5	3	3	0	0
Bla	219	123	89	73	63	47	26	16	17	1
Nord	261	167	127	100	82	44	23	18	40	3
Ger	212	115	82	66	56	33	27	21	2	0.4
Con	686	552	448	389	339	217	157	48	46	7
Mor	152	151	126	116	103	69	57	57	31	13
Pur	106	117	100	101	94	89	89	89	13	8
Tru	430	400	404	368	322	202	123	111	79	30
Tra	289	176	157	144	144	144	144	144	5	4
Ren	388	400	406	393	381	340	340	340	38	30
Ron	323	373	417	400	391	330	255	242	86	53

Residential development and land-cover disturbances accounted for 83.6% of the total variation among lakes (Fig. 4.2A) along the first PCA axis. This disturbance gradient was associated with decreasing water transparency (Secchi) and increasing nutrient (TP, TDP, TN) and algal (Chl. a) concentrations. Lakes Connelly and Truite (upper right side) were the most disturbed at small scale within the nearshore first 50 m riparian strip whereas lakes Rond and René (lower right side) were the most disturbed at the scale of the watershed (Fig. 4.2B). Lakes Connelly and Truite located on flatter watershed had low relative depth and were the less transparent. Lakes Rond and Renée showed the highest nutrient concentrations. On the left side of the ordination plot, lakes Violon, Cabane and Croche, located on steeper watershed, were the most pristine, relatively deep and the most transparent. The other lakes shared intermediate level of disturbance. The second PCA axis explained only 9.1 % of the total variance and was associated with morphometry gradients in lake area and watershed area and drainage ratio (Fig. 4.2A). It mostly discriminated large lakes with high watershed area and drainage ratio (Connelly) or volume (Gervais) from lakes with inverse morphological features (René).

4.5.2 Crustacean zooplankton communities

Mean crustacean summer density varied greatly among lakes along the residential development gradient. The lowest densities were found in the lakes Tracy and Violon (2 ind·L^{-1}) and the highest in Lake René (63 ind·L^{-1}) (Fig. 4.3A). A similar range of variation was observed for mean crustacean summer biomass (Fig. 4.3B), with the lowest biomass in the lakes Violon and Tracy (4 $\mu g \cdot L^{-1}$) and the highest in Lake René (41 $\mu g \cdot L^{-1}$). Increase in total crustacean zooplankton biomass was significantly related to residential and land-cover disturbances at the scale of the watershed (total watershed) and within large riparian strips (> 500 and 1000 m) (Table 4-IV).

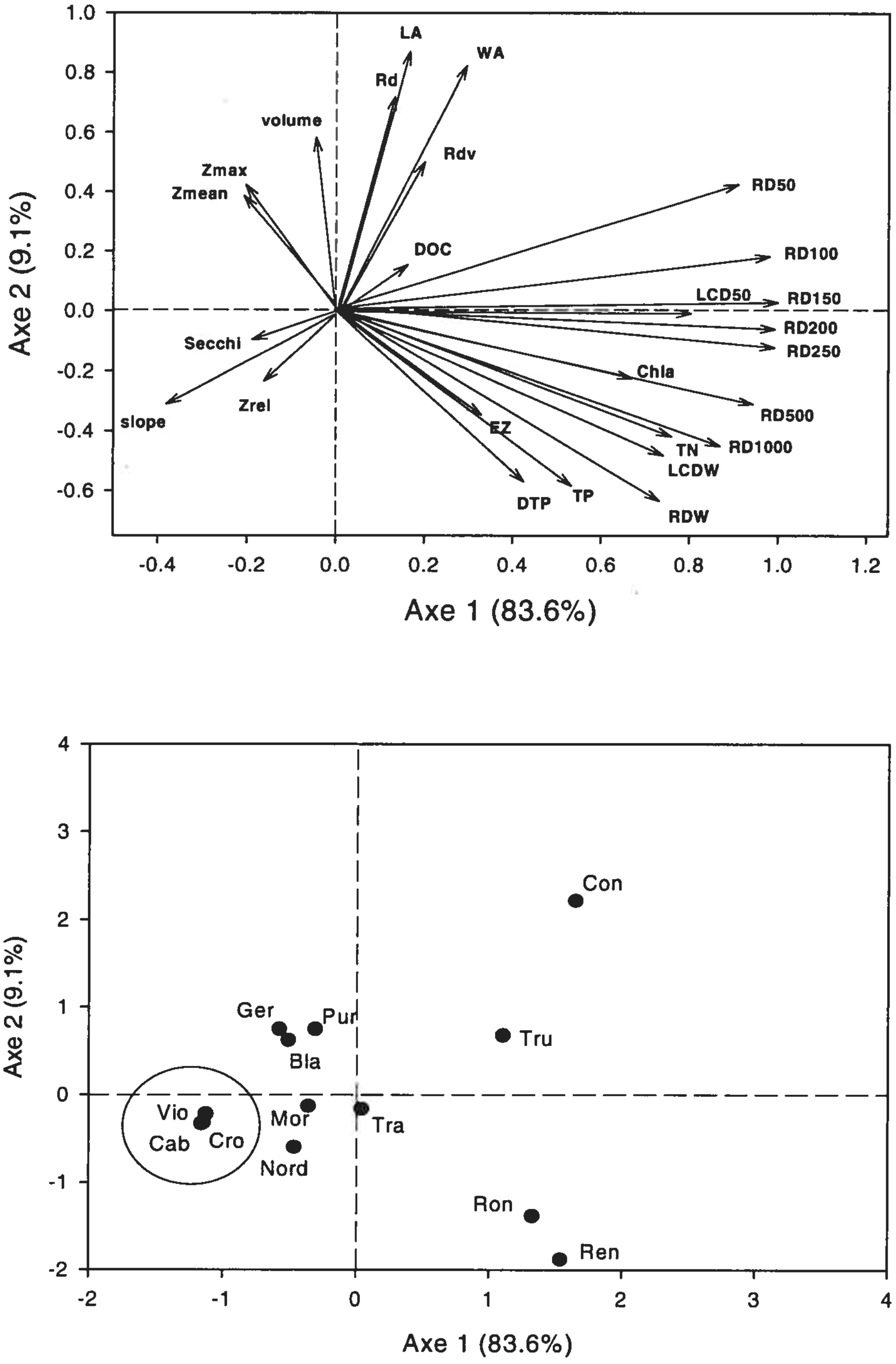
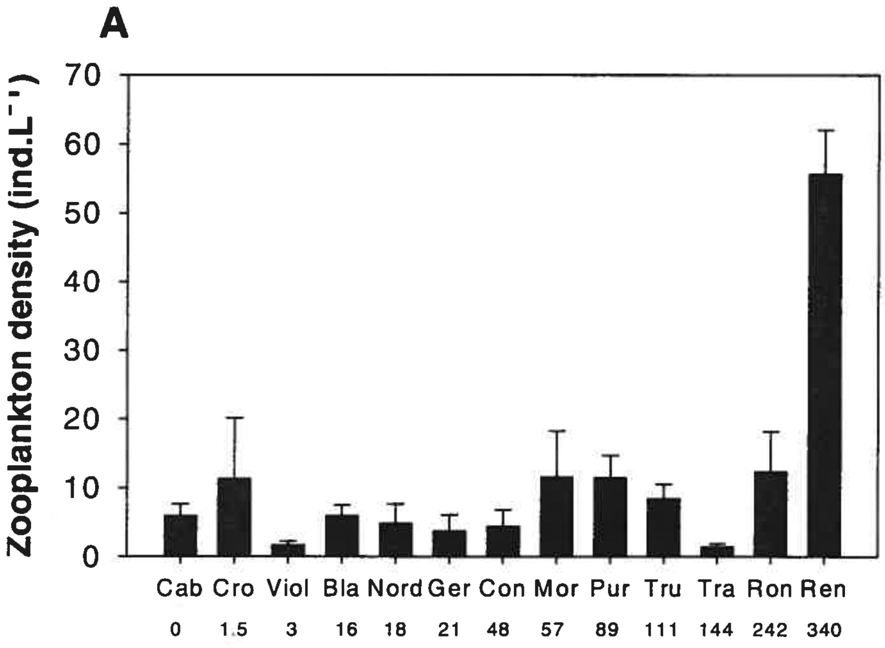


Figure 4.2: Ordination diagram for PCA of anthropogenic, lake and watershed morphometric and physico-chemical variables (upper panel). Lakes are indicated in lower panel; pristine lakes are circled. Lake and morphometric variables codes are identified in Table 4-I and anthropogenic variables codes in Table 4-III.



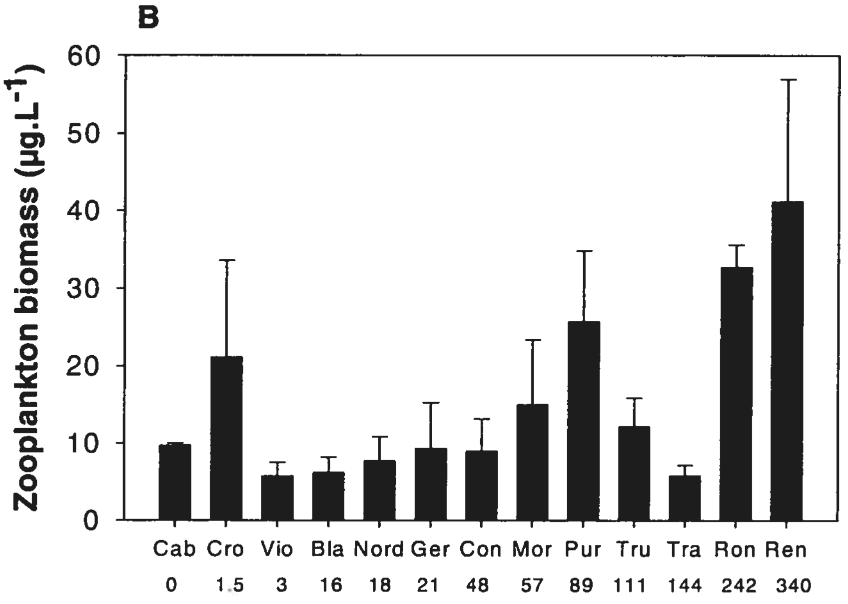


Figure 4.3: (A) Mean summer density (ind·L^{-1}) and (B) mean summer biomass (dry weight: µg·L^{-1}) of macrozooplankton community as an increasing impact of residential development within the watershed of the 13 lakes 2003 (numbers represented dwellings/km^2 = RDW). Error bars are the standard error (n = 3).

Summer crustacean community structure changed among lakes with dominance by large cladocerans or by copepods (Fig. 4.4A). In Lake Tracy, crustaceans were mostly composed of large cladocerans (mostly *Daphnia*) whereas calanoids dominated in Lake Violon and Lake Morency and cyclopoids in Lake Purvis. In Lake Nord, both cyclopoids and calanoids shared the dominance. Relative biomass of *Bosmina*, calanoid copepods, *CerioDaphnia*, *Diaphanosoma* and *Holopedium* did not change over the summer months in each lake (RM-ANOVAs, all $P > 0.05$), whereas the relative biomass of *Daphnia* and cyclopoid copepods changed over the summer months ($P = 0.027$ and $P = 0.003$, respectively). In Lake Rond, *Daphnia* was not present in June, the main cladoceran being *Bosmina*; *Daphnia* appeared and became dominant later in July and August. In Lake Rond, the relative biomass of the cyclopoids decreased in August compared to June and July.

Daphnia species assemblages also varied greatly among lakes with dominance by small-sized species such as *D. mendotae* and *D. ambigua* or large-sized species such as *D. pulicaria* and *D. catawba* (Fig. 4.4B). Two small species (*D. mendotae*, *D. ambigua*) were dominant in Lake René, and only *D. mendotae* in Lake Rond, Lake Connelly and Lake Morency. Large species (*D. pulicaria*, *D. catawba*) were abundant in the Lake Tracy, Lake Truite, and Lake Blanche. *Daphnia dubia* was found in 3 lakes (Purvis, Truite, and Connelly) whereas *D. ambigua* was only present in Lake René. *D. longiremis* was presented in several lakes (Purvis, Nord, Blanche, Croche, Cabane). The relative biomass of *D. pulicaria*, *D. catawba*, and *D. longiremis* did not change over the summer months in each lake (RM-ANOVAs, $P > 0.05$), whereas the relative biomass of *D. mendotae* marginally changed over the summer period ($P = 0.022$). The biomass of *D. mentodae* decreased in July in Lake Purvis and Lake Truite and in August in Lake Cabane.

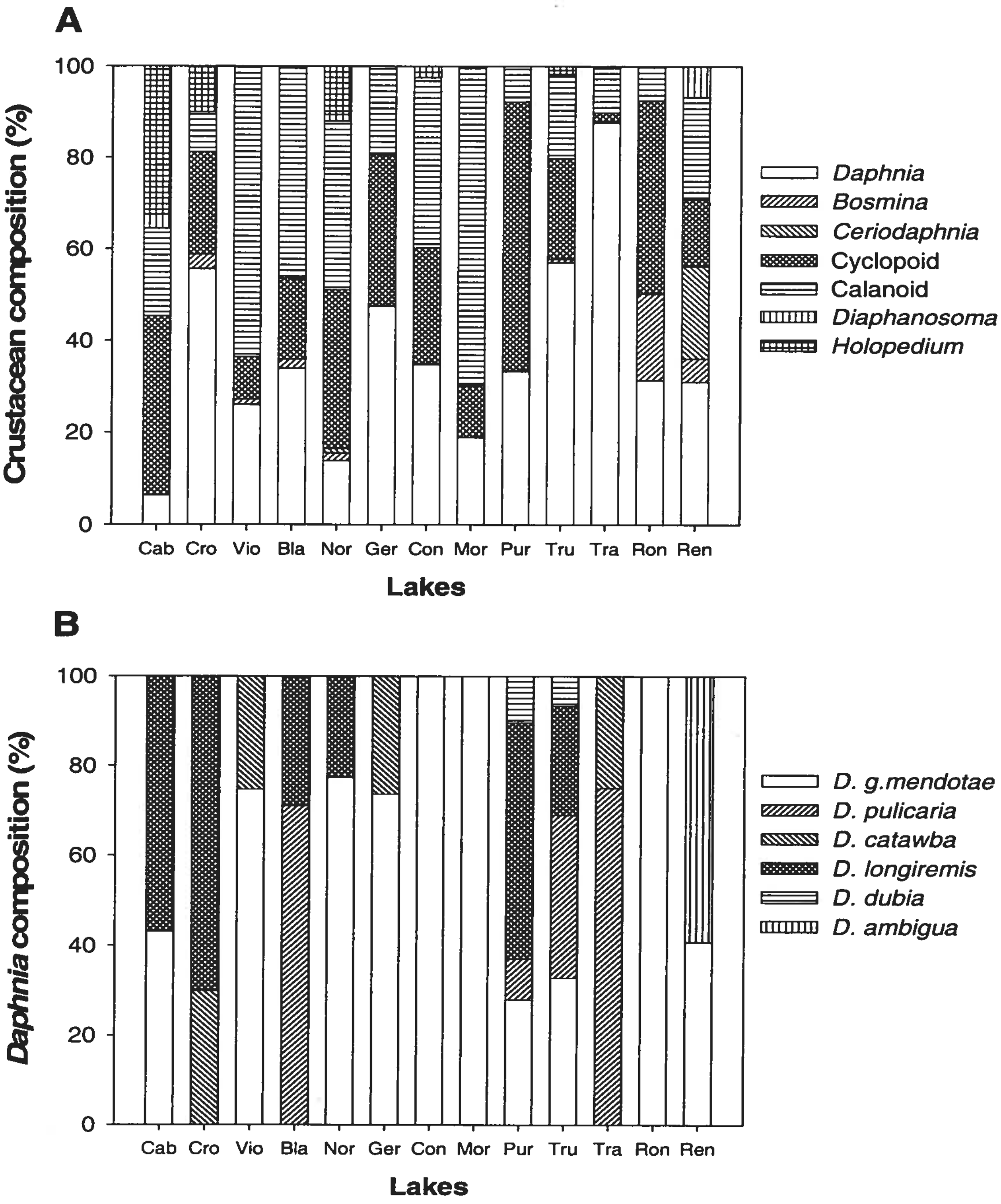


Figure 4.4: (A) Taxonomic composition (as a percentage of mean seasonal biomass) of crustacean functional groups (Bosmina, Holopedium, *Daphnia*, Diaphanosoma, Cerio*Daphnia*, calanoid and cyclopoid) and (B) Taxonomic composition (as a percentage of mean seasonal biomass) of *Daphnia* species (D. pulicaria, D. catawba, D. longiremis, D. g.mendotae, D. dubia and D. ambigua) in the 13 lakes.

4.5.3 Influence of residential and land-cover disturbances on water quality and crustacean biomass

Bivariate regression analyses indicated that residential development and land-cover disturbances were related to increases in nutrients (TP, TN), as well as to increases in crustacean biomass (Table 4-IV). The best relationships (higher r^2) were observed at the scale of the watershed. Disturbance by residential development or land-cover clearing on nearshore riparian strips < 50-1000 m was not related to pelagic TP concentrations and crustacean biomass, but was related to increasing TN (Table 4-IV). Water transparency (Secchi), euphotic depth (ZE) and DOC were not related to disturbances.

Only total crustacean biomass (Crus) and *CerioDaphnia* were associated to watershed disturbance by residential development whereas land-cover clearing within the whole watershed were associated with *Bosmina* biomass (Table 4-IV). Copepod biomass (calanoids and cyclopoids), *Daphnia*, *Diaphanosoma* and *Holopedium* biomass were not related to the disturbance factors (data not shown).

We also evaluated if the influence of residential and land-cover disturbances on crustacean functional groups was mediated by a significant effect of nutrient and algal enrichment and by changes in water transparency. Indeed, we only found significant relationships between nutrients (TP) and biomass of total crustaceans. Neither nutrients nor water transparency variables influenced the *Daphnia* biomass (data not shown). Algal concentration (Chl. *a*) was not associated to changes in the biomass of total crustaceans or any crustacean functional groups.

4.5.4 LCC cascades

LCC models predicted 8 significant cascades between residential development (RD) or land-cover disturbance within the watershead (LCD) and biomass of total crustaceans, functional groups or *Daphnia* species (Figs. 4.5 and 4.6). Path models begin with the RDW and LCDW disturbances at the scale of the watershed and include total phosphorus (TP) and algal concentration (Chl. a) as linking elements. In each path model, relationships between disturbances, TP and Chl.a were always constant; however, relationships with crustaceans and *Daphnia* changed depending of functional groups and *Daphnia* species (Fig. 4.5 and 4.6). Residential development within the watershed had the highest positive effect on TP concentrations (0.80) whereas land-cover disturbance effect on total phosphorus was weaker (0.567). No direct relationship between RDW and LCDW was found with path analysis, whereas TP and Chl. *a* were positively correlated (0.766).

LCC models explained 33 % of among-lake variation in total crustacean biomass. Four crustacean functional groups LCC models were significant and explained between 20.4 and 48.5% of the among-lake variance (Fig. 4.5). Small (*Bosmina, CerioDaphnia*) and large (*Daphnia*) cladocerans responded the most to disturbances whereas *Holopedium* were less sensitive. Copepods (calanoids, cyclopoids) and *Diaphanosoma* LCC models were not significant (Fig. 4.5). TP enrichment always increased biomass of total crustaceans and functional groups (except *Holopedium*). *Diaphanosoma* and *CerioDaphnia* responded the most to TP enrichment (0.924-0.959). In most LCC models, Chl. *a* was not related to changes in crustacean biomass, except for *CerioDaphnia* and *Diaphanosoma* biomass which decreased with TP enrichment (-0.457 and -0.494 respectively) (Fig. 4.5).

Among the *Daphnia* LCC models, only 3 out of 6 models were significant and explained between 41 and 48 % of the among-lake variation in *D, pulicaria*, *D. g.mendotae*, and *D. ambigua*) (Fig. 4.6). *D. longiremis*, *D. catawba* and *D. dubia* LCC models were not significant (Fig. 4.6). Total phosphorus had a positive influence on *D. g.mendotae* and *D. ambigua* and a negative influence on *D. pulicaria*. Furthermore, Chl. *a* had a negative influence on *D. ambigua* (Fig. 4.6).

Table 4-IV: Results of regression analyses (r^2) between residential development (RD) and land-cover disturbance (LCD) on different riparian zones (n=13) versus summer mean (three months) of the water quality variables and crustacean functional groups biomass are located on the left side lower to the separated line. Regression results (r^2) between water quality variables and the biomass of total crustaceans and functional groups (right and upper side of the table in grey and italic). Only coefficients of the significant relationships are shown (Bonferroni correction: $p < 0.005$). Abbreviations are: TP = total phosphorus ($\mu g.L^{-1}$); TN = total nitrogen ($\mu g.L^{-1}$); Crus= total crustacean ($\mu g.L^{-1}$); Bos = *Bosmina* ($\mu g.L^{-1}$); Cerio = *CerioDaphnia* ($\mu g.L^{-1}$); Dia = *Diaphanosoma* ($\mu g.L^{-1}$); Cyclo = Cyclopoid ($\mu g.L^{-1}$).

RD	TP	TN	Crus	Bos	Cerio	Dia	Cyclo	
50m			*0.588*					TP
100m			*0.540*		*0.548*	*0.521*	*0.521*	TN
150m								
200m		0.569						
250m		0.605						
500m		0.679						
1000m		0.728	0.534					
Watershed	0.542	0.668	0.628		0.546			
LCD								
50m								
Watershed				0.686				

Figure 4.5: Path diagrams quantifying land-cover cascade and residential development for crustacean functional groups. Eight path models were calculated: A= Crustacean, B = *Daphnia*, C = calanoid, D = cyclopoid, E = Diaphanosoma, F = Holopedium, G = Bosmina and H = Cerio*Daphnia*. Ovals indicate human disturbance or functional groups, and boxes indicate nutrient elements. The variance explained by the model is in boldface italicized next to the functional group when significant after Bonferroni correction (p = 0.006). The path coefficients are indicated along the arrows. Abbreviations: TP = total phosphorus; Chl a = chlorophyll a.

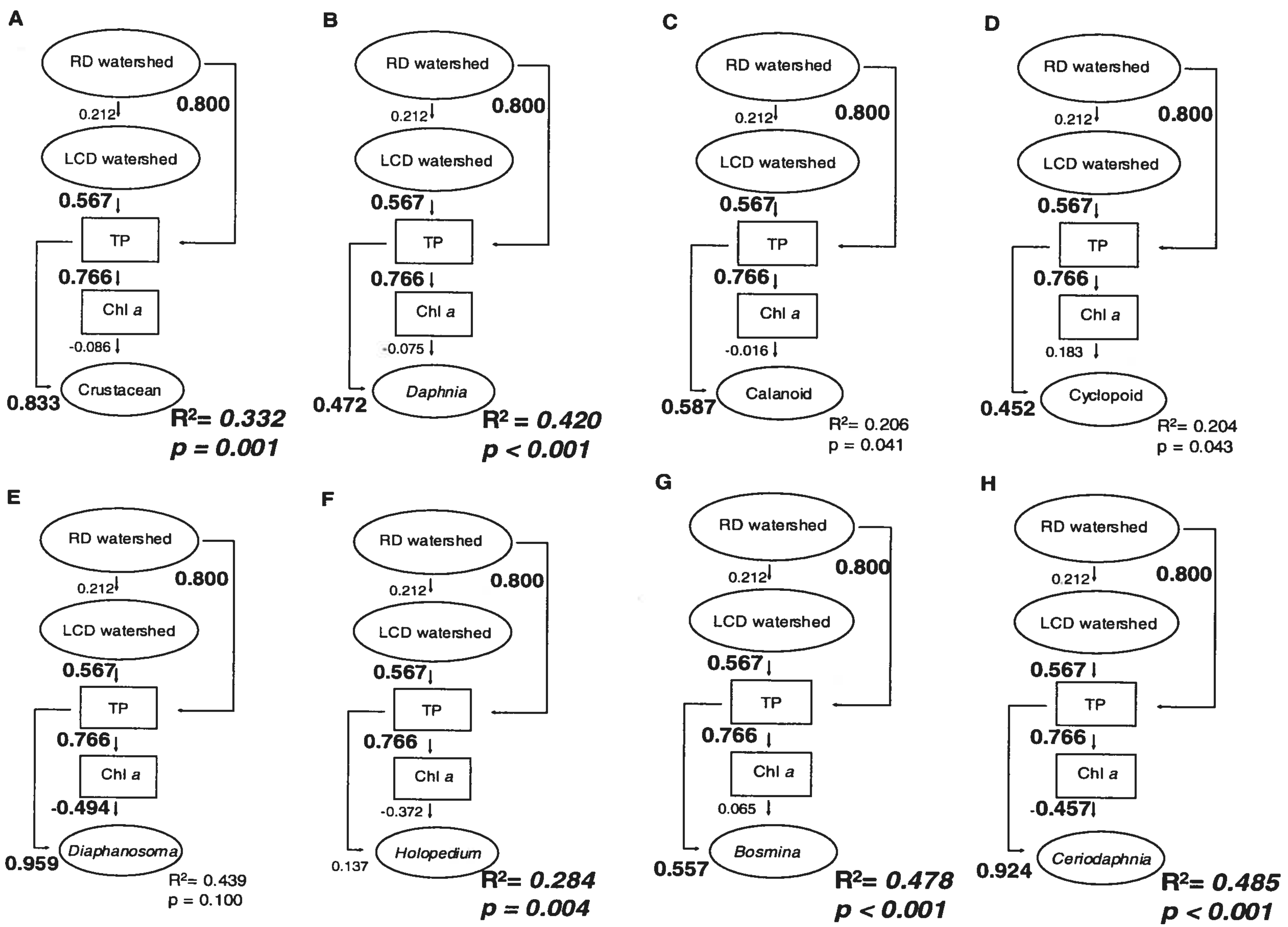
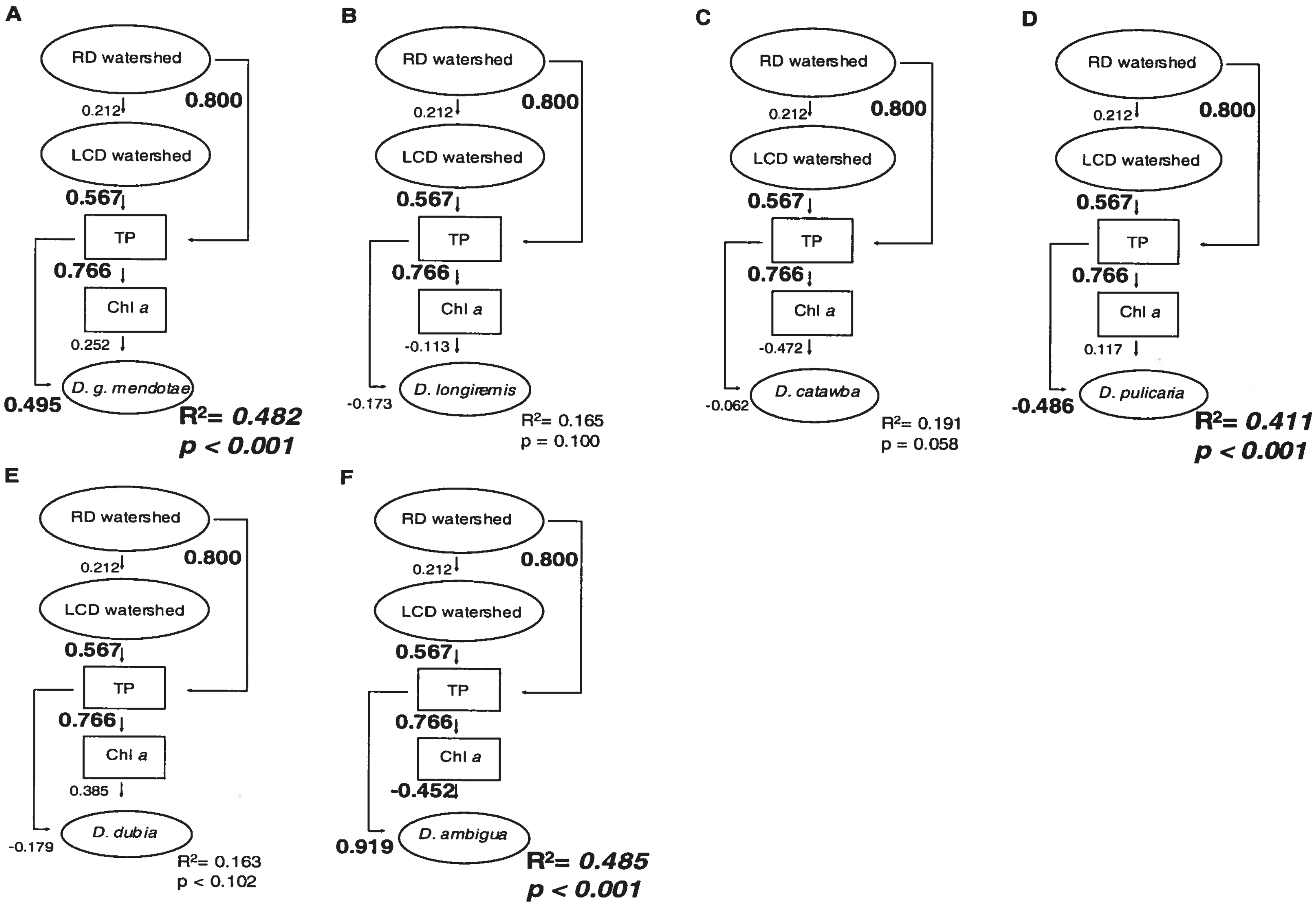

A
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.086
0.833
Crustacean
$R^2 = 0.332$
$p = 0.001$
B
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.075
0.472
Daphnia
$R^2 = 0.420$
$p < 0.001$
C
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.016
0.587
Calanoid
$R^2 = 0.206$
$p = 0.041$
D
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
0.183
0.452
Cyclopoid
$R^2 = 0.204$
$p = 0.043$
E
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.494
0.959
Diaphanosoma
$R^2 = 0.439$
$p = 0.100$
F
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.372
0.137
Holopedium
$R^2 = 0.284$
$p = 0.004$
G
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
0.065
0.557
Bosmina
$R^2 = 0.478$
$p < 0.001$
H
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl *a*
-0.457
0.924
Ceriodaphnia
$R^2 = 0.485$
$p < 0.001$

Figure 4.6: Path diagrams quantifying land-cover cascade and residential development for *Daphnia* species. Six path models were calculated: A = D. g. mendotae; B = D. longiremis; C = D. catawba; D = D. pulicaria; E = D. dubia; F = D. ambigua. Ovals indicate human disturbance or *Daphnia* species, and boxes indicate nutrient elements. The variance explained by the model is in boldface italicized next to the *Daphnia* specie when significant after Bonferroni correction ($p = 0.008$). The path coefficients are indicated along the arrows. Abbreviations: TP = total phosphorus; Chl a = chlorophyll a.


A
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
0.252
D. g. mendotae
0.495
R²= 0.482
p < 0.001
B
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
-0.113
D. longiremis
-0.173
R²= 0.165
p = 0.100
C
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
-0.472
D. catawba
-0.062
R²= 0.191
p = 0.058
D
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
0.117
D. pulicaria
-0.486
R²= 0.411
p < 0.001
E
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
0.385
D. dubia
-0.179
R²= 0.163
p < 0.102
F
RD watershed
0.212
0.800
LCD watershed
0.567
TP
0.766
Chl a
-0.452
D. ambigua
0.919
R²= 0.485
p < 0.001

4.5.5 Variation partitionning of crustacean community

Four significant variables explained 30.5 % of the total variation in crustacean zooplankton community structure during summer, and the two first canonical axes were significant (P = 0.001) (Fig. 4.7A). Water transparency had the highest contribution (Secchi: 12%, $P = 0.001$), followed by residential development (RDW: 9%, $P = 0.001$), nutrient enrichment (TP: 8%, $P = 0.007$) and land-cover disturbance (LDCW: 7%, $P = 0.013$). Axis 1 represented a gradient of water transparency with higher biomass of *Daphnia* associated with clear lakes and opposed to *Holopedium*, calanoids, and cyclopoids found in more coloured lakes (Fig. 4.7A). Three lakes (Tracy, Croche and Blanche) were associated with high water transparency while lakes Nord and Cabane had the lowest water transparency (Fig. 4.7A). Axis 2 represented a gradient of TP enrichment associated to the RDW and LCDW disturbance gradients (Fig. 4.7A). Gradients in TP and Secchi transparency were independent, indicating that *Daphnia* has a strong influence on water transparency, independently of nutrient enrichment. *CerioDaphnia* and *Bosmina* were associated with the disturbance gradients while copepods and *Holopedium* occurred in little perturbed lakes. The lakes associated with the disturbance gradient were René, Purvis and Rond (Fig. 4.7A); they had mean concentrations of total phosphorus higher than 10 $\mu g \cdot L^{-1}$. Temporal variation among dates (June, July and August) did not have an impact on the distribution of crustacean functional groups; no particular cluster was associated to months, and in most lakes, data collected at the three months were clustered together (Fig. 4.6A). Variation partitioning indicated that water transparency and nutrient enrichment (Secchi, TP) explained a similar amount of variance (16.3%) in the crustacean community structure, more than for the disturbance variables (14.6%: RDW and LCDW), while natural variation in lake and watershed morphometry had no influence. Around 6% of the variance was explained by the variables interactions.

Seven significant variables explained 57.2% of the total variation in the biomass of *Daphnia* species, and the canonical axes were significant $P = 0.001$ (Fig. 4.7B). Total phosphorus concentration had the highest contribution (TP: 17%, *P* = 0.002), followed by lake relative depth (Zrel: 12%, *P* = 0.002), lake area (LA: 10%, *P* = 0.004), total nitrogen (TN: 7%, *P*= 0.005), the euphotic depth (EZ: 6%, *P*= 0.049), water transparency (Secchi: 5%, *P* = 0.018), and land-cover disturbance (LCDW: 5%, *P* 0.018). Axis 1 represented a gradient of TP and TN enrichment associated with high land-cover disturbance in large lakes, which was opposed to an inverse gradient in water transparency and lake relative depth (Fig. 4.6B). The small species *Daphnia mendotae* and *D. ambigua* were associated with the nutrient and land-cover disturbance gradients whereas the larger species *D. catawba* and *D. pulicaria* were associated with clear and deep lakes (Fig. 4.7B). Lakes Rond and René were associated with high disturbance while lakes Tracy and Blanche where associated with higher water transparency (Fig. 4.7B). Again, no temporal variation was measured as monthly data did not have an impact on the *Daphnia* species distribution (Fig. 4.7B). Variation partitioning indicated similar amount of variance explained by water quality variables (25.5%: EZ, TP, TN, Secchi) and lake and watershed morphometry (27.3%: LA and Zrel), while land-cover disturbance (LCDW) explained only 10.2% of *Daphnia* species distribution among lakes. Around 20% of the variance was explained by the variables interactions.

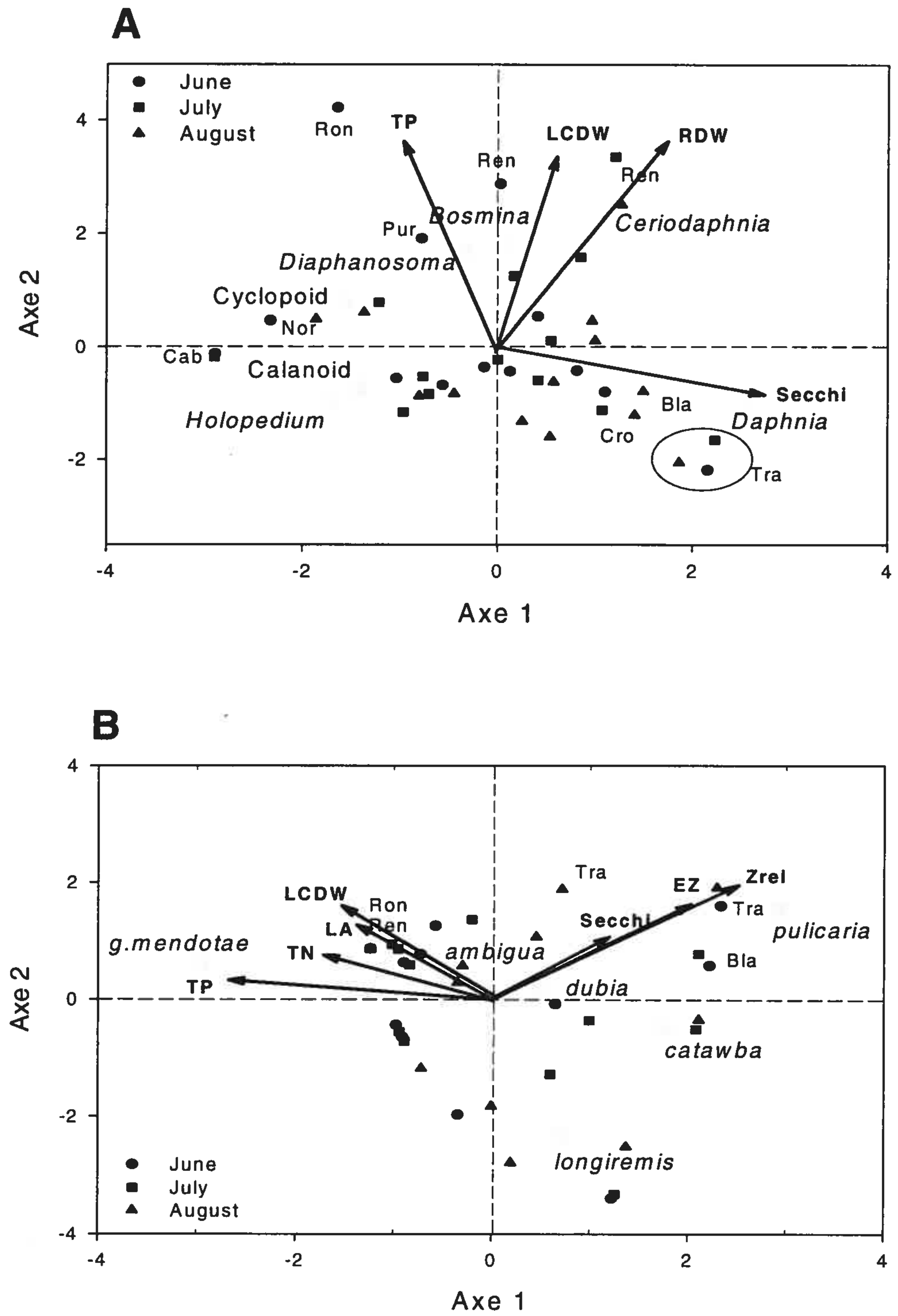


Figure 4.7: (A) RDA of the biomass of macrozooplankton functional groups biomass (*Bosmina*, Holopedium, *Daphnia*, *Diaphanosoma*, *CerioDaphnia*, calanoid and cyclopoid). (B) RDA of the biomass of *Daphnia* species. TP = total phosphorus; TN = total nitrogen; EZ = depth of the euphotic zone; LCDW = land-cover development on the watershed; LA = Lake area; Zrel = relative depth; Secchi = Secchi disk depth.

4.6 Discussion

Lakes in the Laurentian region are distributed along a large range of residential and land-cover disturbances while being somewhat similar based on their origin, trophy and morphology. The disturbance gradient accounted for most of the variation and was associated to a two to three fold increase in nutrients (TP and TN) and a four-fold increase in algal concentration (Chl. *a*). At the scale of the watershed, residential development (RDW) had a greater influence on TP enrichment than land-cover disturbance (LCD: % of open area). The conversion of forest into dwellings, hotels, roads, golf courses and ski slopes reflects the transition of pristine environments to more urbanized and recreational environments which can increase the importation of nutrients into the aquatic systems (Knoll et al. 2003; Hoffmann and Dodson 2005). Both the absence of relationship between RD and LCD at the scale of the watershed in land-cover cascade (LCC) models, and the higher impact of residential development on TP enrichment provide insight toward identification of residential development as the key disturbance stimuli.

Recent urbanization of watersheds in the Laurentian region slightly influenced lake water quality and indirectly zooplankton community. Crustacean zooplankton responded mainly to large scale disturbances within the watershed, whereas small scale disturbances on nearshore riparian strips had a minor influence. This finding is different from the responses of littoral algae and benthic macroinvertebrates in the same lakes which mainly responded to nearshore residential development and land-cover disturbance in the 50-100 m riparian strips (Lambert 2006; Lambert et al. 2007; De Sousa 2007; De Sousa et al. 2007). Human land use typically increases lake productivity by elevating nutrient export from watersheds to lakes (Lathrop et al. 1998, Lamontagne et al. 2000; Knoll et al. 2003; Hoffmann and Dodson 2005), which primarily may affect the littoral zone. However, our study suggests that even though early impact of nearshore residential development occurs in the littoral zone (Lambert et al. 2007; De Sousa et al. 2007), residential development and land-cover disturbance at the scale of the watershed can impact pelagic community even in still relatively pristine region. Our results imply that the pelagic zooplankton community is an ultimate indicator of large-scale disturbances within the watershed while littoral benthic communities are early indicators of nearshore disturbances. Pelagic zooplankton community responses following residential and land-cover watershed disturbances are consistent with large-scale shifts toward eutrophication of canadian lake ecosystems in recreational and recently urbanized region.

Our study supports the hypothesis that TP is the best predictor of changes in crustacean zooplankton biomass in the Laurentian region, as observed in other Canadian poor-nutrient lakes (Yan 1986), and at continental scale along a latitudinal and trophic gradients (Pinto-Coelho et al. 2005). TP enrichment mediated residential development and land-cover cascades on crustacean community. Both regression analyses and LCC models showed that TP enrichment is a key intermediate element in the cascades linking the disturbance stimuli to increasing biomass of crustacean zooplankton. LCC models showed that TP enrichment was also associated with biomass increase of small *Daphnia* species (*D. mendotae, D. ambigua*) and biomass decrease of the large *D. pulicaria*. However, LCC models were not powerful in predicting variation in crustacean biomass. Bottom-up cascading effects of residential and land-cover disturbance at the scale of the watershed explained less than half of the total among-lake variation in crustacean zooplankton and *Daphnia* biomass. The addition of top-down effects by including planktivory variables as explanatory variables in the LCC models would probably allow better to predict of among-lake variation in crustacean zooplankton (Chang et al. 2004).

We did not find a positive influence of increasing algal concentration on crustacean zooplankton based on bivariate regressions and LCC models. LCC models showed only negative effects of increasing Chl *a* on some cladocerans (*CerioDaphnia, Daphnia ambigua*). Along eutrophication gradients, higher Chl. *a* concentration generally reflects dominance of inedible algae (Watson et al. 1997) such as large Chlorophytes and Cyanobacteria which are often detrimental to cladocerans and *Daphnia* (Ghadouani et al. 2003).

Studied lakes were distributed along two mostly independent gradients as shown by the PCA results: a disturbance gradient associated to TP enrichment and a water transparency gradient and lake depth. Along the disturbance and nutrient gradient, Lakes René and Rond were the most urbanized and nutrient-enriched while Lakes Violon and Cabane were the most pristine. Lake Tracy, and Lakes Croche and Blanche in a lesser extent, were clearly associated with water transparency and lake depth. Lakes René and Rond had the stronger TP and TN concentrations in the pelagic zone, reflecting the highest residential and recreational development within their watershed. The disturbance gradient was associated to among-lake changes in total crustacean biomass, suggesting a significant impact. The lower biomass were found in the most pristine, transparent lakes (Violon, Blanche, Tracy) whereas the highest biomass occurred in the most enriched and urbanized lakes (Rond, René). However, lakes of intermediate disturbance level showed variable crustacean biomass and community structure, indicating complex interactions between crustacean zooplankton community and natural and disturbance gradients.

In addition to biomass, crustacean community structure also changed along the disturbance gradient. In our study, the number of crustacean functional groups did not vary among lakes with 4-5 functional groups in the most pristine lakes and 4-6 fucntional groups in the most disturbed lakes. Other studies have shown that watershed development increases zooplankton richness by contributing limiting nutrients to lakes; nonetheless, overload of nutrients could reduce zooplankton richness (Hoffmann and Dodson 2005; Dodson et al. 2007). The difference among lakes in crustacean community structure stands in terms of dominance of the functional groups. In the most urbanized and nutrient-enriched lakes, cladocerans such as *Bosmina*, *CerioDaphnia* and *Diaphanosoma* were dominant while they were present only in few numbers in the pristine and transparent lakes. The association of *Diaphanosoma* with TP enrichment could be partly explained as this cladoceran is usually found in eutrophic systems (Stich 2004). These cladocerans could thus be viewed as indicators of human watershed disturbance in Canadian lakes. Even though our studied lakes are still in an oligo-mesotrophic state, the presence of these functional groups linked to high residential and land-cover disturbances seems to imply that these lakes are already in a eutrophic state (Stemberger and Lazorchak 1994).

Unlike calanoids and *Holopedium*, *Daphnia* was associated with the most transparent and deep lakes. In the RDA, *Daphnia* was not related to the disturbances or the TP enrichment of the watershed. Water transparency is a derivative of TP concentration and algal biomass that usually reflects the disturbances and is not only the result of *Daphnia* grazing, but an integral product of bottom-up and top-down forces. Nonetheless, RDA results indicated that the large *D. pulicaria* was associated with the gradient of lake transparency and depth, as observed in other studies (Curries et al. 1999; Lathrop et al. 1999; Stemberger and Miller 2003). Thus, this indicate the potential of *Daphnia* as an effective filter-feeder capable of creating a clear-water phase through their high grazing efficiency (Sommer et al. 1986; Lathrop et al. 1999; Kasprzak et al. 1999; Beisner 2001; Stemberger and Miller 2003).

Daphnia species showed differential responses to the land-cover disturbance (LCD) and nutrient gradients. Small *D. ambigua* and *D. g.mendotae* were associated to LCD at the scale of watershed, whereas large *D. pulicaria* and *D. catawba* were opposed to these gradients. The presence of small daphnids in the most disturbed and nutrient-enriched lakes may also suggest some planktivory effect, because *D. g. mendotae* was found to better survive intense planktivory in more eutrophic lakes (Gélinas et al. 2007). *D. catawba* is usually found in lakes with pH around 6 (Holt et al. 2003), and these lakes are less productive and less disturbed by human activities. Furthermore, the association of large-bodied *D. pulicaria* and *D. catawba* with higher water transparency and deeper euphotic zone depth is consistent with their role as efficient herbivorous grazer (Kreutzer and Lampert 1999; Tessier et al. 2001; Beisner 2001) and their migrating behaviour (Lampert 1989). Large *D. pulicaria* and *D. catawba* are generally found in deep lakes (Keller and Conlon 1994) where they can avoid predation by size-selective planktivorous fish by migrating in the deep and dark zone. Large *Daphnia* undergo diurnal vertical migration to reduce mortality by moving to deeper water where darkness provides a visual refuge from fish (Lampert 1993; Wright and Shapiro 1990).

As proposed by Dodson et al. (2005), modern zooplankton ecologists are faced with understanding the relative influence of anthropogenic and natural ecological factors on pelagic communities. Our study showed that both natural and disturbance factors had significant effects on crustacean zooplankton structure. Variation partitioning demonstrated that changes in water transparency, and nutrient enrichment associated with the disturbance gradient are important drivers of crustacean community structure. However, only 30 % of the adjusted variation of crustacean functional groups was explained in RDA suggesting that we failed to measure other environmental variables, such as planktivory pressure that may be an important driver of crustacean community structure (Chang et al. 2004). *Daphnia* species assemblages showed a stronger structuring effect of water transparency and lake depth and area which explained 58% of the total adjusted variation, a higher proportion than land-cover disturbance and associated nutrient enrichment. Here again, information on fish assemblages could help to explain more of the variation in *Daphnia* assemblages.

Implications for biomonitoring

Eutrophication remains the most pervasive water quality problem in freshwaters and limnologists should develop biomonitoring tools to assess lake ecosystems. Our study showed that even in relatively pristine canadian lakes still protected from more intense disturbances by agriculture and industrial activity, recent residential development of watershed may subtly affect pelagic ecosystems. Although some more extreme indices of eutrophication such as anoxia at night, high pH during the day, and blooms of cyanobacteria are still infrequent. Land-cover disturbance and residential development reflect partly cascading bottom-up effects through TP enrichment.

As crustacean zooplankton is a key element of the pelagic food web (McQueen et al. 1986; Carpenter and Kitchell 1993), any change in the community, particularly in cladocerans and *Daphnia* species of different body size will have profound impact on the whole pelagic ecosystems in terms of nutrient enrichment and water transparency. Finally, the identification of effective functional groups may help to establish biomonitoring program based on efficient bioindicators (Stemberger et al. 2001). Crustacean zooplankton assemblages are complex and contain many groups and species capable of responding differently and in unpredictable ways to watershed disturbance (this study; Stemberger and Lazorchak 1994; Patoine et al. 2000; Dodson et al. 2005; Hoffmann and Dodson 2005; Galbraith and Burns 2007). However, our study indicated that some crustacean functional groups and *Daphnia* species were found relevant for developing bioindicators of watershed disturbance in canadian lakes undergoing recent residential development. Cladocerans are responding the most to the disturbance gradient. Some cladocerans (*Bosmina*, *CerioDaphnia*) and small daphnids (*D. g.mendotae*, *D. ambigua*) were associated with the disturbance gradient while calanoids and large daphnids (*D. pulicaria, D. catawba*) reflect pristine conditions. Our study provides potential biomonitoring tools based on crustacean zooplankton community structure to assess the response of pelagic communities to watershed disturbance at large scale while two companion studies on littoral communities (Lambert et al. 2007; De Sousa et al. 2007) offered complementary tools based on periphyton mats and macroinvertebrate community to assess the preliminary effects of watershed disturbance at small scale on nearshore riparian zone.

4.7 Acknowledgements

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Chapitre 5

Depth selection patterns of crustacean zooplankton in nutrient-poor Canadian shield lakes

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5.1 Summary

1. Vertical habitat complexity within lakes may affect depth selection patterns of zooplankton by producing strong gradients in light, water temperature, oxygen, and algal concentration, and by providing prey refuges in deeper zones. In response to these vertical gradients, crustacean zooplankton, and especially *Daphnia* species, may develop depth selection patterns and diel vertical migration.
2. To test how zooplankton depth selection patterns vary among nutrient-poor Canadian shield lakes along a gradient of anthropogenic disturbance by residential development and land-cover forest clearing, we calculated weighted mean depth (WMD) distribution of crustacean functional groups and *Daphnia* species during day and night in 8 Canadian shield lakes of the Laurentian region (Southern Québec, Canada).
3. Depth selection patterns of crustacean functional groups and *Daphnia* species were primarily related to the temperature (59-78% of explained variance), and secondly to the depth of the euphotic zone (7-10%) and the oxygen concentration (2-8%). Most WMD of crustacean functional groups and *Daphnia* species were located in the metalimnion or at the depth of the euphotic zone. Crustacean zooplankton avoided warm and oxygenated surface layers and tended to stay in colder but oxygenated deep waters both at day and night times. They also stay deeper in lakes with greater euphotic zone.
4. There was some evidence of upward migrations of large *Daphnia* and copepods in some lakes, and a case of downward migration in a lake inhabited by chaoborid larvae.
5. Multivariate regression trees (MRT) were used to cluster crustacean functional groups and *Daphnia* species into homogenous groups based on natural and disturbance factors. The depth of the euphotic zone, the sampling depth, the time of sampling (day or night) and the biomass of chlorophyll *a* were the main factors clustering crustacean. The drainage area /lake volume ratio, the sampling depth, the land-cover disturbance in the watershed and the concentration of total dissolved phosphorus were the main factors clustering *Daphnia* assemblages.

5.2 Introduction

In lake ecosystems, habitat complexity arises as the result of vertical and horizontal heterogeneity that is reflected in the distribution patterns of zooplankton (Pinel-Alloul, 1995; Pinel-Alloul & Ghadouani, 2007). Thermal stratification and associated physicochemical gradients were shown to influence depth selection patterns and vertical distribution of crustacean zooplankton groups in lakes (Winder, Buergi & Spaak, 2003; Thackeray *et al.*, 2006; Johnson, O'Brien & MacIntyre, 2007) and enclosure experiments (Tolomeyev & Zadereev, 2005). In deep lakes, water stratification provides to zooplankton sharp vertical gradients in light, temperature, oxygen, food concentration, and predation risk. Therefore, optimal depth selection pattern of crustacean zooplankton is a compromise driven by a combination of abiotic (light, temperature, oxygen) and biotic (food resource and predation risk) forces that will mostly be advantageous to their fitness by affecting their metabolism, growth and life history traits (Gielbelhausen & Lampert, 2001; Reichwaldt, Wolf & Stibor, 2005). DVM patterns of *Daphnia* have been the most studied (Stirling, McQueen & Johannes, 1990; Angeli *et al.*, 1995; Ringelberg, 1999; Wissel & Ramacharan, 2003, Alonso, Rocco & Barriga, 2004), although crustacean copepods also adopt DVM behaviour (Ghan, Haytt & McPhail, 1998; Ghan, McPhail & Haytt, 1998).

In addition to the water colum complexity, the anthropogenic land-use of lake watershed may also indirectly affect zooplankton community (Dodson, Lillie & Will-Wolf, 2005; Dodson *et al.*, 2007). Cascading effects on thermal stratification, water chemistry (Galbraith & Burns, 2007), phytoplankton production (Knoll, Vanni & Renwick, 2003), and will subsequently affect the crustacean zooplankton community (Gélinas & Pinel-Alloul, 2007). However, there is still no study comparing depth selection patterns of different crustacean functional groups and *Daphnia* species inhabiting nutrient–poor Canadian shield lakes affected by recent human disturbances.

Crustaceans were classified into functional groups according to their feeding mode and their body size. The utilisation of functional groups implied that they play a similar role in the ecosystem (Stemberger & Lazorchak, 1994). Cladocerans were divided in different feeding groups: the filter-feeders, the filter- and grasping-feeders, and the raptorial-feeders.

First, large cladocerans as *Daphnia, Diaphanosoma* and *Holopedium* were categorized as filter-feeders because they can filter a broad range of particles that usually increases with their body length (Chow-Fraser & Knoechel, 1985; Knoechel & Holtby, 1986). However, they were separated into three distinct functional groups based on their daily average filtering rate: *Diaphanosoma* = 1.6 ml animal^{-1} day^{-1}, *Holopedium* = 4.4 ml animal^{-1} day^{-1} and *Daphnia* = 3.6 to 14.4 ml animal^{-1} day^{-1} (review in Wetzel 1991). Small cladocerans such as *Bosmina* use distinct modes of feeding by combining filter- and grasping-feeding on bacteria, small algae, and flagellates (DeMott & Kerfoot, 1982; Vanderploeg, 1990). Copepod filtration rates are less efficient than cladocerans of similar size and they select large particles (Peters & Downing, 1984). Copepods were divided into two feeding groups: the calanoids that collect a variety of small and large algal particles using passive and active mechanisms (Vanderploeg, 1990) and the cyclopoids which are raptorial omnivores and effective predators but also feed on algae (Adrian & Frost, 1993).

Here, we studied the effects of physicochemical vertical gradients in the pelagic zone and watershed human disturbances on depth residence selection and DVM patterns of crustacean zooplankton in still nutrient-poor Canadian shield lakes of the Laurentian region (Québec, Canada) facing recent human disturbances by increasing residential development and land-cover clearing. We hypothesized that physiochemical variables are strongly correlated with the crustacean depth selection patterns and examined how recent residential and land-cover disturbances may influence these behavioural patterns. We analyzed depth residence selection and DVM patterns of crustacean functional groups and *Daphnia* species in relation to within-lake vertical gradients in light, temperature, oxygen and algal resources, and residential and land-cover disturbances. Furthermore, we constructed empirical models predicting the depth distribution of crustacean functional groups and *Daphnia* species using multivariate regression trees (MRT) analysis, a new approach for modeling species-environment relationships.

5.3 Methods

5.3.1 Study sites

Sampling was conducted in 8 lakes of the Laurentian region, north of Montréal, Canada (45°59'N – 73°60'W). The Laurentian region is of glacial origin (Wisconsin glaciation: 18 000 years ago, Martignole 1975), covered by Canadian shield forest, and characterised by a continental climate with a mean annual temperature of 4°C and mean annual precipitation between 1100 and 1400 mm (25-40% as snow) (Savage 2001).

Disturbance gradients in residential development and land-cover clearing ranged from 3 to 242 dwellings/km^2 and from 0 to 53% of forest cleared (open area) at the scale of the watershed (Table 5-I)., The intensity of the disturbance by residential development and land-cover clearing was even higher near lakeshore with maxima of 686 dwellings/km^2 and 86 % of open area in the 50 m riparian zone (Table 5-I). Wetlands on the watershed area were rarely present and never exceeded 2% of total watershed area (data not shown).

5.3.2 Morphometry and disturbance characteristics of lakes and watersheds

Natural morphometric characteristics of watersheds (area and slope, drainage ratio/lake area) and lakes (area, volume, maximum and mean depth) were measured (MapInfo, V 6.5) from numerical topographic and bathymetric maps (Lambert 2006). To evaluate anthropogenic disturbance by residential development and land forest cover clearing, we estimated the density of dwellings (per km^2) and the percentage of open area on orthorectified aerial photographs (1:30 000 and 1:10 000) acquired in 2002 and 2004 (MapInfo V 6.5) (Lambert 2006) within the 50-m wide riparian zone and within the whole watershed (Table 5-I). Open areas represented zones cleared for buildings, roads, parking lots, and lawns; a golf course and ski down hill trails were also included in the case of Lake Rond.

5.3.3 Water sampling and analysis

Sampling was carried out in July 2003 at the location of maximum depth in each lake. Temperature, oxygen concentration, and pH were measured at 1 m intervals through the water column with a Hydrolab Surveyor® 4, and light attenuation with a photometer Licor 1000. Secchi depth transparency was measured and the euphotic zone (EZ) was estimated as the depth of 1% of surface light irradiance. Water samples were collected with a 4 L Van Dorn bottle at 4 different depths (mid-epilimnion, mid-metalimnion, mid-hypolimnion and at the depth of the euphotic limit). Water samples were transferred into two 1-L polypropylene containers, a dark one for chlorophyll *a* (Chl. *a*) analysis and a clear one for chemical analysis of total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), dissolved organic carbon (DOC) and pH. In the laboratory, Chl. *a* water samples were filtered on GF/C Whatman filters (1.2 µm pore size) and the filters were kept frozen until analysis. Chl. *a* pigments were extracted in cold 95% ethanol for 24h and measured before and after acidification at 665nm and 750 nm (Spectronic Genesys 5 spectrophotometer) (Nusch 1980). TP and TDP concentrations were determined on 50 ml of unfiltered and filtered (Gelman type glass-fiber filters: 0.45 µm pore size) water samples, respectively. TP and TDP samples were analysed as orthophosphate after persulfate digestion in an autoclave (Stainton, Gabel & Amstrong, 1977). TN was analysed with a LACHAT Continuous Flow Quick-Chem 8000 and DOC with a Shimadzu ASI-5000A.

5.3.4 Zooplankton sampling and analysis

As for water, zooplankton was sampled in July 2003 at the deepest site in each lake at 4 different depths (mid-epilimnion, mid-metalimnion, mid-hypolimnion and at the lower depth of the euphotic zone) using a 12 L Patalas plankton trap (153 µm mesh size) at midday and midnight. Depending of lake maximum depth, additional zooplankton samples were also taken randomly at some others depths to give a better precision of the vertical distribution of *Daphnia* species (Violon = 5 depths; Rond = 1; Morency = 3; Connelly = 3; Tracy = 2; Truite = 2; Purvis = 3; Gervais = 4). Samples were preserved in 4 % buffered sucrose-formalin solution (Haney & Hall, 1973). Taxonomic identification, counting and size measurements were done on the entire sample. Zooplankton were placed into a grooved Plexiglas Ward counting cell (10 ml capacity) under a dissecting microscope (Leica MZ20) connected to an image analyser (Image Pro Plus) enabling direct sizing of organisms. Copepod nauplii and rotifers were excluded from the analysis because the 153 µm mesh size plankton net did not adequately collect nauplii stages and small rotifers; it only collected the large rotifer *Asplanchna* and the species with spines like *Keratella* and *Kellicottia*. Body length of cladocerans was measured from the top of the head to the base of the tail spine. Chaoborid larvae were counted in the entire sample. Copepods were measured from the top of the head to the end of the caudal ramus. Generally, a minimum of 20 individuals were measured for each crustacean functional group and a minimum of 100 individuals for each *Daphnia* species, or all individuals present in the entire sample if these minimum numbers could not be achieved after searching the sub-sample. To estimate the biomass of taxa, body lengths were converted to dry weights using published regression models for each crustacean functional group or *Daphnia* species (Malley *et al.*, 1989). Weighted mean depth (WMD) distribution at day and night sampling in each lake for each crustacean functional group and *Daphnia* species were calculated from the Patalas samples as followed:

$$\mathrm{WMD} = \Sigma\, (N_i * d_i)/\ \Sigma\, N_i$$

where N_i = number of one crustacean group or *Daphnia* species at the depth i, and d_i = depth i.

Amplitude and direction of DVM patterns were estimated by the difference between WMD at day and night.

Therefore, according to their feeding behaviour and body size, crustaceans were separated into six functional groups: calanoids, cyclopoids, *Daphnia*, *Holopedium*, *Diaphanosoma* and *Bosmina*. In addition, *Daphnia* species were considered separately since competition between differently sized-species occurs in nature and grazer-resource and prey-predator interactions varies among species (Leibold, 1991; Gonzalez & Tessier, 1997; Kreutzer & Lampert 1999; Tessier, Bizina & Geedey, 2001; Gélinas, Pinel-Alloul & Ślusarczyk, 2007).

5.3.5 Statistical analysis

We first performed a two-way ANOVA on the chlorophyll *a* to estimate the effects due to depths (epilimnion, metalimnion, hypolimnion and depth of the euphotic limit), time (day or night) and the interaction across lakes. We also performed similar two-way ANOVAs on each functional groups biomass to estimate the effect of depths, time and the interaction. Post-hoc Tukey tests were used for pairwise comparison on significant effects. A one-way ANOVA was used to test for differences between day and night weighted mean depths (WMD) of crustacean functional groups and *Daphnia* species. Data were log transformed

($\log_{10}$ +1) to achieve normality of the data according to Kolmogorov-Smirnov tests ($P > 0.05$) (Lilliefors) (Sokal & Rolf, 1995).

Multiple linear regression analyses were used to evaluate the relative influence of physicochemical parameters on the weighted mean depth (WMD) of the functional groups and *Daphnia* species biomass during day and night. The significance level of each regression constant was indicated as $* = p < 0.05$ and their partial r^2 value was reported in brakets.

To better assess the distribution of the crustacean functional groups and *Daphnia* species among lakes in relation to natural and disturbance factors, we used multivariate regression trees (MRT) as a predictive method (Larsen & Speckman, 2004). All additional depths were used in these two analyses. This new modelling method makes no assumption about the form of relationship between functional groups or *Daphnia* species and their environment (linearity is not obligatory). MRT is a form of multivariate regression that predicts species abundance from the explanatory variables (De'ath, 2002). MRT is also a method of constrained clustering where each cluster is defined by a set of environmental variables based on species dissimilarities. The tree grows from repeatedly splitting the data into two nodes from a single explanatory variable that maximise the homogeneity of the two created nodes. A vertical line links two consecutive nodes and predicts proportionally the variance that is explained; thereby, the longest the vertical line is, the largest proportion of the total variance is explained. The terminal nodes are usually called the leaves of the tree. The size of the trees (number of leaves) was based on a cross-validation procedure that generates a series of trees and the smallest tree (with the lowest number of leaves) was selected (De'ath 2002). The variance explained by the MRT is 1 minus the Error given by the program. Concerning the CV-error, a result of 0 represents a perfect prediction and 1 (or a little over) a poor prediction (De'ath 2002). Hellinger's transformations were applied to functional groups and *Daphnia* species biomass data to reduce the influence of rare species (Legendre & Gallagher, 2001). All natural and anthropogenic environmental variables were used in the model: variables characterising the heterogeneity of the water column were included as well as other variables representing the anthropogenic disturbances within the entire watershed. MTR were done in R program and we used the Euclidian distance for splitting the explanatory variables.

Table 5-I. Morphometric characteristics and human disturbance factors for the 8 studied lakes. Human disturbance variables were calculated within the watershed (W) and on the first 50 meters riparian strips (50).

Lakes	**Watershed area** (km²)	**Watershed slope** (%)	**Drainage area /lake area**	**Drainage area /lake volume**	**Lake area** (km²)	**Lake volume** (10^6 m^3)	**Lake max. depth** (m)	**Lake mean depth** (m)	**Secchi disk depth** (m)	**Euphotic zone depth** (m)	**Residential Development** dwellings/km^2		**Land-cover disturbance** Open area (%)	
											W	50m	W	50m
	WA	slope	Dr	Drv	LA	volume	Zmax	Zmean	secchi	ZE	RDW	RD50	LCD W	LCD 50
Violon	4.41	9.2	10.5	1.33	0.38	3.325	22.6	8.9	5.3	8	3	8	0	0
Gervais	8.65	6.2	8	0.37	0.97	23.526	60	24.4	8	16.5	21	212	1	2
Connelly	24.36	6.2	18.6	2.55	1.24	9.561	20.8	7.7	3	7	48	686	7	46
Morency	2.33	14.6	8	1.04	0.26	2.246	20.3	8.7	4.75	8.5	57	152	13	31
Purvis	0.6	10.6	2.2	0.42	0.19	1.446	19.7	7.8	6	11.5	89	106	8	13
Truite	4.23	5.9	7.3	0.89	0.51	4.783	21.6	9.3	6	11	111	430	30	79
Tracy	0.24	8.3	1.9	0.36	0.08	0.676	22.9	8.1	7.25	12	144	289	4	5
Rond	1.5	7.5	8	1.24	0.17	1.206	15.9	7.2	4.5	9.5	242	323	53	86

Table 5-II: Variations in water temperature, oxygen, nutrients (TP, TDP) and algal biomass (Chl. a at day and night), and in Chaoborus density (Chao. at day and night) among sampling depths in each of the 8 studied lakes.

Lake	**Strata**	**Depth** (m)	**TP** (µg·L^{-1})	**TDP** (µg·L^{-1})	**Day Chl a** (µg·L^{-1})	**Night Chl a** (µg·L^{-1})	**Temp** °C	**O$_2$** (mg.L^{-1})	**Day Chao.** Ind.m^{3}	**Night Chao.** Ind.m^{-3}
Vio	Epi	1.5	4	1.4	0.26	1.47	25.5	6.9	0	0
	Meta	6	4.9	1.6	0.56	0.89	9.5	10.6	0	0
	1% light	8	9.1	1.3	1.35	0.59	5.2	9.1	0	0
	Hypo	15	13.6	1.4	1.43	1.5	4	3.75	0	0
Ger	Epi	2.5	4	1.3	0.60	0.57	21.5	6.15	0	0
	Meta	5.5	6.4	1.8	0.22	0.96	10.1	8	0	0
	1% light	16.5	5.2	1.75	1.41	0.48	5.3	7.55	0	0
	Hypo	20	5	1.3	1.25	-	4.5	6.22	0	0
Con	Epi	2	5.9	2.3	1.04	3.52	22	7.7	0	500
	Meta	7	7.9	2.1	1.75	4.03	8.9	6	0	0
	Hypo	15	8.3	2.35	0.67	2.08	4.7	2.65	0	0
Mor	Epi	1.5	7.5	1.8	2.38	-	24	7.8	0	0
	Meta	5.5	11.5	2.4	5.18	3.59	10.65	11.8	0	0
	1% light	8.5	14.2	2.2	3.93	3.67	5.75	9.2	0	0
	Hypo	13	12.8	1.75	4.99	11.67	4.3	1.5	0	0
Pur	Epi	1.5	8.3	3.8	0.89	0.91	24	7.4	0	0
	Meta	6.5	8.5	2.9	1.36	0.41	11	11.7	0	0
	1% light	11.5	16.2	3.95	5.15	5.26	5.7	3.1	0	0
	Hypo	15	19.5	1.2	4.30	0.45	4.9	0.6	0	0
Tru	Epi	3	6.9	2.35	1.62	1.42	20.6	7.7	0	0
	Meta	8	6.5	1.8	4.32	3.10	9.8	9.4	0	0
	1% light	11	5	1.7	2.22	2.99	5.9	7.7	0	0
	Hypo	15	4.2	1.55	0.71	0.73	4.9	5.9	0	0
Tra	Epi	2	4.2	1.7	0.09	0.71	21.2	7.5	0	0
	Meta	6.5	5.1	2.15	0.93	1.15	10.2	10.6	80	500
	1% light	12	9.2	3.45	4.23	1.67	5	1.25	170	2000
	Hypo	15	12.2	3.65	2.56	1.79	4.8	0.4	170	0
Ron	Epi	0.5	8	2.5	1.12	1.72	21.5	10	0	0
	Meta	3.5	8.9	3.15	0.68	1.05	10.1	13	0	0
	1% light	9.5	40.3	4.2	16.37	11.22	6.05	3.55	0	0
	Hypo	12	30.2	2.6	5.77	7.96	4.8	0.4	0	0

5.4 Results

5.4.1 Lake environments and disturbance gradients

Although the studied lakes were located in lacustrine environments of similar origin and geology, they varied by their morphometry, water quality, and anthropogenic disturbances. They were generally of small area but different in terms of depth and volume, watershed area and slope, and drainage ratio (Table 5-I). The lakes were still oligotrophic with total phosphorus (TP) concentrations not exceeding 10 $\mu g \cdot L^{-1}$ in the epilimnion during July; however, higher TP in the hypolimnion up to 30-40 $\mu g \cdot L^{-1}$ suggested nutrient-enriched conditions in some lakes (Table 5-II). Secchi transparency and euphotic depth varied two orders of magnitude among lakes (Table 5-I). Most of the lakes were circumneutral or slightly alkaline (data not shown). Gradients in residential development (RD) and land-cover disturbance (LCD) ranged from 3 to 242 dwellings/km^2 and from 0 to 53% of forest cleared (open area) at the scale of the watershed. The intensity of the disturbances was the highest at small scale within the 50 m riparian strip with a maximum of 686 dwellings/km^2 in Lake Connelly and 86% of open area in Lake Rond (Table 5-I).

In the studied lakes, physicochemical parameters varied with depth (Figs. 5.1 and 5.2; Table 5-II). All lakes were thermally stratified in July. Epilimnetic temperature varied between 22°C and 25°C whereas hypolimnetic temperature varied between around 4-5 °C. Four lakes (Morency, Tracy, Purvis, Rond) developed hypolimnetic oxygen deficit and anoxia during summer stratification. Algal concentration (Chl. *a*) significantly varied among depths (Table 5-III), the epilimnion had the lowest Chl. *a* which was significantly different from the euphotic zone depth (post-hoc Tukey result): most of the lakes displayed deep chlorophyll maxima up to 16 $\mu g \cdot L^{-1}$ (Table 5-II). These deep chlorophyll layers were associated with oxygen production up to 11-13 $mg \cdot L^{-1}$ in the metalimnion (Figs. 5.1 and 5.2; Table 5-II). No significant effects of time and interaction (depth*time) were found in the chlorophyll *a* (Table 5-III).

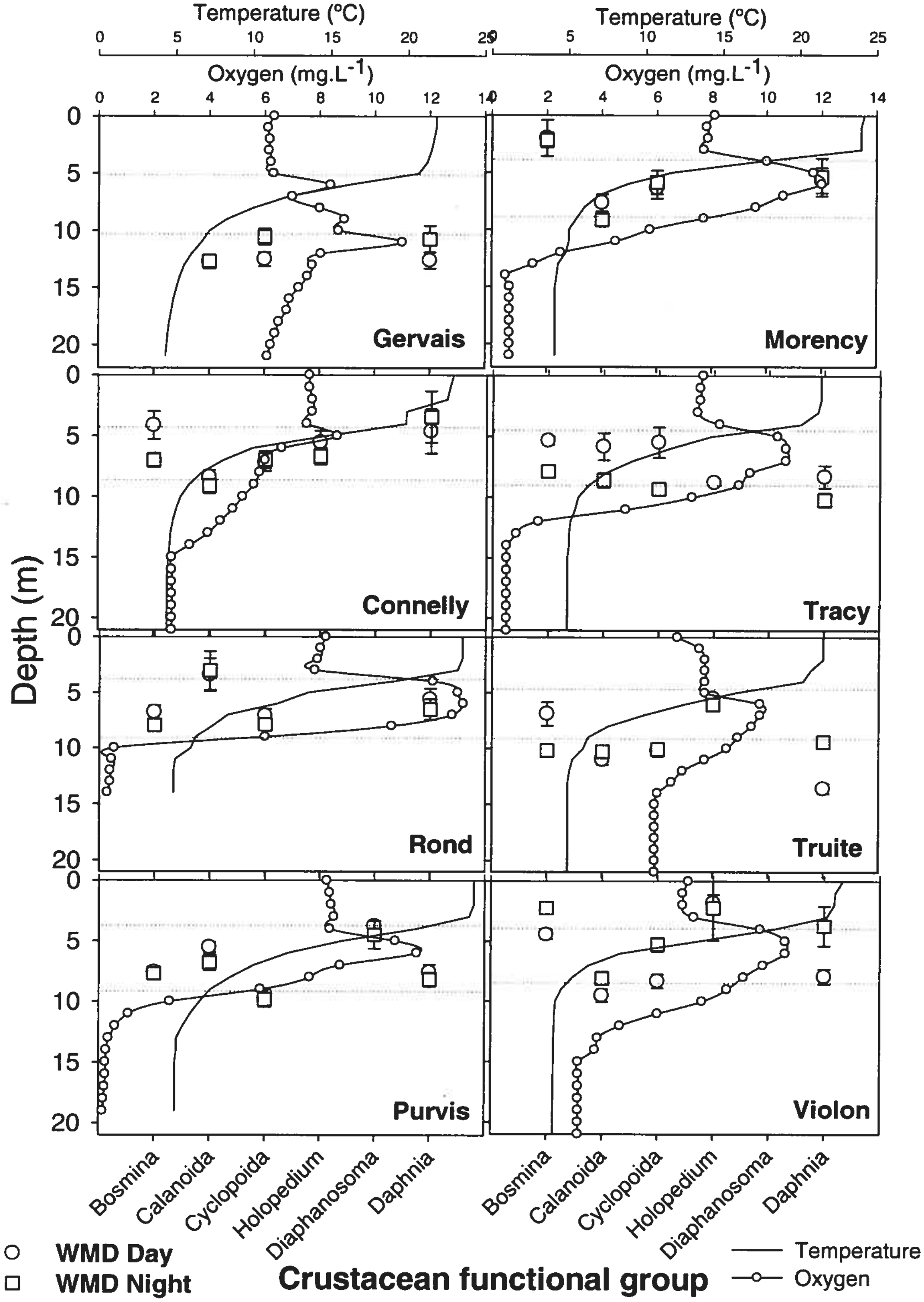

Figure 5.1: Weighted mean depth (m) of the six crustacean functional groups in each lake during day and night. Stratification is indicated by the vertical profile of temperature, oxygen concentration is indicated by the vertical profile. The dotted lines indicate the boundaries between the metalimnion and the two other layers (epilimnion and hypolimnion).

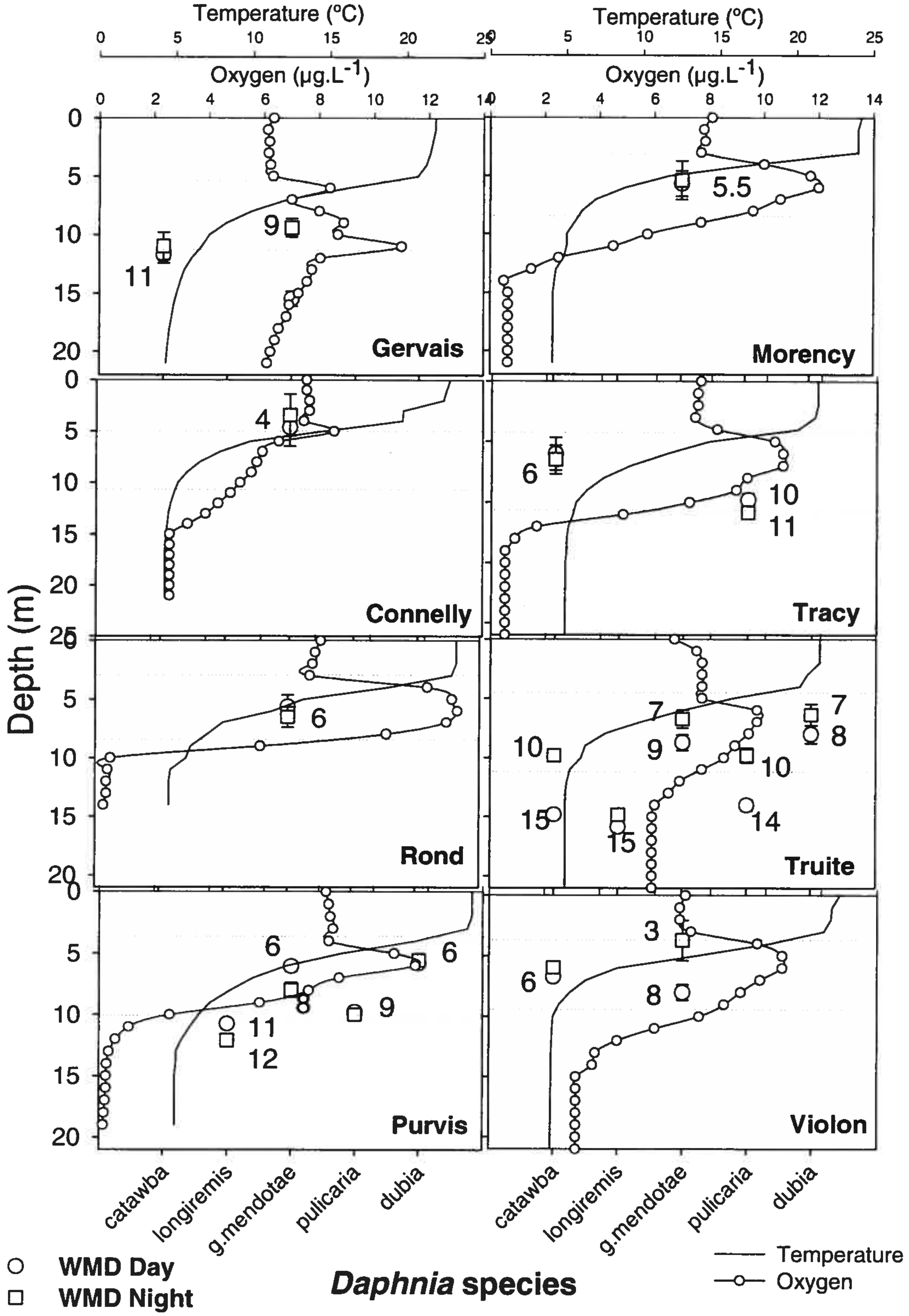

Figure 5.2: Weighted mean depth (m) of the five *Daphnia* species in each lake during day and night. Stratification is indicated by the vertical profile of temperature, oxygen concentration is indicated by the vertical profile. The dotted lines indicate the boundaries between the metalimnion and the two other layers (epilimnion and hypolimnion).

5.4.2 Crustacean zooplankton community

Three functional groups composed the majority of the crustacean community, *Daphnia*, calanoids and cyclopoids (Fig. 5.3). Two-ways ANOVAs showed no significant effects of depth, time or their interaction on the biomass of *Bosmina*, calanoids, cyclopoids, *Diaphanosoma* and *Holopedium* (Table 5-III). Results of the two-way ANOVA showed significant effects of depths and time in *Daphnia* biomass, however, the interaction was not significant (Table 5-III). The post-hoc Tukey test showed that night biomass was higher than daytime biomass, the lowest biomass was located in the hypolimnion and the hightest was in the metalimnion. *Daphnia* was a key component of the crustacean community in the epilimnion of most lakes representing at least 25% of the total crustacean biomass at day time, except in the lakes Violon, Morency and Truite where calanoids and cyclopoids dominated. *Daphnia* dominance in the epilimnion increased during night, except in lakes Purvis and Tracy. *Daphnia* was the most abundant group in the metalimnion in all lakes with percentages generally higher than 50%, except during the day in Lake Truite and during night in Lake Connelly. Crustacean composition in deeper strata (euphotic zone depth, hypolimnion) was similar during day and night in each lake. In deep strata, *Daphnia* was dominant in the lakes Gervais, Truite and Tracy, whereas the calanoids were abundant in lakes Violon, Connelly and Morency, and the cyclopoids in lakes Purvis and Rond.

Daphnia species assemblages also varied among lakes (Fig. 5.4). Small *Daphnia* (*D. g.mendotae*, *D. dubia*, *D. longiremis*) were dominant in most of the lakes (Violon, Connelly, Morency, Purvis, Truite, Rond), whereas large *Daphnia* (*D. pulicaria*, *D. catawba*) were the most frequent in two lakes (Gervais, Tracy) only.

Table 5-III: Two-way ANOVAs testing for the differences in biomass between depths, time and their interaction for each functional group (Bosmina, Calanoid, Cyclopoid, Holopedium, Diaphanosoma and *Daphnia*) and for the chlorophyll a.

Functional groups	Source	df	MS	*F*	*P*
Bosmina	Depth	3	0.013	0.409	0.747
	Time	1	0.001	0.025	0.875
	Depth*Time	3	0.003	0.086	0.967
	error	54	0.031		
Calanoid	Depth	3	0.02	0.141	0.935
	Time	1	0.173	1.22	0.274
	Depth*Time	3	0.061	0.432	0.731
	error	54	0.142		
Cyclopoid	Depth	3	0.181	1.125	0.347
	Time	1	0.004	0.026	0.872
	Depth*Time	3	0.052	0.322	0.809
	error	54	0.161		
Holopedium	Depth	3	0.013	1.467	0.234
	Time	1	0.004	0.496	0.484
	Depth*Time	3	0.002	0.228	0.877
	error	54	0.009		
Diaphanosoma	Depth	3	0.002	2.179	0.101
	Time	1	0.001	1.59	0.213
	Depth*Time	3	0.001	0.912	0.441
	error	54	0.001		
Daphnia	Depth	3	1.348	8.505	**< 0.001**
	Time	1	1.757	11.086	**0.002**
	Depth*Time	3	0.211	1.331	0.274
	error	54	0.158		
	Source	df	MS	*F*	*P*
Chl *a*	Depth	3	0.275	3.893	**0.014**
	Time	1	0.005	0.065	0.799
	Depth*Time	3	0.018	0.255	0.858
	error	54	0.071		

5.4.3 Depth selection and DVM patterns

Generally, weighted mean depths (WMD) of functional groups were located in the metalimnion and around the depth of the euphotic zone but some exception occurred (Figs. 5.1 & 5.2). Day and night WMD of functional groups were very similar in most of the lakes (one-way ANOVAs, $P > 0.05$). We observed the opposite trend of DVM in Lake Tracy; WMD of all functional groups were higher in the water column during daytime and lower at night (Fig. 5.1). High abundance of *Chaoborus* larvae was associated to this inverse migratory behaviour (Table 5-II).

In general, WMD of the two small *Daphnia*,which body length never exceeded 1 mm, *D. g.mendotae* and *D. dubia* were located higher in the water column (4-7 m) compared to the large *D. pulicaria* and *D. catawba* (7-11 m) which maximum body size reach 1.8 mm and 2.1 mm, respectively (Fig. 5.5). The two small species had opposite depth distribution; *D. dubia* was mainly found in upper strata (epilimnion and metalimnion) and also at night at the depth of the euphotic zone, but not in the hypolimnion. In contrast, *D. longiremis* was mainly found in deep strata (euphotic zone depth and hypolimnion). The three other *Daphnia* were found in the 4 strata but they were of different size (Fig. 5.5).

DVM amplitude (expressed as the displacement of WMD from day to night) did seem to increase with body size of crustacean groups, although the regression was barely significant ($r^2 = 0.345$, $p = 0.064$: results without Lake Tracy) because of important variability from lake to lake for each functional group (Fig. 5.6A). Crustaceans in Lake Tracy did downward migration at night of 2-4 m amplitude (Fig. 5.6A). Large *Daphnia* species (body size > 1.4 mm) displayed upward migration at night, with again the inverse pattern for *D. pulicaria* in Lake Tracy where we observed a downward migration of 1 m (Fig. 5.6B).

Figure 5.3: Crustacean functional groups composition (%) of biomass during day and night in each 4 depth (epilimnion, metalimnion, 1% light depth and hypolimnion).

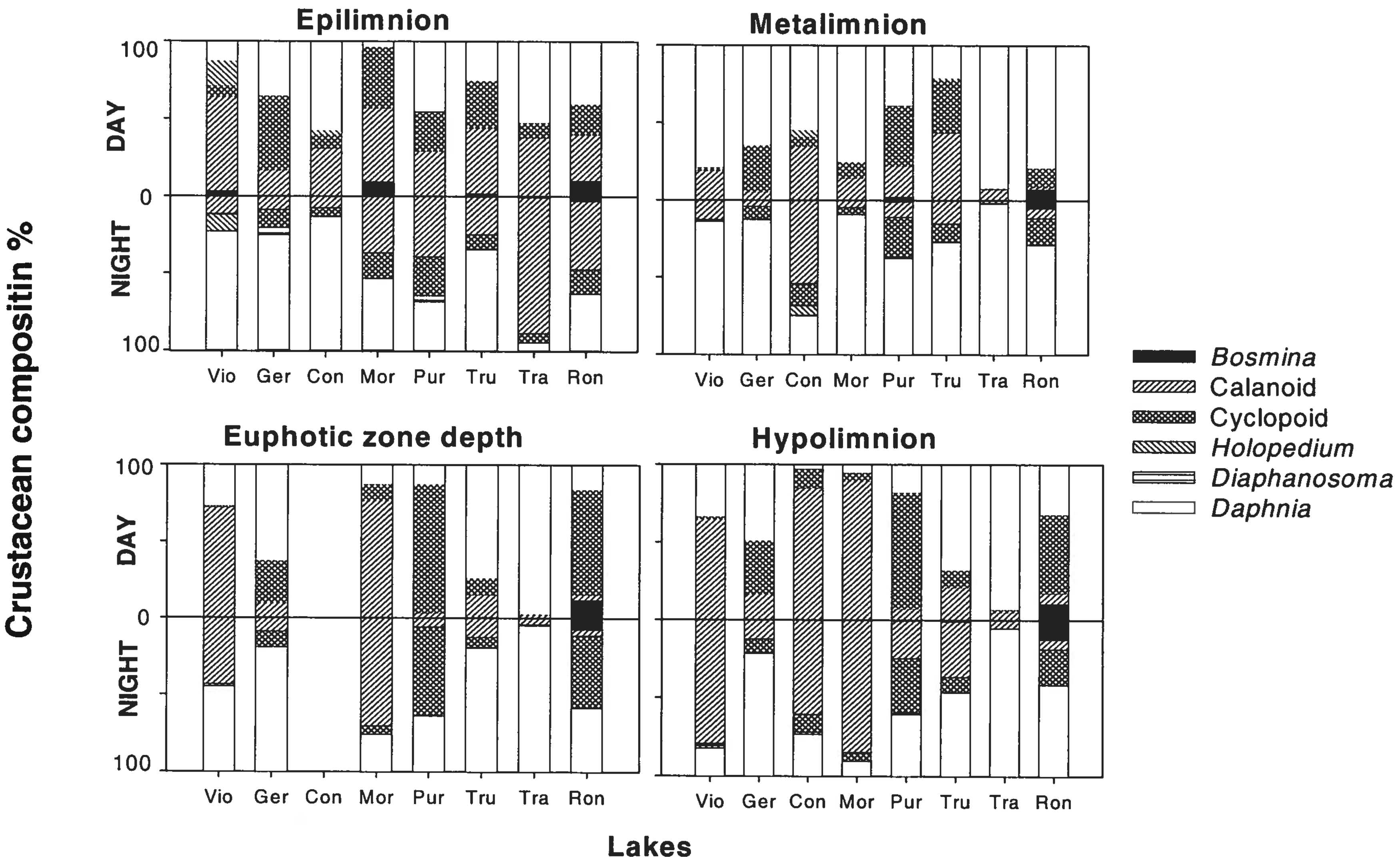
Epilimnion
Metalimnion
Euphotic zone depth
Hypolimnion
Crustacean compositin %
100
DAY
0
NIGHT
100
Vio
Ger
Con
Mor
Pur
Tru
Tra
Ron
Lakes
Bosmina
Calanoid
Cyclopoid
Holopedium
Diaphanosoma
Daphnia

Figure 5.4: *Daphnia* specie composition (%) of biomass during day and night in each 4 depth (epilimnion, metalimnion, 1% light depth and hypolimnion).

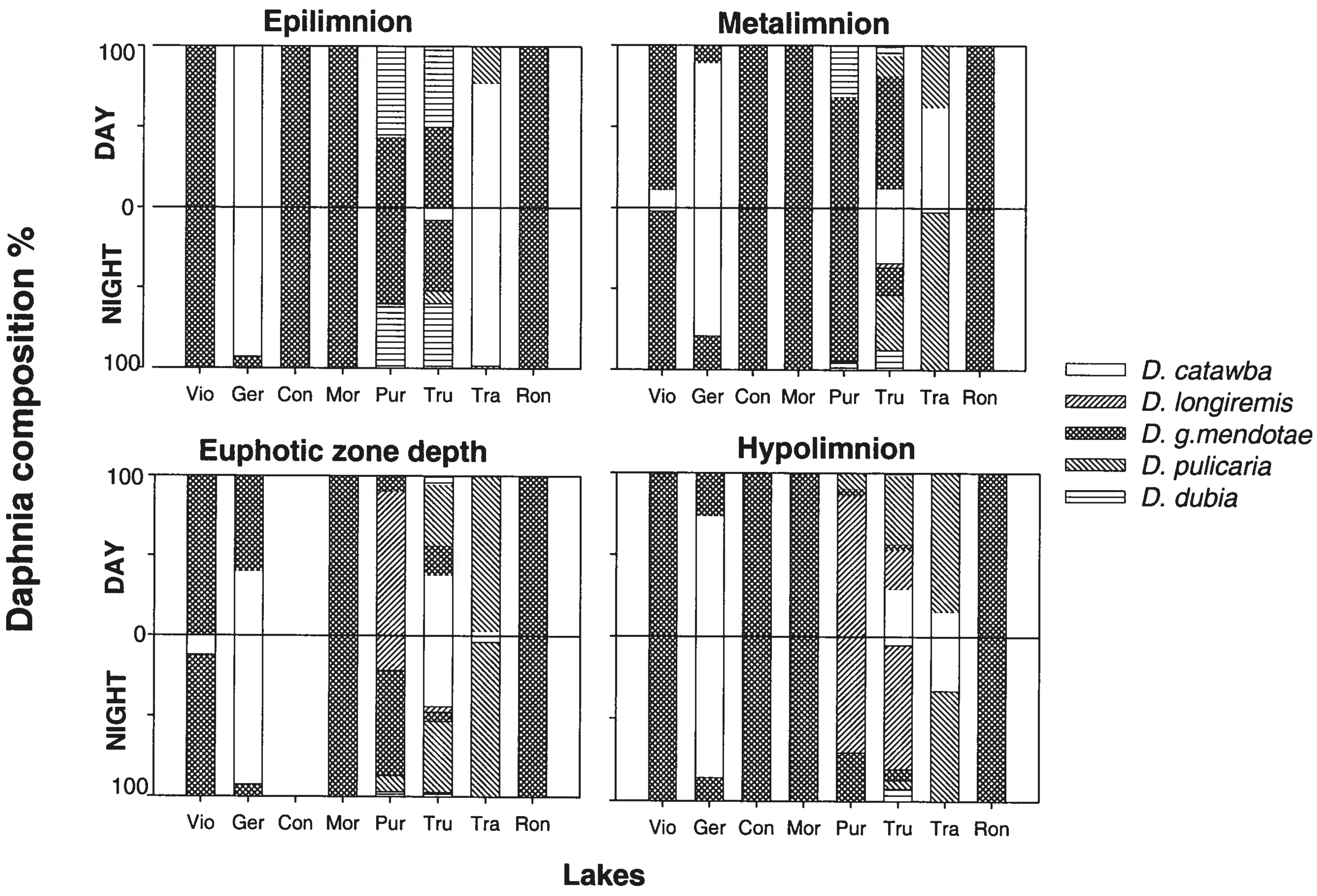
Epilimnion
Metalimnion
Euphotic zone depth
Hypolimnion
Daphnia composition %
DAY
NIGHT
100
0
100
Vio
Ger
Con
Mor
Pur
Tru
Tra
Ron
Lakes
D. catawba
D. longiremis
D. g.mendotae
D. pulicaria
D. dubia

Table 5-IV: Mean biomass of the terminal leaves from the multiple regression trees of the crustacean functional groups and the *Daphnia* species. Standard deviation is in brackets.

	Zooplankton						
	Bosmina	Calanoids	Cyclopoids	*Holopedium*	*Diaphanosoma*	*Daphnia*	*Explanatory variables*
Leaves							
1	0.01 (0.01)	12.99 (11.3)	1.38 (1.5)	0.25 (0.4)	0	4.48 (4.7)	EZ < 9; Depth > 6.5
2	0.04 (0.1)	10.16 (18.2)	2.32 (2.4)	0.37 (0.2)	0	10.66 (13.4)	EZ < 9; Depth < 6.5; Day
3	0.01 0.0)	3.62 (2.5)	1.45 (1.5)	1.33 (2.5)	0	31.20 (21.6)	EZ < 9; Depth < 6.5; Night
4	1.21 (1.5)	2.22 (1.6)	21.18 (15.9)	0	0.01 (0.0)	14.20 (13.8)	EZ > 9; Chla > 4
5	0.29 (0.5)	5.15 (4.2)	2.63 (3.2)	0.06 (0.1)	0.14 (0.1)	7.01 (5.4)	EZ > 9; Chla > 4; Depth < 5
6	0.21 (0.5)	2.73 (2.5)	2.73 (3.2)	0.26 (0.8)	0.03 (0.1)	22.86 (41.0)	EZ > 9; Chla > 4; Depth > 5

	Daphnia					
Leaves	*D. catawba*	*D. longiremis*	*D. g.mendotae*	*D. pulicaria*	*D. dubia*	
1	5.05 (5.7)	3.44 (2.1)	2.67 (6.0)	3.11 (4.7)	0.37 (0.3)	Drv < 1; OW > 7; Depth < 10.25
2	2.12 (2.9)	1.57 (4.0)	8.25 (10.2)	1.61 (2.5)	2.44 (1.6)	Drv < 1; OW > 7; Depth > 10.25
3	8.91 (6.8)	0	1.75 (1.5)	0.88 (0.5)	0	Drv < 1; OW < 7; TDP < 2
4	6.70 (13.6)	0	0	42.38 (76.1)	0	Drv < 1; OW < 7; TDP > 2
5	4.89 (7.7)	0	10.68 (14.1)	0	0	Drv > 1

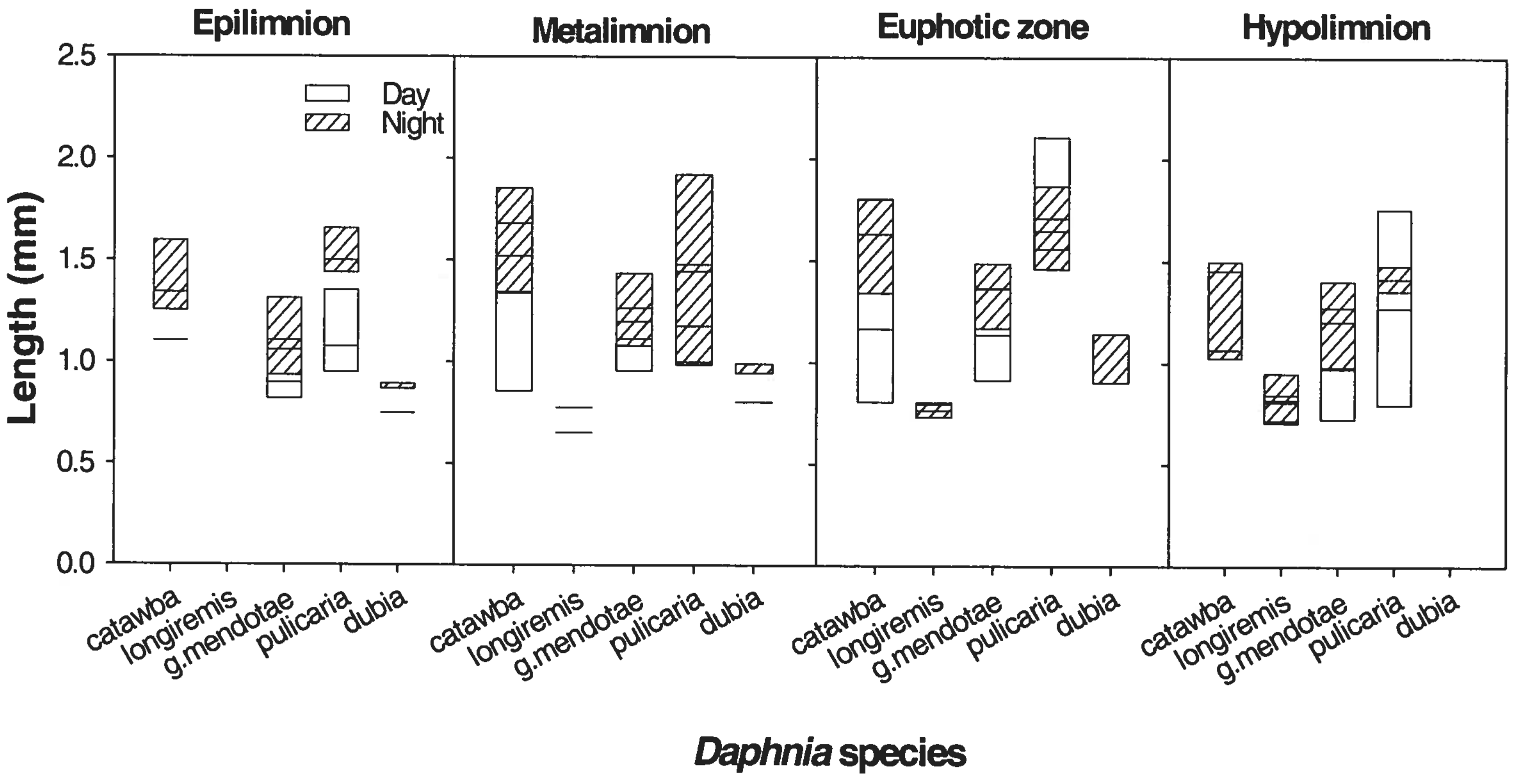

Figure 5.5: Box-plot of mean body size (mm) of *Daphnia* species in each 4 depths (epilimnion, metalimnion, euphotic zone and hypolimnion).

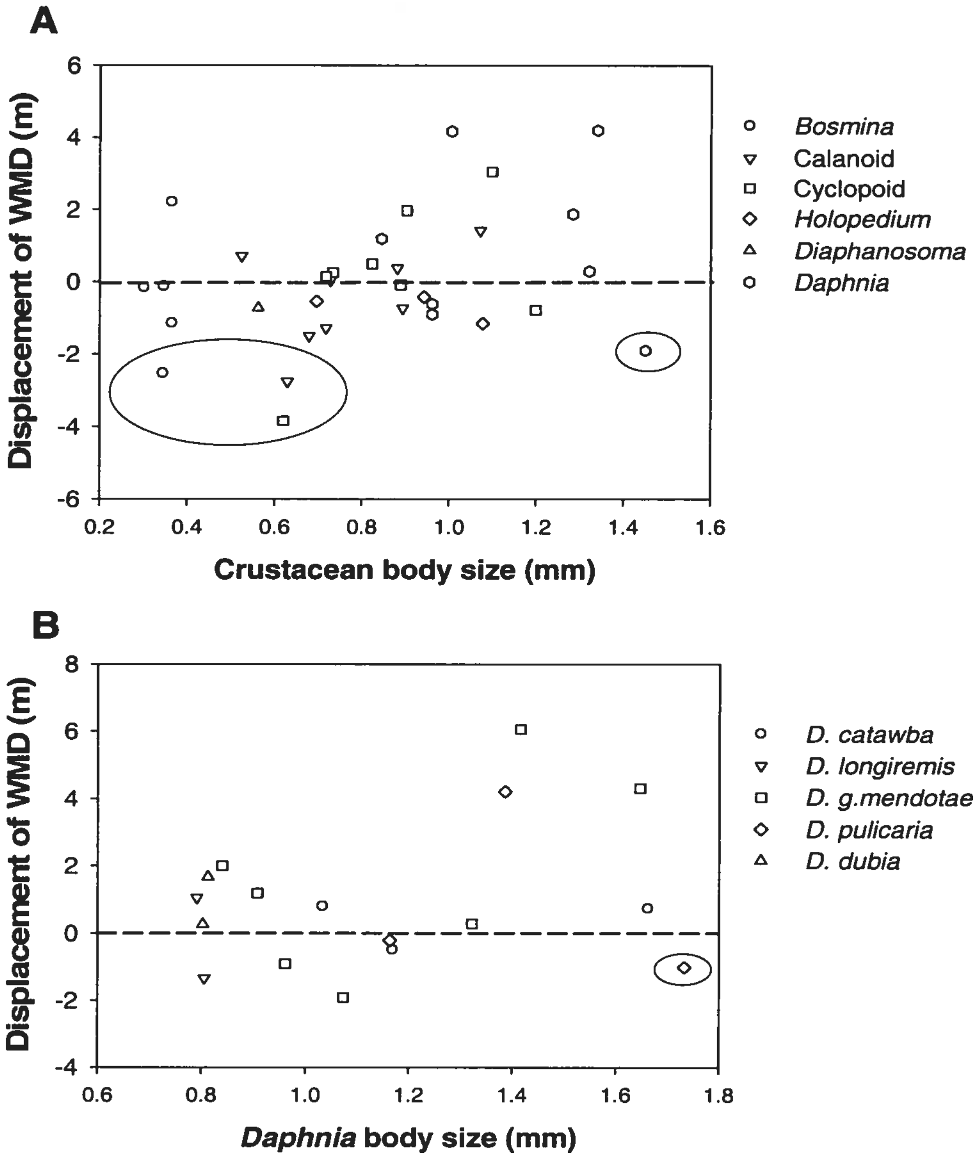

Figure 5.6: Weighted mean depth (WMD) displacement between daytime and night time in relation to body size (mm) for A) each crustacean functional group and B) *Daphnia* species. Positive displacement indicates a lower residence depth during daytime, inversely for negative displacement. The circled dots represent negative diel migration behaviour of functional groups (A) and *D. pulicaria* (B) in Lake Tracy.

5.4.4 Environmental control of depth selection and DVM patterns

Multiple linear regressions showed that depth selection patterns of both crustacean groups and *Daphnia* species were influenced by three abiotic variables (temperature, euphotic zone depth, oxygen) (eqs. 1-4). Overall, the models explained more than 87 % of the variation in WMD of functional groups (eq. 1) and more than 74% of the variation in WMD of *Daphnia* species (eq. 3) during day time. The models were even better for explaining depth distribution patterns during night with more than 86% of WMD variation explained (eqs. 2-4). Water temperature was positively correlated to WMD and accounted for a major proportion (58-78%) of the explained variation. The relative influence of the depth of the euphotic zone and oxygen was weaker, explaining 7-10% and 2-8% respectively (eqs. 1-4). Crustacean zooplankton avoided warm and clear surface waters and tended to stay in cold and less oxygenated deep waters both at day and night times. They also stay deeper in lakes with greater euphotic zone. Regression analysis of our data set yielded the following relationships:

Eq. 1: $FG_{DAY} = 10.035 \pm 0.453 - 0.387 \pm 0.032\ T^* + 0.453 \pm 0.083\ EZ^* - 0.245 \pm 0.091\ O_2^*$

$(r^2 = 0.74) \qquad (r^2 = 0.09) \qquad (r^2 = 0.05)$

Eq. 2: $FG_{NIGHT} = 8.722 \pm 1.127 - 0.378 \pm 0.029\ T^* + 0.470 \pm 0.078\ EZ^* - 0.235 \pm 0.090\ O_2^*$

$(r^2 = 0.78) \qquad (r^2 = 0.10) \qquad (r^2 = 0.02)$

Eq. 3: $D_{DAY} = 9.991 \pm 3.873 - 0.407 \pm 0.172\ T^* + 0.642 \pm 0.285\ EZ^* - 0.500 \pm 0.234\ O_2^*$

$(r^2 = 0.58) \qquad (r^2 = 0.07) \qquad (r^2 = 0.08)$

Eq. 4: $D_{NIGHT} = 10.463 \pm 2.675 - 0.358 \pm 0.083\ T^* + 0.424 \pm 0.191\ EZ^* - 0.389 \pm 0.115\ O_2^*$

$(r^2 = 0.72) \qquad (r^2 = 0.10) \qquad (r^2 = 0.05)$

Multivariate regression trees (MRT) explained 70.8% of the total variation in the biomass of crustacean functional groups and formed 6 distinct leaves, some of which contained as few as 10-11 observations (Fig. 5.7) and represented a fairly effective prediction (CV error = 0.633). More information on samples (lake, sampling depth and time) included in each leaf is presented in the Appendix 5.1. The depth of the euphotic zone (EZ), chlorophyll *a* concentration (Chl *a*), sampling depth (depth) and time of sampling (day or night) were the 4 explanatory variables included in the model. The first node (node 1) was associated to the depth of the euphotic zone (EZ) and accounted for 36% of the explained variance. It distinguished crustacean communities accordingly to lake water transparency and light transmission. On the left side of the tree, crustacean communities in lakes with EZ less than 9 m (Morency, Connelly and Violon) were dominated by calanoids and *Daphnia* (Table 5-IV, Appendix 5.1). The second node (node 2) was associated with sampling depth and accounted for 12% of the explained variance and the node 3 separated day and night samples and accounted for 9% of the explained variance. In deeper strata (depth > 6.5 m), calanoids were the most important (leaf 1), whereas in surface waters (depth < 6.5 m) *Daphnia* became more abundant, especially at night (leaves 2 and 3) (Table 5-IV). On the right side of the tree (node 1), crustacean communities in lakes with EZ deeper than 9 m (Rond, Gervais, Truite, Tracy, and Purvis) were dominated either by cyclopoids (leaf 4) or daphnids (leaves 5 and 6) depending of algal concentration (Chl. *a*, node 4, 10% of the explained variance). Node 5 associated to depth accounted for 4% of the explained variance. Cyclopoids were dominant in lakes Rond and Purvis having Chl. *a* concentration higher than 4 $\mu g.L^{-1}$ (leaf 4), while *Daphnia* were more abundant in lakes with lower algal concentration (Chl. a < 4 $\mu g.L^{-1}$) in surface (leaf 5) or deep (leaf 6) strata (Table 5-IV).

MRT explained 86% of the total variance in *Daphnia* species biomass and formed 5 leaves (Fig. 5.8) and represented a good prediction (CV error = 0.321). Drainage area/lake volume ratio (Drv), land-cover disturbance within the watershed (LCDW), total dissolved phosphorus (TPD), and depth of sampling (Depth) were the 4 explanatory variables included in the model. The first node (node 1) associated to the drainage area /lake volume ratio (Drv) accounted for 49% of the explained variance. In the left side of the tree, lakes with a Drv smaller than 1 were subdivided in 4 leaves accordingly to land-cover disturbance within the watershed (LCDW) (node 2: 15% of explained variance), and subsequently to the sampling depth (node 3: 15%) and TDP concentrations (node 4: 6.5%). Samples included in leaves 1 and 2 showed the more diverse *Daphnia* assemblages, with all 5 species present (Table 5-IV). They correspond to deep (leaf 1: euphotic zone depth, hypolimnion) and upper (leaf 2: epilimnion and metalimnion) strata of the lakes Truite and Purvis (Appendix 5.2). The small *D. longiremis* and *D. g. mendotae*, as well as the large *D. pulicaria* and *D. catawba* were more abundant in the leaf 1, whereas the small *D. g.mendotae* and *D. dubia* were more important in the leaf 2 (Table 5-IV). Leaves 3 and 4 corresponded to lakes Gervais and Tracy (Appendix 5.2); they were characterised by the dominance of large *Daphnia*. Leaf 3 was mainly composed of all samples from the nutrient-poor and clear Lake Gervais and the epilimnion samples of Lake Tracy where *D. catawba* was the dominant specie. Leaf 4 corresponded to all metalimnion and hypolimnion samples of Lake Tracy where *D. pulicaria* was the dominant species. On the right side of the three, 4 lakes (Morency, Connelly, Rond and Violon) had a Drv greater than 1 and formed a large cluster of samples (leaf 5: 54 samples) composed only of two *Daphnia* species (*D. g.mendotae*, D. *catawba*), the smallest being dominant (Table 5-IV).

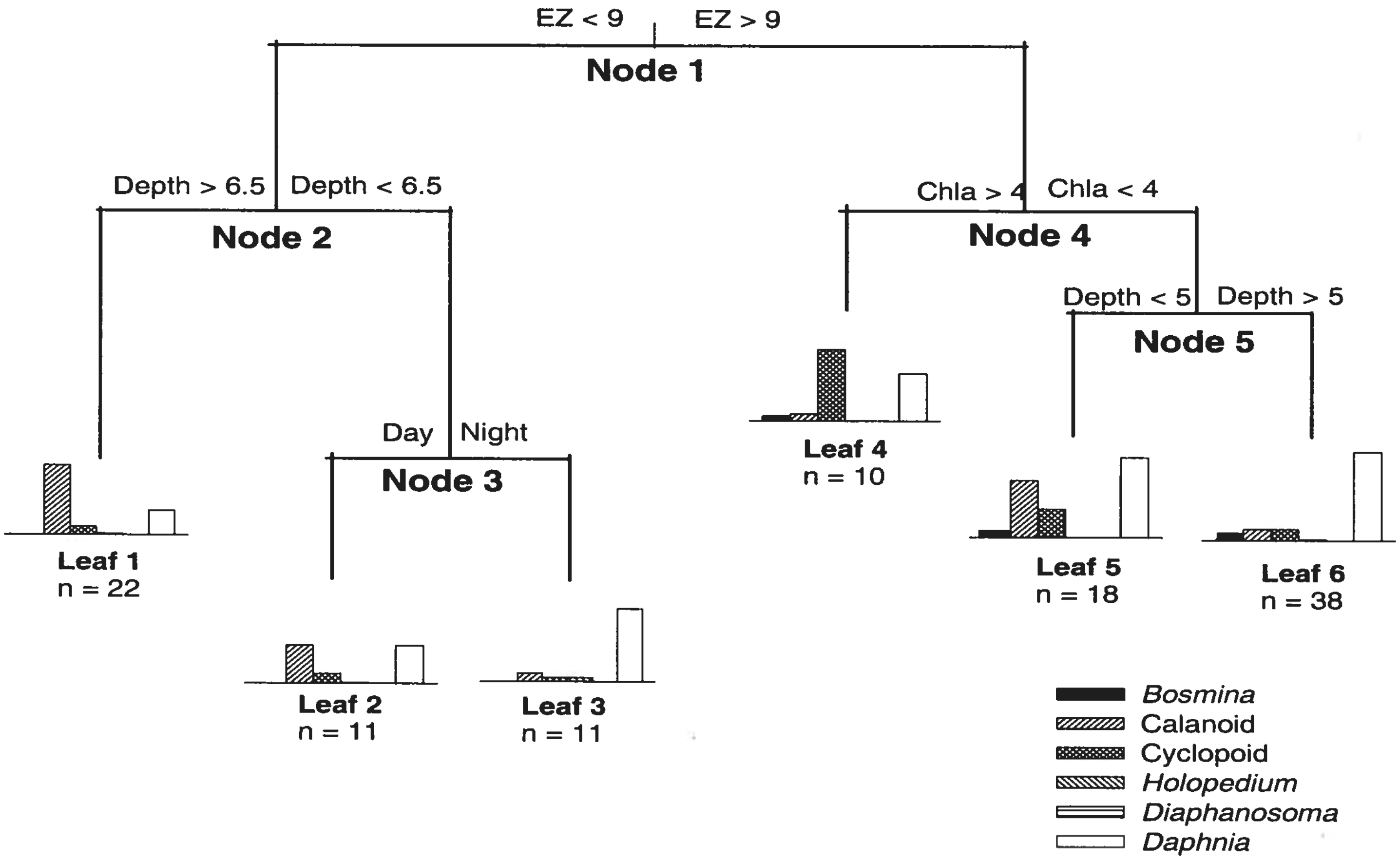

Figure 5.7: Multivariate regression tree of the crustacean functional groups. n = sample size into the leaf.

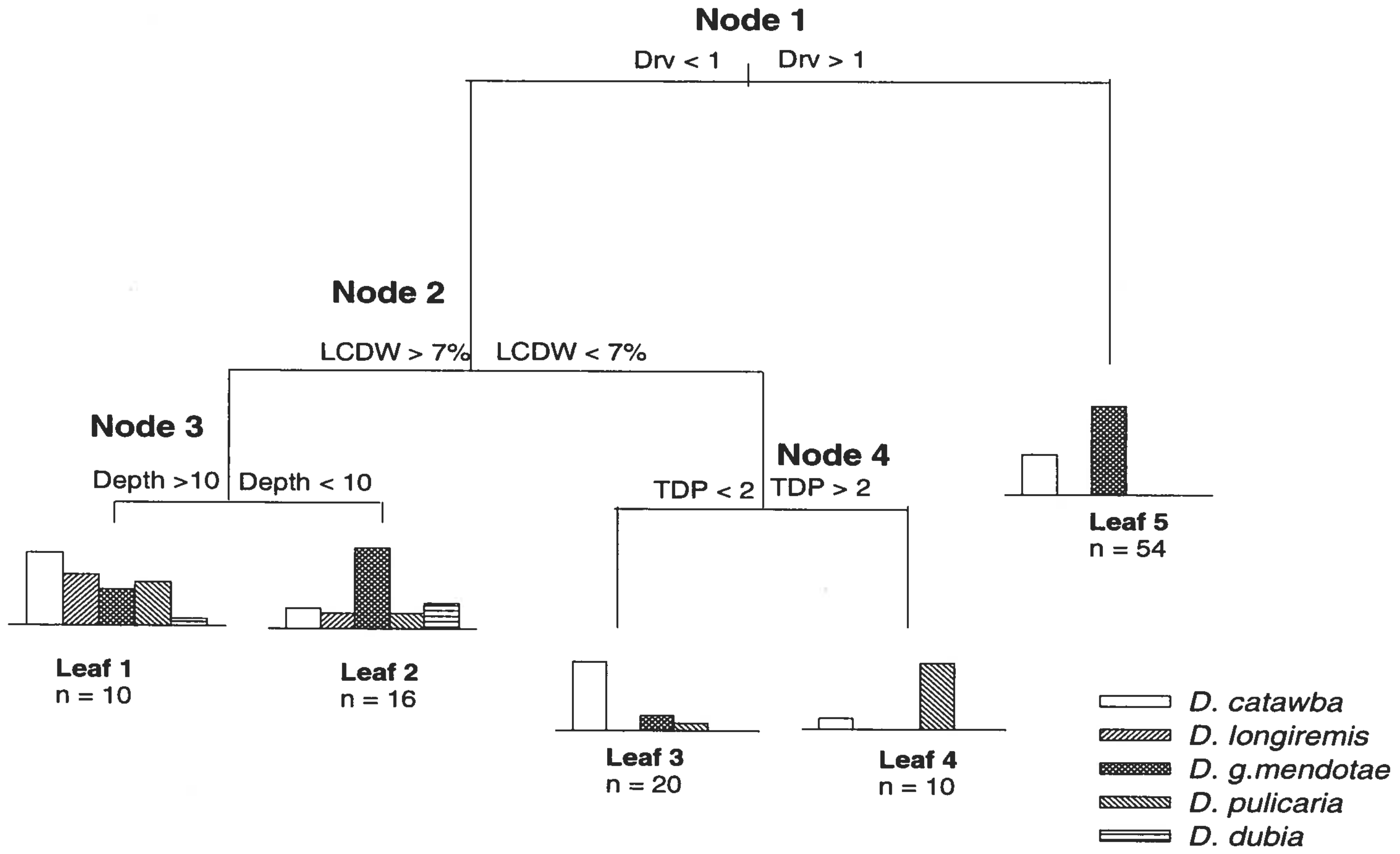

Figure 5.8: Multivariate regression tree of the *Daphnia* species. n= sample size into the leaf.

5.5 Discussion

Our study gives support for the hypothesis that water physicochemical stratification governs depth selection patterns of crustacean functional groups. As suggested by Loose & Dawidowcz (1994), temperature is a key factor regulating the depth selection, as seen in our study where crustaceans and *Daphnia* tended to avoid warm surface waters. Avoiding surface does not imply that this behaviour evolved to avoid high temperatures since the metabolism of heterothermic animals is governed by temperature; reproduction and all physiological processes are temperature dependent. It rather evolved to cope with other circumstances related to the surface temperature like evading high predation threat. Even though, our study design did not allow us to clearly evaluate the impacts of biological factors such as predation pressure, others studies have shown that predation as well as food availability, water clarity, oxygen concentration all counted in structuring depth selection patterns and DVM behaviour of crustaceans and *Daphnia* species (Winder, Spaak & Mooij, 2004; Muluk & Beklioglu, 2005). Several other abiotic factors like water transparency, thermocline depth, chlorophyll *a* deep maxima, and annual fish stocking were also reported to influence mean depth residence of *D. galeata* in a high mountain lake (Winder, Spaak & Mooij, 2004). In our study, oddly, thermocline and Secchi disk depth, chlorophyll *a* or total phosphorus did not improve the prediction of depth residence selection.

Our study suggested some interactions between depth residence selection patterns and crustacean body size. Only the small cladocerans like *Bosmina* and small *Daphnia* (*D. Dubia*, *D. g. mendotae*) as well as gelatinous species as *Holopedium* less vulnerable to fish predation tended to distribute in warmer upper strata compared to large *Daphnia* (*D. pulicaria*; *D. catawba*). The difference in mean selection depth between small and large-bodied species might be explained in part by size-selective predation strategy avoidance (Brooks & Dodson, 1965; Leibold, 1991; De Meester *et al.*, 1999). This is reinforced by the fact that in the most transparent lake (Gervais: Secchi disk = 12m), crustacean stayed deeper. However, this relationship may also reflect, in combination with low algal concentration, the grazing pressure of *Daphnia* and its consequence on water clarity since the large *D. pulicaria* was the dominant specie in Lake Gervais. *Daphnia* are unspecific filter feeders that graze large amount of algae and increase water transparency (Kasprzak, Lathrop & Carpenter, 1999; Kreutzer & Lampert 1999; Lathrop, Carpenter & Robertson, 1999; Tessier, Bizina & Geedey, 2001).

The similarity in depth distribution patterns among day and night that we observed in some lakes could be explained either by our sampling scale (only 4 depths distanced by several meters) that did not allow to assess fine-scale distribution patterns (Pearre 2003) or by the consistence in resource availability and distribution among lakes (Pijanowska & Dawidowicz, 1987). However, our study gives some evidence of diel vertical migration (DVM) behaviour in four lakes. One interesting result is the inverted DVM pattern occurrence observed in Lake Tracy due to high populations of chaoborid larvae, as already shown by Tollrian & Harvell (1999). In Lake Tracy, WMD of *Chaoborus* larvae was around 11.4 m during the day and most crustacean functional groups stayed above 10 m to evade the predation pressure.

MTR approach was a successfully approach in relating depth selection patterns of crustacean functional groups to physicochemical, biological and anthropogenic factors. For the crustacean functional groups, the key driving factors were the euphotic zone depth, day or night time sampling, sampling depth and chlorophyll *a* concentration. These factors are also contributing to *Daphnia* vertical distribution and diurnal migration patterns reported in other studies (De Meester *et al.*, 1999; Ringelberg, 1999; Van Gool & Ringelberg, 2002; Winder, Spaak & Mooij, 2004). As seen with regression analysis, depth selection patterns of crustaceans were primarily governed by the depth of the euphotic zone. Higher euphotic depth extending deeper than the thermocline allow enough light to reach the upper layers of the hypolimnion and can trigger the formation of deep chlorophyll maxima, as seen in some of our lakes (Pinel-Alloul, Gélinas & Ghadouani, 2007). The presence of these deep layers of algal resources presumably accounted for the vertical distribution of most crustaceans and *Daphnia* in the metalimnion and at the depth of the euphotic zone. Hence, food availability can also be one mechanism that drives their depth residence within the water column. There were at least three more variables that help explaining the clustering of the crustacean functional groups. The depth, more precisely, 6.5 m which in most Laurentian lakes corresponds or is relatively close to the thermocline which is a variable known to regulate mean depth distribution (Winder, Spaak & Mooij, 2004). In our study, crustacean depth residence was deeper than the thermocline and large crustaceans (*Daphnia*, copepods) made upward DVM in the most transparent lakes (Gervais, Truite, Tracy). The most plausible explanation might be to decrease their vulnerability to planktivorous or invertebrate predation (Lampert, 1989; Ringelberg, 1999; Van Gool & Ringelberg, 2002; Ringelberg & Van Gool, 2003) or to avoid ultraviolet light (Alonso, Rocco & Barriga, 2004; Persaud & Williamson, 2005). In lakes with the euphotic zone deeper than 9 meters, *Daphnia* dominance was associated to lower chl. *a* probably due to its high grazing potential (Soranno et al., 1993; Kasprzak, Lathrop & Carpenter, 1999; Lathrop, Carpenter & Robertson, 1999). In contrast, in two transparent lakes (Rond and Purvis) with chl. *a* biomass higher than 4 $\mu g.L^{-1}$ cyclopoids were dominant. McLauren (1974) proposed demographic advantages for marine copepods living at lower temperature under high food conditions. MRT leaves of crustacean functional groups showed that high biomass of *Bosmina* was found in leaf 4, in association with higher chl. *a* concentration. This species was found to be related to eutrophic conditions (Sommer *et al.*, 1986) or to watershed disturbance by residential development (Gélinas & Pinel-Alloul, 2007).

For *Daphnia* species, the key factors in MRT were drainage area/lake volume ratio, total dissolved phosphorus, land-cover disturbance within the watershed and sampling depth. Lakes with drainage area /lake volume greater than 1 contained only two *Daphnia* species (*D. g.mendotae* and *D. catawba*). In lakes with drainage area/lake volume smaller than 1, the presence of cottages, roads, lawns and ski hills within the watershed (open area) increase the amount of nutrient entering the lake (Dodson, Lillies & Will-Wolf, 2005). In those disturbed lakes, habitat partitioning separated *Daphnia* species based on their body size. Higher biomass of the small *Daphnia* species, (*D. g.mendotae* and *D. dubia*) were mostly found above the euphotic zone depth, whereas large *Daphnia* (*D. catawba* and *D. pulicaria*) were found in deeper strata. Small-sized *Daphnia* species are less susceptible to fish planktivores that visually select larger body size prey than large-sized *Daphnia* (Brooks & Dodson, 1965; Tollrian & Dodson, 1999). Furthermore, in lakes with low land-cover disturbance in their watershed and low TDP concentrations, *D. catawba* dominated over *D. pulicaria*. Thus *D. catawba* seems to be associated with more pristine conditions than *D. pulicaria*. The most surprising results of all may be that catchment effects are felt at the species level (*Daphnia*) but not at the functional group level. The higher density of roads on disturbed catchment might be one factor that facilitate the establishment of *Daphnia* due to salt spreading in winter to prevent ice-formation. Calcium is a required element in *Daphnia* moulting (Hessen & Alstad, 2000).

Multivariate regression trees (MTR) are powerful tools for clustering crustacean communities based on the biomass of functional groups in relation to natural and anthropogenic environmental variables. Furthermore, this method allowed us to use dependent variables correlated among themselves (Larsen & Speckman, 2004) and did not assume linearity between explanatory variables and species (De'ath, 2002). Our MTR approach allows us to demonstrated more clearly how small changes in morphometric (drainage ratio), physicochemical (water transparency and nutrients), biological (algal concentration) and anthropogenic (land-cover disturbance) conditions of lakes can govern both the composition and depth residence of crustacean zooplankton in still nutrient-poor canadian shield lakes. Indeed, human disturbances within lake watersheds have cascading bottom-up effects on water nutrient enrichment that could indirectly influence crustacean zooplankton community (Dodson, Lillies & Will-Wolf, 2005; Gélinas & Pinel-Alloul, 2007). Therefore, as seen in this study with the MTR models, depth selection patterns of crustacean zooplankton are governed by a combination of factors related to the vertical heterogeneity in the water column associated to human disturbances within the watershed, unexpectingly at the specie level.

5.6 Acknowledgements

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5.7 Appendices

Appendix 1. Composition of leaves in the MRT model for crustacean functional groups. Legends represent the lake, the depth and the time of sampling (d = day, n = night). Abbreviations of the lakes: Mor = Morency, Con = Connelly, Vio = Violon, Ron = Rond, Pur = Purvis, Ger = Gervais, Tru = Truite and Tra = Tracy.

Leaf 1	**Leaf 2**	**Leaf 3**	**Leaf 4**	**Leaf 5**	**Leaf 6**	
Mor 8.5 d	Mor 1.5 d	Mor 1.5 n	Ron 9.5 d	Ger 1 d	Ger 5.5 d	Ron 6.5 d
Mor 13 d	Mor 3.5 d	Mor 3.5 n	Ron 12 d	Ger 2.5 d	Ger 8 d	Ron 6.5 n
Mor 17.5 d	Mor 5.5 d	Mor 5.5 n	Ron 9.5 n	Ger 1 n	Ger 10.5 d	Tru 5.5 d
Mor 8.5 n	Con 1 d	Con 1 n	Ron 12 n	Ger 2.5 n	Ger 16.5 d	Tru 11 d
Mor 13 n	Con 2 d	Con 2 n	Tru 8 d	Tra 2 d	Ger 20 d	Tru 15 d
Mor 17.5 n	Con 4 d	Con 4 n	Pur 9.5 d	Tra 4 d	Ger 24.5 d	Tru 17 d
Con 7 d	Vio 1.5 d	Vio 1.5 n	Pur 11.5 d	Tra 2 n	Ger 5.5 n	Tru 5.5 n
Con 10 d	Vio 2.5 d	Vio 2.5 n	Pur 15 d	Tra 4 n	Ger 8 n	Tru 8 n
Con 12.5 d	Vio 4 d	Vio 4 n	Pur 9.5 n	Ron 0.5 d	Ger 10.5 n	Tru 11 n
Con 15 d	Vio 5 d	Vio 5 n	Pur 11.5 n	Ron 3.5 d	Ger 16.5 n	Tru 15 n
Con 7 n	Vio 6 d	Vio 6 n		Ron 0.5 n	Ger 20 n	Tru 17 n
Con 10 n				Ron 3.5 n	Ger 24.5 n	Pur 5.5 d
Con 12.5 n				Tru 3 d	Tra 6.5 d	Pur 6.5 d
Con 15 n				Tru 3 n	Tra 9.5 d	Pur 5.5 n
Vio 8 d				Pur 1.5 d	Tra 12 d	Pur 6.5 n
Vio 10.5 d				Pur 3.5 d	Tra 15 d	Pur 15 n
Vio 12.5 d				Pur 1.5 n	Tra 17.5 d	
Vio 15 d				Pur 3.5 n	Tra 6.5 n	
Vio 8 n					Tra 9.5 n	
Vio 10.5 n					Tra 12 n	
Vio 12.5 n					Tra 15 n	
Vio 15 n					Tra 17.5 n	

Appendix 2. Composition of leaves in the MRT of *Daphnia* species. Legends represent the lake, the depth and the time of sampling (d = day, n = night). Abbreviations of the lakes are: Mor = Morency, Con = Connelly, Vio = Violon, Ron = Rond, Pur = Purvis, Ger = Gervais, Tru = Truite and Tra = Tracy.

Leaf 1	**Leaf 2**	**Leaf 3**	**Leaf 4**	**Leaf 5**	
Tru 11 d	Tru 3 d	Ger 1 d	Tra 6.5 d	Mor 1.5 d	Ron 0.5 d
Tru 15 d	Tru 5.5 d	Ger 2.5 d	Tra 9.5 d	Mor 3.5 d	Ron 3.5 d
Tru 17 d	Tru 8 d	Ger 5.5 d	Tra 12 d	Mor 5.5 d	Ron 6.5 d
Tru 11 n	Tru 3 n	Ger 8 d	Tra 15 d	Mor 8.5 d	Ron 9.5 d
Tru 15 n	Tru 5.5 n	Ger 10.5 d	Tra 17.5 d	Mor 13 d	Ron 12 d
Tru 17 n	Tru 8 n	Ger 16.5 d	Tra 6.5 n	Mor 17.5 d	Ron 0.5 n
Pur 11.5 d	Pur 1.5 d	Ger 20 d	Tra 9.5 n	Mor 1.5 n	Ron 3.5 n
Pur 15 d	Pur 3.5 d	Ger 24.5 d	Tra 12 n	Mor 3.5 n	Ron 6.5 n
Pur 11.5 n	Pur 5.5 d	Ger 1 n	Tra 15 n	Mor 5.5 n	Ron 9.5 n
Pur 15 n	Pur 6.5 d	Ger 2.5 n	Tra 17.5 n	Mor 8.5 n	Ron 12 n
	Pur 9.5 d	Ger 5.5 n		Mor 13 n	Vio 1.5 d
	Pur 1.5 n	Ger 8 n		Mor 17.5 n	Vio 2.5 d
	Pur 3.5 n	Ger 10.5 n		Con 1 d	Vio 4 d
	Pur 5.5 n	Ger 16.5 n		Con 2 d	Vio 5 d
	Pur 6.5 n	Ger 20 n		Con 4 d	Vio 6 d
	Pur 9.5 n	Ger 24.5 n		Con 7 d	Vio 8 d
		Tra 2 d		Con 10 d	Vio 10.5 d
		Tra 4 d		Con 12.5 d	Vio 12.5 d
		Tra 2 n		Con 15 d	Vio 15 d
		Tra 4 n		Con 1 n	Vio 1.5 n
				Con 2 n	Vio 2.5 n
				Con 4 n	Vio 4 n
				Con 7 n	Vio 5 n
				Con 10 n	Vio 6 n
				Con 12.5 n	Vio 8 n
				Con 15 n	Vio 10.5 n
					Vio 12.5 n
					Vio 15 n

Chapitre 6

Conclusion générale

Le zooplancton module les interactions entre les niveaux trophiques et la dynamique des réseaux pélagiques lacustres. En particulier, les daphnies par leur double rôle de brouteur généraliste sur le phytoplancton et de proie préférée des poissons et des invertébrés ont un rôle crucial et intégrateur aux niveaux des effets ascendants ‵bottom-up' et descendants ‵top-down' dans les réseaux trophiques lacustres. Elles jouent également un rôle primordial dans le maintien de la transparence de l'eau des lacs. Les daphnies étant des proies sélectionnées par les prédateurs planctonophages, elles développent des réponses adaptatives qui réduisent les effets de la prédation et leur permettent de survivre. Ces réponses sont spécifiques aux types de prédateurs présents dans le milieu. De plus, un prédateur peut déclencher différentes réponses adaptatives; les plus connues sont des modifications des traits morphologiques et démographiques ou du comportement, communément reconnue comme la plasticité phénotypique. La recherche visait à définir les réponses adaptatives des crustacés, et des daphnies en particulier, vis-à-vis des facteurs naturels (ressources algales, prédation) et anthropiques (développement résidentiel) et leurs conséquences sur la dynamique des réseaux trophiques pélagiques des lacs du Québec.

Cette thèse comporte un premier volet (Chapitre 2) qui apporte une nouvelle perspective sur la plasticité phénotypique des daphnies, en particulier leurs capacités d'adaptation face aux changements spatiaux et temporels des facteurs naturels liés à l'impact des prédateurs. L'originalité de ce volet résulte de l'approche *in situ* en milieu naturel adoptée pour l'étude des impacts de la prédation des jeunes perchaudes de l'année et des invertébrés planctoniques. En effet, jusqu'alors, la vaste majorité des études ont été menées en laboratoire dans des conditions expérimentales qui sont peu représentatives des conditions naturelles et elles utilisaient des kairomones de poissons adultes (substances chimiques associées aux excrétas des poissons) pour simuler la présence des prédateurs. De surcroît, peu d'études se sont intéressées aux adaptations des daphnies dans un contexte naturel en mesurant les effets directs de la prédation par les jeunes poissons. La pression de prédation exercée par les jeunes poissons de l'année, tels les larves de perchaudes, varie au cours de la saison estivale en fonction de leur développement ontogénique et de leur croissance. Les jeunes perchaudes, contrairement aux adultes, ont un impact majeur mais bref sur les crustacés pélagiques. Dès lors, la survie des daphnies repose en grande partie sur leur capacité à s'adapter à ces prédateurs en modifiant leurs traits morphologiques et démographiques ou leur comportement migratoire. Leur grande plasticité phénotypique leur permet de s'adapter spécifiquement aux prédateurs présents dans leur milieu. Les poissons et les invertébrés prédateurs sont deux types de prédateurs des daphnies qui leur imposent des contraintes différentes.

Dans ce contexte, nous avons étudié les réponses adaptatives de deux populations de daphnies coexistant dans le milieu pélagique du lac Brome vis-à-vis de la prédation par les jeunes perchaudes de l'année et les invertébrés Chaoboridés. Deux espèces de daphnies ayant une taille différente sont retrouvées dans le lac Brome, une espèce de grande taille, *D. pulicaria,* et une espèce de petite taille, *D. g.mendotae*. Les deux espèces sont soumises à une prédation brève mais intense de la part des jeunes perchaudes âgées d'environ 6 semaines. Suivant l'hypothèse de la sélection de prédation positive, les espèces de daphnies de grande taille, les plus visibles, devraient être celles sélectionnées par les jeunes perchaudes. Nos résultats (Chapitre 2) indiquent qu'au contraire, ceux sont les juvéniles des deux espèces de daphnies qui sont les proies préférées des jeunes perchaudes, et non les adultes ou seulement l'espèce de grande taille. Notre étude supporte l'hypothèse contraire de sélection négative des daphnies par les jeunes perchaudes de taille inférieure à 15 mm. Les jeunes perchaudes de moins de 15 mm sont limitées par la petitesse de l'ouverture buccale qui est proportionnelle à leur taille. Elles ne peuvent pas ingérer les daphnies de taille supérieure à 1.75 mm. La croissance des jeunes perchaudes de la taille de 15 mm jusqu'à 25 mm permet de relâcher la contrainte due à la petitesse de l'ouverture buccale; lorsqu'elles ont atteint une plus grande taille au milieu de l'été, elles peuvent alors ingérer des daphnies de plus grande taille. Pour contrer la prédation, les juvéniles et les adultes des deux espèces de daphnies ont d'abord eut recours à des réponses adaptatives de type comportemental. Les daphnies ont fuit les prédateurs dans les eaux de surface en nageant jusqu'à des profondeurs de 9 m en dessous de la zone euphotique, dans l'hypolimnion froid et désoxygéné inaccessible aux perchaudes. A l'inverse, vers la fin de la période de prédation à la mi-juillet, les daphnies résidaient à une plus faible profondeur et ont alors eu recours à des réponses adaptatives démographiques. Comme réponse adaptative, les daphnies adultes ont réduit leur taille à la maturité, ce qui diminuait la taille des femelles parthénogénétiques et les rendait moins vulnérables à la prédation sélective positive (sélection des grandes tailles) opérée par les jeunes perchaudes de 25 mm. De plus, la plus grande espèce de daphnie (*D. pulicaria*) a fait une diapause estivale et produite des œufs de durée (ephippium). Cette étude a démontré, pour la première fois en milieu naturel, la grande plasticité phénotypique des populations de daphnies qui utilisent en alternance des défenses démographiques et comportementales comme réponses adaptatives face à l'évolution ontogénique de l'impact de prédation des jeunes perchaudes de l'année. Les résultats de cette étude ont été publiés par la revue internationale « Journal of Plankton Research ».

Le chapitre 3 ajoute des éléments supplémentaires au chapitre 2. Nous avons testé l'hypothèse que la présence de différents types de prédateurs provoque chez les daphnies des réponses adaptatives spécifiques à chacun des types de prédateurs. En particulier, nous avons comparé en milieu naturel les défenses morphologiques développées par les deux espèces de daphnies en présence des deux types de prédateurs (vertébrés et invertébrés) dans le lac Brome. Progressivement, au cours de l'été, il y a eu apparition des prédateurs invertébrés, les larves de *Chaoborus* et le Cladocère *Leptodora kindtii*, qui se sont ajoutés à la prédation exercée par les jeunes perchaudes de l'année. Nos résultats indiquent que l'espèce de petite taille, *D. g.mendotae,* réagit fortement à la présence des prédateurs invertébrés, puisque ceux-ci sélectionnent préférentiellement les proies de petite taille. La défense morphologique produit par *D. g.mendotae* est une augmentation du capuchon céphalique, une extension de la tête qui augmente le degré de difficulté d'ingestion par les prédateurs invertébrés. Pour l'espèce de grande taille, *D. pulicaria*, la défense morphologique étudiée, l'élongation de l'épine caudale, n'était pas induite par la co-occurrence des prédateurs invertébrés et des jeunes perchaudes de l'année. Cette absence de réponses au niveau morphologique peut s'expliquer par le fait que cette espèce est trop grande pour être sélectionnée par les larves de Chaoboridés et qu'elle développait surtout des réponses adaptatives de type comportemental ou démographique pour contrer la prédation par les jeunes perchaudes de l'année, tel que démontré au chapitre 2. Les résultats de cette étude seront publiés par la revue internationale « Hydrobiologia ».

Les deux premiers chapitres de la thèse (2 et 3) mettent en évidence la grande plasticité phénotypique des réponses anti-prédateurs des daphnies dans le lac Brome face à la pression de prédation multiple et variable exercée par les jeunes perchaudes de l'année et les larves de Chaoboridés. La contribution majeure de notre étude est la mise en évidence en milieu naturel d'un processus de prédation sélective négative s'appliquant sur les juvéniles des deux espèces de daphnies, alors que le paradigme le plus reconnu est celui de la prédation sélective positive sur les espèces de daphnies de grande taille. Nous avons montré pour la première fois en milieu naturel et à l'intérieur d'un même lac, que les espèces de daphnies peuvent développer en alternance différentes stratégies pour contrer la prédation, telles que des défenses morphologiques, démographiques et comportementales. Malgré la cooccurrence de divers types de prédateurs dans le milieu naturel, l'espèce de daphnie de grande taille, *D. pulicaria*, n'a pas développé de défense morphologique, tandis que la petite espèce, *D. g.mendotae*, a développé des défenses morphologiques tout au long de l'été en réponse à la présence de prédateurs invertébrés. Par contre les deux espèces ont développé des défenses comportementales ou démographiques durant l'été en fonction de la variation temporelle de l'abondance et du type de sélection exercés par les prédateurs. Lorsque la disparition des jeunes perchaudes dans le milieu a relâché la pression de prédation qu'elles exerçaient sur les daphnies, les défenses probablement coûteuses devenues inutiles, ont disparu.

Le deuxième volet de la thèse apporte une contribution significative sur les réponses des crustacés planctoniques et des daphnies face au développement résidentiel sur le bassin versant et les rives des lacs du sud des Laurentides (chapitres 4 et 5). Le but final de ce volet de recherche est de voir si les communautés de crustacés planctoniques et les assemblages d'espèces de daphnies sont indicateurs du niveau de développement résidentiel et de perturbation humaine des bassins versants des lacs de villégiature de la zone boréale. La région des Laurentides a subi au cours des dernières deux décennies un accroissement accéléré du niveau d'urbanisation des lacs. Le niveau de développement résidentiel est reflété par la densité des habitations, la présence de routes, de golfs et d'infrastructures hôtelière et récréative (pentes de ski alpin) dans le paysage composé de vallées et montagnes. Notre étude a montré que l'abondance et la structure des crustacés zooplanctoniques étaient modifiées par les perturbations anthropiques du bassin versant (Chapitre 4). La communauté des crustacés pélagiques variait en fonction du niveau de développement résidentiel et de perturbation du territoire sur l'ensemble du bassin versant alors que le développement des zones riveraines en bordure des lacs n'avait pas une influence significative. Le niveau de phosphore total dans les lacs prédisait très bien l'augmentation de la biomasse des crustacés planctoniques le long du gradient de perturbation. L'apport en nutriments est un élément clef dans les cascades d'effets des perturbations du bassin versant sur les écosystèmes pélagiques des lacs des Laurentides.

Pour cette étude, nous avons adopté un modèle d'analyse en cascade (Chapitre 4) qui permet de relier les composantes anthropiques (développement résidentiel et pourcentage d'ouverture) aux groupes fonctionnels de crustacés à l'aide de relations directes et indirectes en passant par des éléments intermédiaires comme les apports en nutriments et l'augmentation de la biomasse algale. Bien que les deux composantes anthropiques influençaient les niveaux de phosphore total, l'effet du développement résidentiel était potentiellement plus important que celui du pourcentage d'aire ouverte dans le bassin versant. Les modèles de cascades démontrent justement l'importance du développement résidentiel sur l'enrichissement en phosphore à titre d'élément pivot ayant un effet direct sur la biomasse des groupes fonctionnels. Les réponses variaient toutefois selon les groupes fonctionnels de crustacés : la biomasse des Cladocères (*Bosmina, CerioDaphnia* et *Diaphanosoma*) et des petites daphnies (*D. g. mendotae, D. ambigua*) augmentaient avec l'enrichissement en phosphore le long du gradient de perturbation. Part contre, la biomasse des Calanoïdes et des grandes daphnies (*D. pulicaria, D. mendotae*) décroissait le long du gradient de perturbation. Les modèles en cascade n'étaient pas significatifs pour *Holopedium gibberum* et trois espèces de daphnies, *D. catawba*, *D. longiremis* et *D. dubia*. Les modèles en cascades pour les espèces de daphnies montraient que les hausses de phosphore étaient associés à des hausses de biomasses des petites daphnies (*D. g. mendotae* et *D. ambigua*) et à une baisse pour les grandes daphnies (*D. pulicaria*). Toutefois, les modèles en cascades liant les niveaux de perturbations aux caractéristiques des communautés de crustacés pélagiques expliquaient moins de la moitié de la variance totale, ce qui suggère que d'autres facteurs comme la planctivorie pouvaient aussi influencer les communautés de crustacés planctoniques.

La partition de la variance expliquée par les facteurs naturels et anthropiques variait selon les groupes fonctionnels de crustacés et les espèces de daphnies. Pour la structure des groupes fonctionnels de crustacés, les variables de qualité d'eau (enrichissement en nutriments et transparence de l'eau) et les variables de perturbation (développement résidentiel et pourcentage de zones ouvertes) étaient les plus structurantes. Par contre pour les espèces de daphnies, c'était les variables de qualité d'eau et les variables morphologiques du lac et du bassin versant qui étaient les plus importantes.

Les résultats de cette étude offrent un potentiel d'application pour la gestion et le suivi environmental des lacs de villégiature du sud du Québec. Nous avons mis en évidence les groupes fonctionnels de crustacés et les espèces de daphnies ayant un potentiel de bioindicateurs de l'urbanisation des lacs (Chapitre 4). Chez les groupes fonctionnels de crustacés, les espèces de petite taille, *Bosmina* et *CerioDaphnia*, étaient associées aux perturbations du bassin versant par le développement résidentiel. Ces espèces sont généralement des indicateurs précoces de l'eutrophisation des lacs. Comme elles ont un faible pouvoir de filtration, leur prédominance peut avoir des conséquences désastreuses au niveau des floraisons d'algues et pour la transparence de l'eau. Les résultats de cette étude (Chapitre 4) feront l'objet d'un article soumis pour la revue « Canadian Journal of Fisheries and Aquatic Sciences ».

Dans le Chapitre 5, nous démontrons que la profondeur de résidence moyenne des crustacés est gouvernée par l'hétérogénéité de la colonne d'eau, principalement le gradient vertical de température et la profondeur de la zone euphotique. L'originalité du dernier chapitre provient de l'utilisation d'une nouvelle méthode statistique (arbre de régressions multivarié) qui intègre l'hétérogénéité spatiale de la colonne d'eau et les niveaux de perturbation sur le bassin versant dans un seul modèle afin d'expliquer la répartition de la biomasse des groupes fonctionnels. Cette méthode statistique sélectionne les variables environnementales significatives et pour chaque variable établit la valeur critique de séparation qui permet de structurer la biomasse des crustacés. Les variables expliquant la répartition de la biomasse des crustacés dans la colonne d'eau sont celles reflétant l'hétérogénéité de la colonne d'eau comme le gradient de température, la profondeur de la zone euphotique, la concentration en chlorophylle *a* et la profondeur d'échantillonnage. La profondeur de résidence moyenne des crustacés et des espèces de daphnies se situait surtout au niveau du métalimnion ou à la base de la zone euphotique. Les gros crustacés planctoniques évitaient les eaux de surface tant le jour que la nuit et se concentraient plutôt en eaux profondes, plus froides mais encore assez bien oxygénées. La profondeur de résidence moyenne était plus grande lorsque les lacs étaient plus transparents. Un élément intéressant de l'étude est la mise en évidence de comportement migratoire journalier chez les plus grandes espèces de daphnies et les copépodes, soit associé à une remontée durant la nuit dans la majorité des lacs, ou une descente durant la nuit dans un lac en particulier. Le comportement migratoire ascendant résulte probablement d'une stratégie pour contrer la pression de prédation exercée par les poissons planctonophages, hypothèse non confirmée. Par contre, la présence en abondance de prédateurs invertébrés dans le lac Tracy provoque un comportement de migration inverse. De plus, notre étude suggère que la profondeur de résidence moyenne durant le jour ou la nuit augmente avec l'augmentation de la taille des groupes fonctionnels de crustacés. Les facteurs abiotiques (température, lumière et oxygène) ont un rôle primordial dans le contrôle de la profondeur de résidence moyenne. Toutefois, d'autres facteurs comme le niveau de perturbation du couvert forestier, des nutriments (phosphore total dissous) et de la biomasse des algues (Chl. *a*) ont aussi un rôle à jouer dans la distribution verticale des crustacés planctoniques. Les modèles définis par les arbres de régressions multiples mettent en évidence la nécessité d'intégrer les variables anthropiques liées au développement résidentiel du bassin versant ainsi que les variables décrivant l'hétérogénéité de la colonne d'eau pour expliquer la structure et la distribution vertical des crustacés zooplanctoniques. La communauté des crustacés zooplanctoniques et les assemblages d'espèces de daphnies dans la zone pélagique ont un rôle important à deux niveaux puisque les brouteurs efficaces comme les daphnies maintiennent la transparence des eaux et assure le transfert d'énergie et de matières au niveau des poissons planctonophages. Les résultats de cette étude (Chapitre 5) feront l'objet d'un article soumis pour la revue « Freshwater Biology ».