

Université de Montréal

Contrôle environnemental de l'hétérogénéité spatiale de la biomasse et de la structure en  
taille des communautés planctoniques aux échelles intra- et inter-lacs

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Cette thèse intitulée :

Contrôle environnemental de l'hétérogénéité spatiale de la biomasse et structure en taille  
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## RÉSUMÉ

Un des défis actuels en écologie du plancton est de déterminer la contribution relative des processus abiotiques et biotiques dans le contrôle environnemental des communautés planctoniques selon différentes échelles spatiales et suivant un continuum d'hétérogénéité environnementale. Cette thèse répond à ces attentes et vise deux principaux objectifs: (1) déterminer l'hétérogénéité spatiale de la biomasse et de la structure en taille des communautés planctoniques aux échelles intra- et inter-lacs; (2) évaluer la contribution relative des facteurs environnementaux ascendants "Bottom-Up" et/ou descendants "Top-Down" à l'origine de cette hétérogénéité. Afin de répondre à ces objectifs, quatre études ont été réalisées à différentes échelles spatiales intra-lac et inter-lacs.

A l'échelle intra-lac, nous avons déterminé dans un lac de tourbière l'influence de la prédation par les invertébrés (Chaoboridae) et de la physico-chimie des eaux sur la distribution horizontale et verticale de la biomasse zooplanctonique et sur sa structure en taille (Chapitre 1). Dans le lac Geai, l'hétérogénéité du zooplancton était aussi importante sur l'axe horizontal que vertical. La prédation était le facteur le plus important influençant la répartition horizontale et verticale du zooplancton. La taille et la densité des Chaoboridae, ainsi que la conductivité des eaux influençaient la répartition horizontale du zooplancton dans le lac. Sur l'axe vertical, la biomasse zooplanctonique diminuait avec la profondeur. Le zooplancton évitait les eaux hypolimnétiques froides et anoxiques où se retrouvaient de fortes densités de gros prédateurs Chaoboridae.

La seconde étude à l'échelle intra-lac avait pour objectif d'évaluer dans un lac sub-alpin les effets de la prédation par les juvéniles de perche (*Perca fluviatilis*) sur la distribution horizontale et verticale des daphnies et des copépodes cyclopoïdes au cours d'un cycle jour-nuit (Chapitre 2). La répartition horizontale et verticale du zooplancton était inverse à celle des poissons. Sur l'axe vertical, le zooplancton était situé de jour dans l'hypolimnion évitant ainsi la prédation par les juvéniles de perche situés dans les eaux épilimnétiques. Une forte opposition horizontale a été identifiée autant de jour que de nuit. La majorité de la densité zooplanctonique a été enregistrée en zone littorale, tandis que la biomasse de perche était principalement pélagique. Nous avons proposé l'hypothèse que la répartition inverse horizontale et verticale du zooplancton face à leur prédateur était due à la prédation des poissons, ainsi que par leur comportement d'anti-prédation (migrations horizontale et verticale). Au cours de la nuit, les cyclopoïdes qui constituaient le principal item du régime alimentaire des perches, étaient plus abondants dans les eaux métalimnétiques plus froides qui étaient évitées par les jeunes perches.

A l'échelle inter-lacs, nous avons testé l'influence de la géologie sur la relation phosphore-chlorophylle *a* (Chapitre 3). Des modèles phosphore-chlorophylle *a* déterminant la réponse quantitative de la biomasse algale totale et pour 4 classes de taille ( $< 3 \mu\text{m}$ ,  $3 - 20 \mu\text{m}$ ,  $< 20 \mu\text{m}$ , et  $> 20 \mu\text{m}$ ) face aux gradients de TP ont été établis pour les lacs du sud du Québec. Nous avons finalement évalué l'influence d'autres paramètres physico-chimiques sur ces relations. Les lacs étudiés reposaient sur un socle granitique caractéristique du bouclier canadien. Ces lacs présentaient des concentrations en chlorophylle *a* plus faibles par unité de phosphore que les lacs retrouvés sur des socles sédimentaires. Les lacs les plus productifs étaient dominés par des algues de grandes tailles ( $> 20 \mu\text{m}$ ), tandis que les algues de petites tailles ( $< 20 \mu\text{m}$ ) étaient plus abondantes dans les lacs de type oligotrophe. L'identification de l'alcalinité comme variable complémentaire à nos modèles de prédiction a permis de proposer l'hypothèse d'un contrôle algal par broutage par le gros zooplancton herbivore dans les lacs plus productifs et alcalins.

Les sources de variations spatiales de la biomasse zooplanctonique ont été quantifiées aux échelles intra- (entre les strates) et inter-lacs (entre les lacs) (Chapitre 4). L'influence des facteurs environnementaux abiotiques et biotiques "Bottom-Up" et "Top-Down" sur les variations de la biomasse et de la structure en taille du zooplancton ( $53-100 \mu\text{m}$ ,  $100-202 \mu\text{m}$ ,  $202-500 \mu\text{m}$ ,  $> 500 \mu\text{m}$ ) ont été évalués dans les 3 strates limnétiques des lacs du sud du Québec. La variation de la biomasse zooplanctonique était plus importante entre les lacs qu'entre les strates d'un même lac. Cependant, les variations entre les strates n'étaient pas constantes d'un lac à l'autre. Les facteurs "Bottom-Up" ont été identifiés comme la plus importante source de variation épilimnétique de la biomasse zooplanctonique entre les lacs. Les facteurs "Top-Down", soit la présence ou l'absence de piscivore dans les lacs, expliquaient la structure en taille des communautés zooplanctoniques ainsi que leur variation verticale (entre les strates). Les lacs où les piscivores étaient absents (dominance des planctivores) présentaient des communautés zooplanctoniques dominées par des petits individus.

L'ensemble de ces résultats permet de conclure que l'hétérogénéité des communautés planctoniques augmente avec l'échelle d'observation. À petites échelles (intra-lac, inter-strates), les facteurs biotiques (prédation) exercent un contrôle sur les communautés planctoniques, tandis qu'à plus grandes échelles (inter-lacs), ce sont les facteurs abiotiques (physico-chimie et morphométrie) qui expliquent en premier lieu la variabilité du plancton. La complémentarité des facteurs abiotiques et biotiques "Bottom-Up" et biotiques "Top-Down" dans le contrôle des communautés planctoniques est omniprésente quel que soit l'échelle d'observation.

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## LISTE DES SIGLES ET ABRÉVIATIONS

°C	degré Celsius
%	pourcentage
$\alpha$ ou P =	niveau de probabilité
dB	décibel
DHM	Migration Horizontale Journalière (Diel)
DOC	carbone organique dissous
DVM	Migration Verticale Journalière (Diel)
EB (< 20 $\mu\text{m}$ )	algue phytoplancton ingérable < 20 $\mu\text{m}$
ha	hectare
IB (> 20 $\mu\text{m}$ )	algue phytoplancton non-ingérable > 20 $\mu\text{m}$
km	kilomètre
km <sup>2</sup>	kilomètre carré
L	litre
log <sub>10</sub>	logarithme en base 10
NTU	unités de turbidité néphélogométrique
m	mètre
m <sup>2</sup>	mètre carré
m <sup>3</sup>	mètre cube
mg	milligramme
MICRO	microphytoplancton
mm	millimètre
Nano	nanophytoplancton
NaPi	nano + picophytoplancton
Pico	picophytoplancton
PSM	"plankton sampling mechanism"
Pt	unité de couleur en chloroplatinate
TChl <i>a</i>	chlorophylle <i>a</i> totale
TN	azote total
TN/TP	rapport azote-phosphore
TP	phosphore total
T.S.	target strength
$\mu\text{g}$	microgramme
$\mu\text{S}\cdot\text{cm}^{-1}$	microSiemens par centimètre
YOY	jeune de l'année (perche 0+)

## DÉDICACE ET REMERCIEMENTS

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## INTRODUCTION GÉNÉRALE

Dès les années 1960-70, le zooplancton était considéré comme un des plus importants maillons de la chaîne alimentaire, dite classique (Steele 1974). Dans cette chaîne simpliste, les herbivores zooplanctoniques occupaient une place prépondérante puisqu'ils consommaient les algues, tandis qu'ils étaient à leur tour mangés par les poissons. Au cours des dernières décennies, plusieurs travaux ont permis de diversifier ce modèle et d'en déterminer sa complexité (Figure 1A). On s'est vite rendu compte qu'à l'intérieur même de chacun des maillons trophiques, il existait de multiples interactions qui influençaient à la fois les niveaux trophiques supérieur et inférieur de la chaîne alimentaire. Cependant, c'est en milieu marin que l'on détermina l'existence (Figure 1B) et l'impact de la chaîne microbienne (bactéries, protozoaires, ciliés et algues de différentes tailles) sur le fonctionnement du réseau trophique (Pomeroy 1974, Sieburth et al. 1978, Azam et al. 1983).

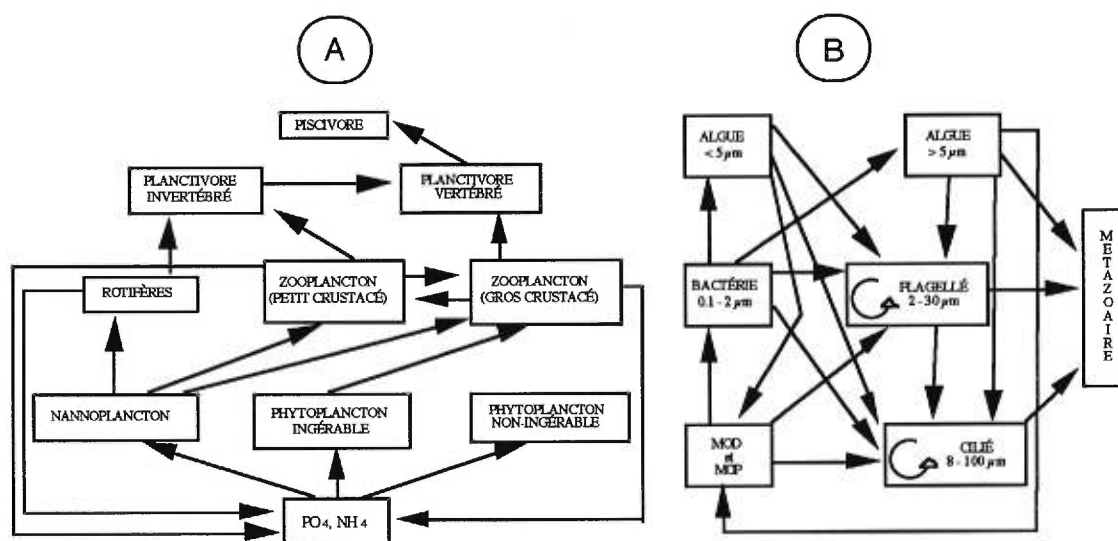


Figure 1. Relation trophique : A) entre les maillons de la chaîne alimentaire excluant la chaîne microbienne (Carpenter et al. 1985); B) entre la chaîne microbienne et le phytoplancton (Sherr et Sherr 1988).

Le pont entre ces deux chaînes trophiques (Figures 1A et 1B) ne s'est fait que tardivement vers la fin des années 1980 (Porter et al. 1988). Bien que nous savions que ces organismes, et plus particulièrement les bactéries, intervenaient dans le recyclage de la matière organique et des nutriments (ex: Azam et al. 1983, Wetzel 1983), ce n'est qu'en

étudiant les interactions entre ces deux chaînes trophiques que l'on confirma à nouveau le rôle clé du zooplancton dans la chaîne alimentaire et plus particulièrement dans le transfert du carbone de la chaîne microbienne vers les poissons (Riemann 1985, Stockner et Porter 1988, Pace et al. 1990). Plus spécifiquement, c'est le macrozooplancton (*Daphnia* spp.) qui, en consommant des proies reposant sur un large spectre de taille (1 à 50  $\mu\text{m}$ ), et pouvant se retrouver à différents niveaux trophiques (picoplancton hétérotrophe et autotrophe, nanophytoplancton et microphytoplancton), permet un meilleur transfert de l'énergie vers les niveaux supérieurs (Christoffersen et al. 1993). Le microzooplancton (petits cladocères, copépodes et rotifères) peut également contribuer au transfert du carbone (Figure 2), mais avec une moins bonne efficacité que les daphnies (Stockner et Porter 1988, Stockner et Shortreed 1989, Lyche et al. 1996).

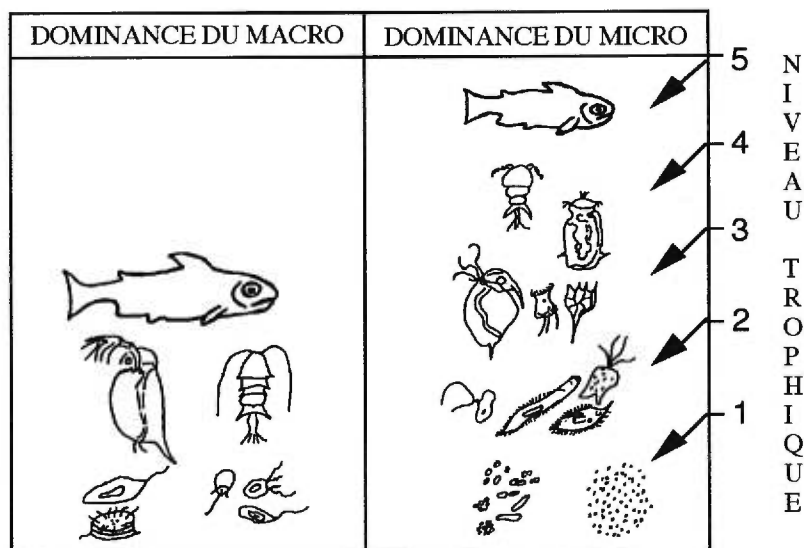


Figure 2. Différence dans les transferts du carbone vers les niveaux supérieurs de la chaîne trophique selon la dominance d'une communauté macro- ou microzooplanctonique (modifié selon Stockner et Shortreed 1989).

Selon Pinel-Alloul (1995a), la prédominance des rotifères dans les lacs sujets à une forte prédation par les invertébrés laisse entrevoir un rôle accru de la chaîne microbienne dans le transfert de l'énergie et du carbone dans les réseaux planctoniques, mais une production globale plus faible de l'écosystème pélagique à cause de l'augmentation du nombre de maillons trophiques. Une dominance du microzooplancton peut ainsi créer une coupure dans les transferts énergétiques vers les niveaux trophiques supérieurs (Mills et Forney 1988, Neill 1988). La présence du macrozooplancton est

donc essentielle dans la chaîne alimentaire, puisqu'il fait le lien entre la chaîne microbienne, les algues et les prédateurs invertébrés et vertébrés. Son rôle clé dans les écosystèmes aquatiques a d'ailleurs été démontré dans de nombreux travaux menés en enclos et en milieux naturels. Il intervient au niveau de la clarté des eaux (Mills et Schiavone 1982, Mazumder et al. 1990a, Mazumder et Lean 1994, Lathrop et al. 1996), dans le transfert du carbone et des contaminants (Reimann 1985, Rasmussen et al. 1990), sur la structure et la dynamique de la chaîne microbienne (Güde 1988, Jürgens et al. 1994), ainsi qu'au niveau du recyclage (Elser et Hassett 1994, Sterner et Hessen 1994) ou de la disponibilité des éléments nutritifs (Mazumder et al. 1992, Mazumder 1994a). L'influence de la structure des communautés zooplanctoniques a non seulement un impact significatif sur la taille, la survie, et la production lacustre des poissons (Stockner et Shortreed 1989, Post et Rudstam 1992; Post et al. 1992; Figure 2), mais également sur la productivité des lacs en limitant le développement algal (Mazumder 1994ab, Taylor et Carter 1997).

De part sa position stratégique dans la chaîne alimentaire (Figure 1A), le zooplancton peut ainsi être considéré comme un excellent bioindicateur des changements environnementaux. Des variations dans la structure en taille, l'abondance ou le nombre d'espèces ou de groupes fonctionnels (micro ou macrofiltreur efficace ou inefficace, prédateur, etc.) dans la communauté peut permettre d'identifier des signes d'acidification (Carter et al 1986, Pinel-Alloul et al. 1990a, Shaw et Kelso 1992), de limitation en calcium (Tessier et Horwitz 1990) ou d'eutrophisation et de prédation (Stemberger et Lazorchak 1994, Hessen et al. 1995). Plusieurs études montrent que ces organismes peuvent servir d'indicateurs de contamination en métaux lourds (Yan et al. 1990; Keller et Yan 1991; Meili 1991; Watras et bloom 1992, Meili 1993; Tremblay et al. 1995; Paterson et al. 1998), de zones polluées (Hakkari 1972; Gras et Rodriguez-Babio 1993) et de perturbations (feux de forêt et déboisement) enregistrées au niveau du bassin versant (Pinel-Alloul et al. 1998a).

Plusieurs processus ou facteurs ont été identifiés comme sources potentielles de modifications de la structure des communautés zooplanctoniques. La taille et la profondeur des plans d'eau ont été reconnus comme les facteurs morphométriques les plus influents. On note une augmentation de la richesses en espèces (Pinel-Alloul et al. 1979, Dodson 1992, Shaw et Kelso 1992, Keller et Conlon 1994) suivant le gradient de taille et de profondeur des lacs. Cependant, la relation entre la biomasse et ces deux variables morphométriques est plus nuancée. Il semble que la biomasse zooplanctonique

augmente avec la taille du lac (Hanson and Peters 1984), mais diminue avec la profondeur des plans d'eau (Hanson and Peters 1984, Yan 1986, Quiros 1991). Ces relations seraient directement reliées à la productivité des systèmes lacustres, puisque le recyclage des éléments nutritifs est plus important dans les lacs de grande superficie et de faible profondeur (Riley et Prepas 1985, Fee et Hecky 1992, Hakanson 1995).

Bien que la biomasse zooplanctonique augmente avec l'enrichissement en phosphore (Hanson and Peters 1986, Yan 1986, Pace 1986), il existe une certaine controverse quant à la modification de la taille de la communauté zooplanctonique suivant le gradient d'eutrophisation. Les milieux enrichis présenteraient des communautés zooplanctoniques dominées par des individus de petites tailles (Gliwick 1969, Hillbricht-Ilkowska 1977, Mills et Schiavone 1982, Beaver et Crisman 1989, Sager et Richman 1991). Bays et Crisman (1983) mentionnent à ce sujet que l'accroissement de la biomasse zooplanctonique totale à la suite d'un enrichissement trophique est principalement attribuable au microzooplancton. A l'opposé, Pace (1986) conclut que bien que la biomasse zooplanctonique est positivement reliée à l'augmentation du phosphore, les variations de la structure en taille de la communauté en sont indépendantes. Cette controverse pourrait s'expliquer par divers processus survenant au cours de l'eutrophisation, tel que des modifications de la composition en espèces zooplanctoniques (ex: Brooks 1969, Gannon et Stemberger 1978), de la structure en taille de la communauté algale (Watson et Kalff 1981, Watson et McCauley 1988; Watson et al. 1992), de la compétitivité des organismes (DeMott 1989, Gliwicz 1990), ainsi que par la prédation par les poissons (Brooks et Dodson 1965, Brooks 1969, Zaret 1980).

Les études en enclos et les expériences de biomanipulation (Shapiro et al. 1975) ont permis de mieux comprendre l'effet combiné des poissons, de la communauté algale et des nutriments sur les modifications de la structure en taille du zooplancton. *A priori*, la présence de planctivores (en absence de piscivore) est accompagnée d'une diminution de la biomasse de macrozooplancton (Mazumder et al. 1990b, Lafontaine et McQueen 1991, Lazzaro et al. 1992, McQueen et al. 1992). L'enrichissement du milieu provoque une augmentation de la biomasse algale (Vollenweider 1968, Dillon et Rigler 1974), tandis que le macrozooplancton contrôle la biomasse algale (Hrbáček et al. 1961, Brooks et Dodson 1965, Shapiro 1980). La biomasse algale peut ainsi être régulée par de fortes interactions induites entre l'apport de nutriments, le broutage par le zooplancton et la prédation par les poissons (McQueen et al. 1986, Mazumder et al. 1988, 1990bc, 1992, Power 1992). Ces notions d'enrichissement et de prédation ont amené au milieu des



années 1980, le développement de nombreux concepts et paradigmes permettant d'expliquer les variations de la structure des communautés planctoniques (Tableau I).

Tableau I. Principaux modèles (avec schéma explicatif) décrivant l'impact combiné des nutriments et des réseaux trophiques sur la biomasse algale (traits pointillés) et zooplanctonique (traits pleins) (modification de Pinel-Alloul et al. 1998b).

Modèle (référence)	Planctivore dominant	Herbivore dominant	Caractéristiques principales des modèles
cascades trophiques (Carpenter et al. 1985)			chaque niveau trophique est inversement et directement relié à ses niveaux trophiques inférieur et supérieur immédiats
bottom-up et top-down (McQueen et al. 1986)			contrôle de la biomasse à la fois par les ressources et par les prédateurs
proie-dépendant (Persson et al. 1988)			suivant l'augmentation du nombre de niveau trophique, il y a une limitation de la production du maillon supérieur selon les ressources disponibles, et la biomasse des proies est limitée par le prédateur
ratio-dépendant (Arditi et Ginzburg 1989)			augmentation de la biomasse des algues et du zooplancton proportionnellement à l'augmentation des nutriments peu importe le type de réseau trophique
size-distribution hypothesis (Mazumder et al. 1992)			distribution en taille et biomasse du plancton déterminées par la prédation, le broutage influence la disponibilité des nutriments et la compétition entre le petit (gris pâle) et le gros (gris foncé) phytoplancton pour les nutriments
modèle sigmoïde (Mazumder 1994abc)			réponse non linéaire des algues au phosphore avec plus grande production dans les milieux non stratifiés (traits gris); Production limitée par le broutage

phosphore ( $\mu\text{g.L}^{-1}$ )

Les paradigmes le plus discutés dans la littérature sont sans contredit les modèles d'interactions trophiques en cascades (Carpenter et al. 1985) et de contrôle ascendant bottom-up (BU) et descendant top-down (TD) des communautés (McQueen et al. 1986, 1989). Ces modèles indiquent que la présence de poissons planctivores permettra le développement d'une communauté de petits individus zooplanctoniques (prédation sur le macrozooplancton) et provoquera un accroissement de la biomasse algale. Dans le cas

inverse, en absence de planctivores (présence de piscivore), le macrozooplancton dominera la communauté zooplanctonique et ainsi limitera le développement algal. Cependant selon la théorie du BU-TD, en milieux eutrophes, les effets des poissons dans le bas de la chaîne trophique seraient beaucoup plus restreints. Ces théories ont fait l'objet de nombreuses controverses à savoir si les forces BU (impact des nutriments) ou TD (prédation par les poissons et herbivores) déterminaient la structure de la chaîne trophique (McQueen et al. 1986, Matson et Hunter 1992). L'influence simultanée et interactive de ces processus sur la biomasse planctonique et la structure des communautés pélagiques a été reconnue à juste titre (Hunter et Price 1992, Power 1992).

*A priori*, les processus d'eutrophisation et de prédation semblent facilement expliquer les variations de la structure en taille des algues et du zooplancton, cependant ces processus sont très complexes (Lammens et al. 1990, DeMelo et al. 1992). De plus, les effets TD s'amenuisent des plus hauts vers les plus bas niveaux de la chaîne trophique et inversement pour les effets BU (Brett et Goldman 1996, 1997). On constate que la présence de macrozooplancton en milieux enrichis ne s'accompagne pas toujours d'une diminution de la biomasse algale (ex: Benndorf 1990, Faafeng et al. 1990, Vanni et al. 1990, Sarnelle 1993), mais plutôt par l'apparition d'algues non-ingérables incluant des cyanobactéries (Mazumder et al. 1992).

La majorité des études qui ont testé ces théories ont été conduites en enclos ou en bassins artificiels, tandis que beaucoup moins de travaux ont été réalisés en milieu naturel (DeMelo et al. 1992). Dans les lacs, plusieurs réponses adaptatives des organismes face à la prédation, (tels que le polymorphisme, migration horizontale, verticale et transversale, période de latence, augmentation du taux de fécondité, etc...), peuvent complexifier les effets BU et TD (Pourriot 1995). On note également dans certains cas que l'absence de prédation par les poissons planctivores, ne favorise pas nécessairement le macrozooplancton (*Daphnia* spp.), mais plutôt le développement d'autres prédateurs invertébrés (ex: *Mysis*, *Chaoborus*, *Notonecta*, *Bytotrephes*, *Leptodora*, *Diaptomus*) qui peuvent également exercer un contrôle sur le zooplancton (ex: DeBernardi et al. 1987, Hanazato et Yasuno 1989, Benndorf 1990, Yan et al. 1991, Arnott et Vanni 1993, Paul et al. 1995; Herwig et Schindler 1996). Le rôle des prédateurs invertébrés sur les communautés planctoniques est complexe par rapport à celui des poissons (Pinel-Alloul 1995a).

A part le modèle sigmoïde de Mazumder (1994abc), aucun des modèles expliquant les variations de la biomasse planctonique (Tableau I), ne considère les autres caractéristiques limnologiques telles que par exemple: la morphométrie des lacs, la

stratification thermique, l'acidité ou la coloration des eaux. La présence de stratification thermique et la notion de refuge (macrophytes, eaux froides anoxique ou oxique) ont été citées comme d'importants éléments pouvant affecter la réponse des communautés planctoniques face à la prédation et à l'enrichissement (Timms et Moss 1984, McQueen 1990, Shapiro 1990, Wright et Shapiro 1990, Moss et al. 1994). Tout récemment, Pinel-Alloul et al. (1995) introduisaient "the multiple driving forces hypothesis", indiquant que le contrôle de la structure des communautés zooplanctoniques repose sur la contribution relative des facteurs abiotiques (morphométrie et physico-chimie), biotiques "bottom-up" (ressource phytoplanctonique) et "top-down" (prédation par les poissons). Ce nouveau paradigme permet ainsi une meilleure intégration de l'ensemble des forces abiotiques et biotiques influençant la structure des communautés zooplanctoniques.

Il est cependant reconnu que l'influence relative des facteurs abiotiques et biotiques varie à l'intérieur d'un lac et entre les systèmes selon les échelles d'observation tant spatiale que temporelle (Carpenter et Kitchell 1988, Rodriguez et al. 1993, Pinel-Alloul et al. 1995). Il est d'ailleurs encore difficile de généraliser sur les phénomènes perturbant les communautés planctoniques, puisque d'une part les effets BU et TD sont beaucoup plus complexes et engendrent de multiples réponses indirectes des communautés (voir ci-haut), et d'autre part nous connaissons encore mal la dynamique des populations planctoniques à différentes échelles spatiales et temporelles. **Un des défis de l'écologie contemporaine est donc de déterminer l'importance de ces processus écologiques à différentes échelles spatiales et temporelles et selon un continuum d'hétérogénéité environnementale (Power 1992, Hunter et Price 1992).**

Les interactions multiples entre les organismes planctoniques et les caractéristiques physiques, chimiques et biologiques de leur environnement varient selon un continuum hiérarchique d'échelles spatiales et temporelles (Horne et Platt 1984, Carpenter 1988, Barry et Dayton 1991). Introduisant le diagramme de Stommel (Figure 3a), Haury et al. (1968) montrent clairement que les agrégations spatiales du zooplancton marin dépendent à la fois des échelles spatiales et temporelles. Une telle hiérarchie a également été notée en milieu dulcicole (Imboden 1990), tant pour le zooplancton (Malone et McQueen 1983, Pinel-Alloul et Pont 1991), que pour le phytoplancton (Harris 1980, 1986, Reynolds 1990). Divers processus biologiques et/ou physiques sont donc à l'origine de l'hétérogénéité spatiale et temporelle des communautés planctoniques.

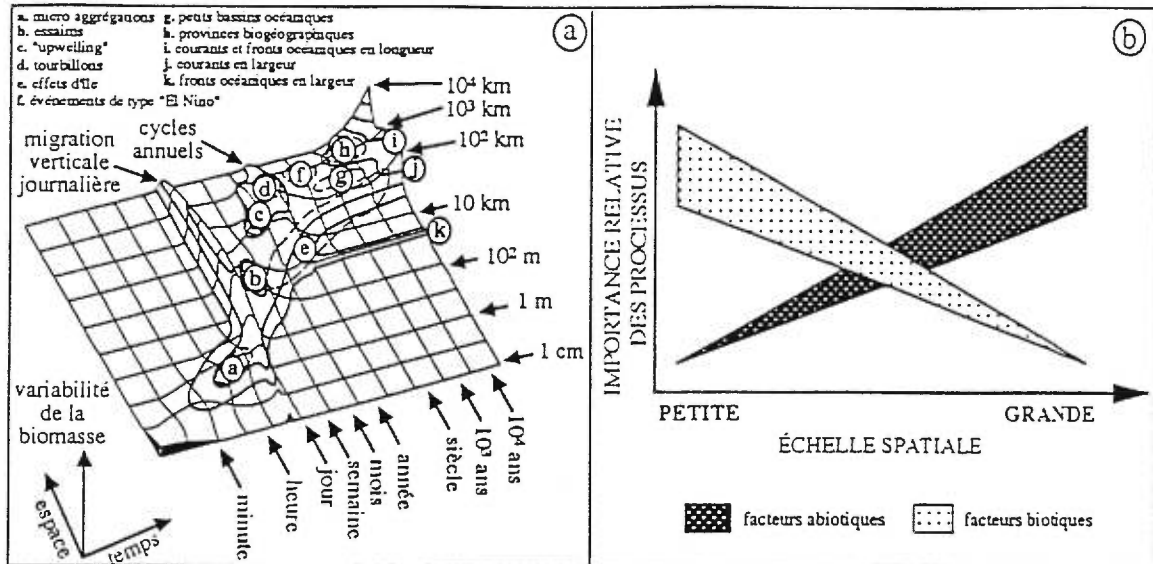


Figure 3. Variabilité du plancton selon l'échelle d'observation en milieu marin (Haury et al. 1978) et en milieu dulcicole (Pinel-Alloul 1995b).

Faisant une synthèse sur les processus abiotiques et biotiques affectant l'hétérogénéité spatiale du zooplancton marin et dulcicole, Pinel-Alloul (1995b) suggérait un effet d'échelle sur l'importance relative des facteurs abiotiques et biotiques dans le contrôle environnemental des communautés zooplanctoniques (Figure 3b). Selon ce modèle, l'importance relative des processus abiotiques augmente à grandes échelles, tandis qu'à l'inverse la contribution des processus biotiques augmente à petites échelles. A grande échelle, les effets régionaux tels que la géologie ont été mentionnés comme d'importants facteurs influençant les niveaux de productivité et la physico-chimie des eaux (Dillon et Kirchner 1975, Gorham et al. 1983, Grobler et Silverbauer 1985, Lachance et Gamache 1985). De tels gradients environnementaux sont à l'origine des variations de la biomasse et de la structure des communautés planctoniques (ex: Duarte et Kalf 1989, Pinel-Alloul et al. 1990ab, Tessier et Horwitz 1990). A petite échelle, plusieurs phénomènes, tels que les migrations verticales (Zaret and Suffern 1976, Lampert 1993, Ringelberg 1993) et horizontales (Kairesalo 1980, Davis 1985, Johannsson et al 1991) et les différents types d'agrégations planctoniques (Figure 3a) engendrent une forte hétérogénéité spatiale et temporelle, ainsi qu'une grande variabilité dans les réponses des communautés planctoniques face aux différents facteurs abiotiques (morphométrie, physico-chimie) et biotiques (prédation, compétition, ressource).

Ce projet de doctorat s'inscrit dans cette problématique d'hétérogénéité spatiale des communautés planctoniques et vise deux principaux objectifs : (1) déterminer l'hétérogénéité spatiale de la biomasse et de la structure en taille des communautés planctoniques aux échelles intra- et inter-lacs; (2) évaluer la contribution relative ou individuelle des facteurs environnementaux ascendants (BU) et/ou descendants (TD) à l'origine de la variabilité de la structure en taille et de la biomasse des communautés planctoniques. Des recherches en milieux naturels à différentes échelles permettront ainsi d'obtenir une meilleure compréhension de la complexité des interactions trophiques dans les réseaux planctoniques.

Afin de répondre à nos objectifs, nous avons développé une nouvelle approche dans l'évaluation de la biomasse et la structure en taille du zooplancton et du phytoplancton. Pour ces deux compartiments trophiques, nous avons dans un premier temps obtenu par filtration sélective la distribution en taille des communautés. Par la suite, l'évaluation de la biomasse des diverses classes de taille phyto- et zooplanctoniques ont été estimées respectivement par fluorométrie et par brûlage (voir détails dans la thèse). Nous avons ainsi obtenu 4 classes de taille pour le phytoplancton (telles que définies par Sieburth et al. 1978): picophytoplancton (Pico:  $< 3 \mu\text{m}$ ), nanophytoplancton (Nano:  $3 - 20 \mu\text{m}$ ), nano- plus picophytoplancton ( $< 20 \mu\text{m}$ ), et microphytoplancton (Micro:  $> 20 \mu\text{m}$ ), ainsi que 4 classes de taille pour le zooplancton:  $53-100 \mu\text{m}$ ,  $100-202 \mu\text{m}$ ,  $202-500 \mu\text{m}$ ,  $> 500 \mu\text{m}$ . La méthode de fractionnement et d'évaluation de la biomasse du zooplancton nous a permis de traiter un plus grand nombre d'échantillons, d'éviter les pénibles procédures de comptage, de mesure et d'identification, et d'obtenir l'information dans un laps de temps plus court que celui que requiert la taxonomie. L'utilisation de la structure en taille du phytoplancton et du zooplancton nous a d'ailleurs permis d'obtenir des réponses beaucoup plus fonctionnelle des communautés planctoniques face aux gradients environnementaux abiotiques et biotiques que si nous aurions utilisé les biomasses totales. Selon Mazumder et al. (1992), les impacts de la prédation sur le phyto- et le zooplancton sont plus importants dans la distribution en taille des communautés qu'au niveau de leur biomasse totale.

Cette thèse est présentée en quatre chapitres qui traitent du contrôle de la biomasse et de la structure en taille des communautés planctoniques par les facteurs ascendants "Bottom-up" et / ou descendants "Top-Down" aux échelles intra- et inter-lacs (Tableau II). Le chapitre 1 présente une étude de la répartition horizontale et verticale de la biomasse et de la structure en taille du zooplancton dans un lac de tourbière (Lac Geai)

sans poissons, dont les principaux prédateurs sont deux espèces de Chaoboridae (*Chaoborus americanus* et *C. trivittatus*). Les objectifs de cette étude étaient : 1) d'évaluer l'hétérogénéité spatiale horizontale et verticale de la biomasse et de la structure en taille du zooplancton; 2) de déterminer quels étaient les facteurs, biotiques et / ou abiotiques, qui contrôlaient les patrons de distribution de la biomasse zooplanctonique sur les deux axes spatiaux; 3) d'identifier les facteurs communs qui pouvaient expliquer l'hétérogénéité horizontale de la biomasse du zooplancton dans les trois strates limnétiques (épi-, méta-, et hypolimnion).

Tableau II. Structure de la thèse indiquant les différentes approches adoptées afin de déterminer l'impact des facteurs environnementaux sur les communautés planctoniques aux échelles intra- et inter-lacs.

Contrôle environnemental	ÉCHELLE D'OBSERVATION	
	<u>INTRA-LAC</u>	<u>INTER-LACS</u>
Bottom-Up et Top-Down	contrôle de la distribution horizontale et verticale de la biomasse et de la structure en taille du zooplancton dans un lac de tourbière <b>(Chapitre 1)</b>	contrôle de la biomasse et de la structure en taille du zooplancton dans les 3 strates limnétiques des lacs du sud du Québec <b>(Chapitre 4)</b>
Bottom-Up ou Top-Down	contrôle de la répartition horizontale et verticale du zooplancton par les poissons dans un lac sub-alpin au cours d'un cycle nyctéméral <b>(Chapitre 2)</b>	contrôle de la structure en taille de la biomasse phytoplanctonique selon la productivité et la géologie des bassins versants des lacs du sud du Québec <b>(Chapitre 3)</b>

Au chapitre 2, nous abordons les interactions entre le zooplancton et les prédateurs vertébrés dans un lac sub-alpin (Lac Annecy). Les objectifs de ce travail étaient de déterminer les effets de la prédation par les juvéniles de perche (*Perca fluviatilis*) sur la distribution horizontale et verticale des daphnies et des copépodes cyclopoïdes au cours d'un cycle jour-nuit. Nous testions (1) s'il y avait une distribution inverse entre les poissons et le zooplancton; (2) et si les patrons de distribution variaient au cours du cycle nyctéméral.

Les objectifs du troisième chapitre étaient (1) d'explorer les relations entre la biomasse algale totale, sa structure en taille ( $< 3 \mu\text{m}$ ,  $3 - 20 \mu\text{m}$ ,  $< 20 \mu\text{m}$ , et  $> 20 \mu\text{m}$ ) et les variations de la concentration en phosphore total des lacs du sud du Québec situés dans des régions de géologie différentes; (2) de générer une nouvelle série de modèles prédictifs TP-Chl *a* déterminant la réponse quantitative de la biomasse algale totale et de ses 4 classes de taille face aux gradients de TP dans les lacs du sud du Québec; (3) de déterminer l'influence d'autres paramètres physico-chimiques sur les relations TP-Chl *a* pour la biomasse algale totale et de ses 4 classes de taille. Dans ce travail, nous testions : (1) si la relation TP-Chl *a* pour la biomasse algale totale et pour ses quatre classes de taille était différente entre des groupes de lacs situés dans deux régions géologiques; (2) si les pentes des nouveaux modèles de régression TP-Chl *a* développés pour les classes de taille algale augmentaient de façon consistante de la plus petite à la plus grande classes de taille.

Enfin, le dernier chapitre a pour buts (1) de quantifier les sources de variations de la biomasse zooplanctonique aux échelles inter-lac et intra-lac; (2) de déterminer l'influence des facteurs environnementaux abiotiques et biotiques "Bottom-Up" et "Top-Down" sur les variations de la biomasse et de la structure en taille du zooplancton ( $53-100 \mu\text{m}$ ,  $100-202 \mu\text{m}$ ,  $202-500 \mu\text{m}$ ,  $> 500 \mu\text{m}$ ) dans les 3 strates limnétiques des lacs du sud du Québec. Nous testions les hypothèses que (1) les changements inter-lacs constituent la plus grande source de variation de la biomasse zooplanctonique totale et de ses classes de taille; (2) que les facteurs abiotiques expliquent majoritairement les variations de la structure en taille de la biomasse zooplanctonique dans les eaux épilimnétiques; (3) que dans les strates meta- et hypolimnétiques, la biomasse des plus grosses fractions zooplanctoniques ( $202-500 \mu\text{m}$  et  $> 500 \mu\text{m}$ ) étaient contrôlée par les facteurs biotiques, tandis que celle des plus petites fractions ( $53-100 \mu\text{m}$  et  $100-202 \mu\text{m}$ ) répondaient plutôt aux variations des facteurs abiotiques.

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CHAPITRE 1

SPATIAL DISTRIBUTION OF ZOOPLANKTON BIOMASS SIZE FRACTIONS  
IN A BOG LAKE : ABIOTIC AND (OR) BIOTIC REGULATION ?

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## RÉSUMÉ

Bien que l'hétérogénéité spatiale du zooplancton soit reliée aux variations des facteurs abiotiques et biotiques ainsi qu'à leurs interactions, très peu d'études se sont attachées à préciser l'importance relative de ces processus dans la régulation de la distribution vertical et horizontale du zooplancton dans un lac. Le principal objectif de cette étude était de déterminer l'importance relative des facteurs abiotiques et biotiques dans le contrôle de la répartition verticale et horizontale de la biomasse du zooplancton fractionnée en quatre classes de taille (53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$ , 202-500  $\mu\text{m}$ , > 500  $\mu\text{m}$ ) dans un lac de tourbière (lac Geai, Québec). La distribution spatiale du zooplancton était hétérogène à la fois sur l'axe horizontal et sur l'axe vertical et présentait un patron similaire pour toutes les classes de taille. Sur l'axe horizontal, l'hétérogénéité spatiale s'est avérée très importante dans la strate épilimnétique. La biomasse du zooplancton était concentrée dans le côté est du lac, le secteur où la conductivité et l'abondance des petites larves de Chaoboridés étaient les plus fortes. Sur l'axe vertical, la biomasse du zooplancton était plus importante dans l'épilimnion et diminuait fortement en profondeur. Ce patron de distribution verticale semblait dû à l'évitement des eaux froides et anoxiques et à la fuite des grandes larves de Chaoboridés dans l'hypolimnion. En général, la prédation par les invertébrés était l'un des principaux facteurs de contrôle de la répartition spatiale de la biomasse du zooplancton dans le lac Geai. Toutefois, la taille de ces prédateurs avait une plus grande influence que leur densité.

## ABSTRACT

Although spatial heterogeneity of zooplankton has been explained by variations in abiotic and biotic factors as well as their cascading interactions, few studies have paid attention to the relative importance of these processes in structuring the vertical and horizontal distribution of zooplankton within a lake. The main objective of this study was to determine the relative importance of abiotic and biotic processes in the regulation of vertical and horizontal distribution of four size fractions (53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$ , 202-500  $\mu\text{m}$ , > 500  $\mu\text{m}$ ) of the zooplankton biomass in a bog lake (Lake Geai, Québec). Spatial heterogeneity of zooplankton biomass was found in both the horizontal and vertical dimensions of the lake, and spatial patterns were quite similar for all size fractions. On the horizontal axis, spatial heterogeneity was stronger in the epilimnetic stratum. Zooplankton biomass was mainly aggregated in the east side of the lake in an area of higher conductivity and greater density of small chaoborid larvae. On the vertical axis, zooplankton biomass was concentrated in the epilimnetic waters and decreased with depth. This vertical pattern of distribution might be due to the avoidance of cold and anoxic waters and a high density of large chaoborid larvae in the hypolimnion. In general, invertebrate predation has been identified as the primary factor regulating zooplankton biomass distribution in Lake Geai. However, the size structure of chaoborid predators was more important than their density in the control of the spatial distribution of zooplankton.

## 1.1 INTRODUCTION

For the last few decades, spatial heterogeneity of freshwater zooplankton was shown to be an important feature in limnological studies. Although some studies assumed an homogeneous horizontal distribution of plankton population (Pinel-Alloul et al. 1990; Pinel-Alloul et al. 1995), zooplankton spatial heterogeneity within a lake has been found to occur both in the vertical and horizontal axes of the pelagic habitat (Pinel-Alloul et al. 1988; Pinel-Alloul and Pont 1991; Lacroix and Lescher-Moutoué 1995). Spatial heterogeneity in plankton communities has also been detected on scales ranging from centimetres to kilometres and many abiotic and biotic factors were found to explain such variability (see Pinel-Alloul 1995 for a review).

Water stratification influences strongly the vertical distribution of zooplankton species (Richerson et al. 1978). Cold profundal and poorly-oxygenated waters offer a refuge for the prey and a higher source of food (Zaret and Suffern 1976; Murtaugh 1985). Other factors such as light diel cycle, feeding competition, and vertebrate predation could also explain zooplankton diel migration and vertical distribution (Zaret and Suffern 1976; Angeli et al. 1995; Ringelberg 1995).

Horizontal distribution of zooplankton has received less attention than its vertical distribution pattern. Most studies have focused on the spatial variation of zooplankton species along transects with more or less equi-spaced stations at scales at which zooplankton variability was expected to be important (Malone and McQueen 1983; Pinel-Alloul et al. 1988; Pinel-Alloul and Pont 1991; Lacroix and Lescher-Moutoué 1995). Horizontal spatial heterogeneity in zooplankton depends on lake size and configuration, sampling scale, time scales, and abiotic and biotic factors inherent to the lakes (Malone and McQueen 1983; Pinel-Alloul et al. 1988; Pinel-Alloul and Pont 1991; Patalas and Salki 1992 and 1993).

Some observations suggest that both abiotic and biotic factors would control zooplankton spatial distribution in lakes, but no study has simultaneously assessed the relative importance of these factors in the vertical and horizontal axes of a lake. This study attempts to do so for four zooplankton biomass size fractions in a small bog lake in southern Quebec. Objectives are **1**) to evaluate the vertical/horizontal heterogeneity of zooplankton biomass; **2**) to determine which factors, biotic or/and abiotic, control the distribution patterns of zooplankton biomass on both axes; **3**) and to identify common

factors that could explain horizontal heterogeneity of zooplankton biomass in the limnetic strata (epi-, meta-, hypolimnion).

Bog lakes are of interest for the study of zooplankton spatial patterns since they are small and well stratified when deep, and they offer peculiar limnological conditions (weak ionic contents, low pH, fishless environment). In particular, the absence of fish in these water bodies allows stronger interactions either between the zooplankton species or among zooplankters and invertebrate predators (Arnott and Vanni 1993). Little is known of the regulation of zooplankton communities in acidic bog lakes in spite that they are among the most common lake types in eastern Canada (Neary et al. 1990). Although water acidity is recognized to affect diversity and structure of invertebrates communities (Haines 1991), no study has been carried out to determine how acidity level or other abiotic and biotic factors in bog lakes could affect zooplankton spatial distribution. Arnott and Vanni (1993) provided some indications on the main factors controlling zooplankton community in bog lake (Figure 1). At the opposite of circumneutral lakes where fish predation seems to have major control zooplankton structure (Rodriguez et al. 1993), zooplankton communities in acidic and fishless bog lakes should rather be controlled by both abiotic (low pH) and biotic (invertebrate predation) factors. Because the Arnott and Vanni's model did not consider spatial variation of abiotic factors regulating zooplankton community, the determination of the relative importance of these processes by considering their spatial variability may contribute to a better understanding of the Arnott and Vanni's model.

## 1.2 MATERIALS AND METHODS

### 1.2.1 Study site

The study was carried out in Lake Geai (Figure 2), located at the Station de Biologie des Laurentides (SBL) de l'Université de Montréal (46° N., 74° W.), approximately 80 km north of Montreal. Lake Geai is a small bog lake (area: 0.99 ha; max depth : 7.5 m), with acidic (mean pH : 5.6) and dystrophic waters (DOC: 8.5 mgL<sup>-1</sup>; color : 114.5 mg Pt.L<sup>-1</sup>). The lake is not influenced by human activity and it is well sheltered from winds, being surrounded by a dense forest (within a radius of 300 m) of *Betula papyrifera* mixed with sparse *Acer saccharum*, *Picea mariana*, *Abies balsamea* and *Thuja occidentalis* (Harper and Cloutier 1985). It has a dimictic thermal regime but may some years be meromictic. There is neither permanent outlet or inlet during the summer. A floating mat of *Sphagnum* and *Ericaceae* covers the south and west-south shorelines

Figure 1 : Relative importance of abiotic and biotic factors affecting zooplankton assemblage structure along a pH stress gradient (from Arnott and Vanni, 1993).



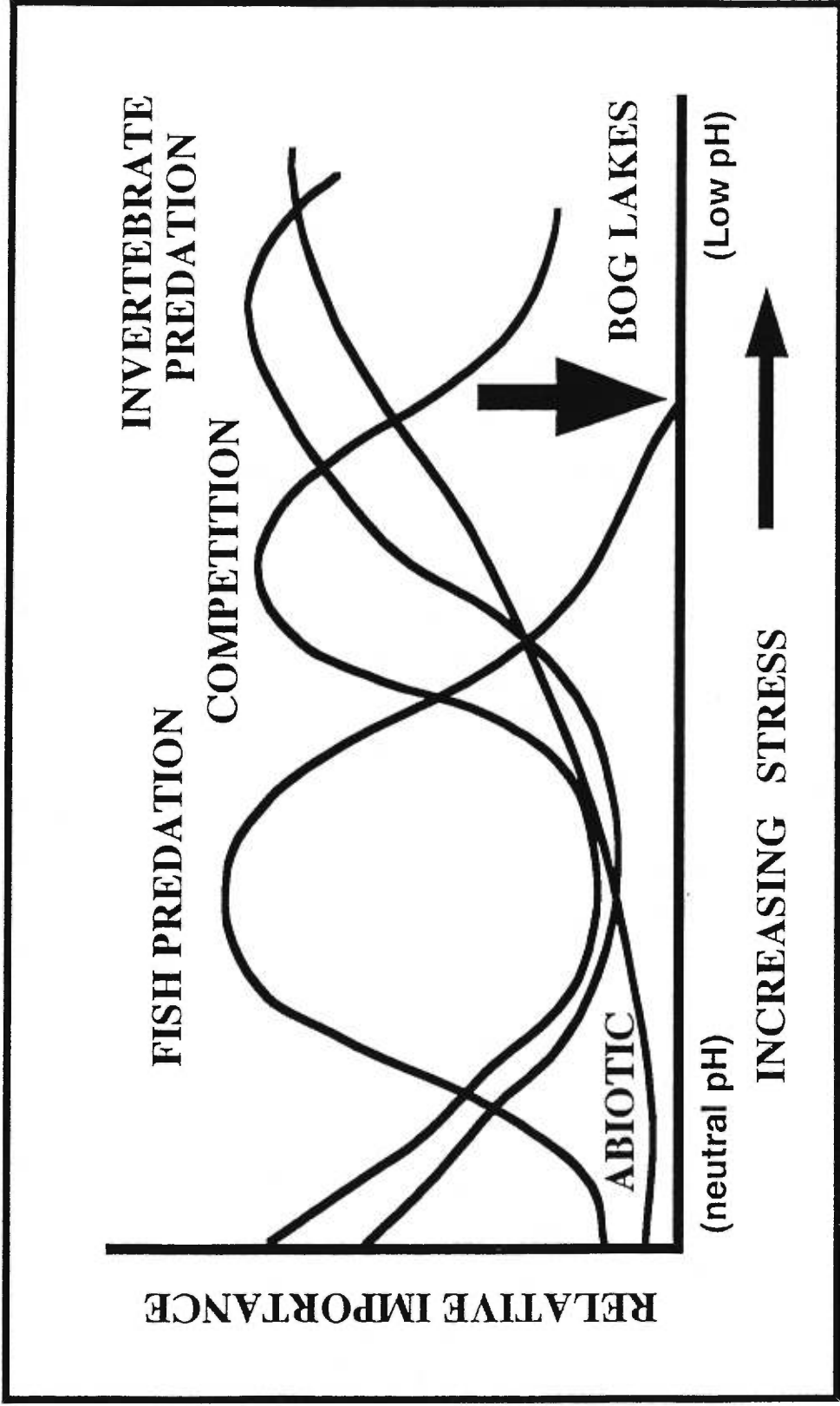


Figure 2). Two chaoborid species (*Chaoborus americanus* Loew, *C. trivittatus* Johansen) are the most abundant pelagic invertebrates in this fishless lake (Harper and Cloutier 1985). Other potential predators for zooplankton not considered in this study are also present in Lake Geai (e.g. : notonectids, corixids, dytiscids, etc.).

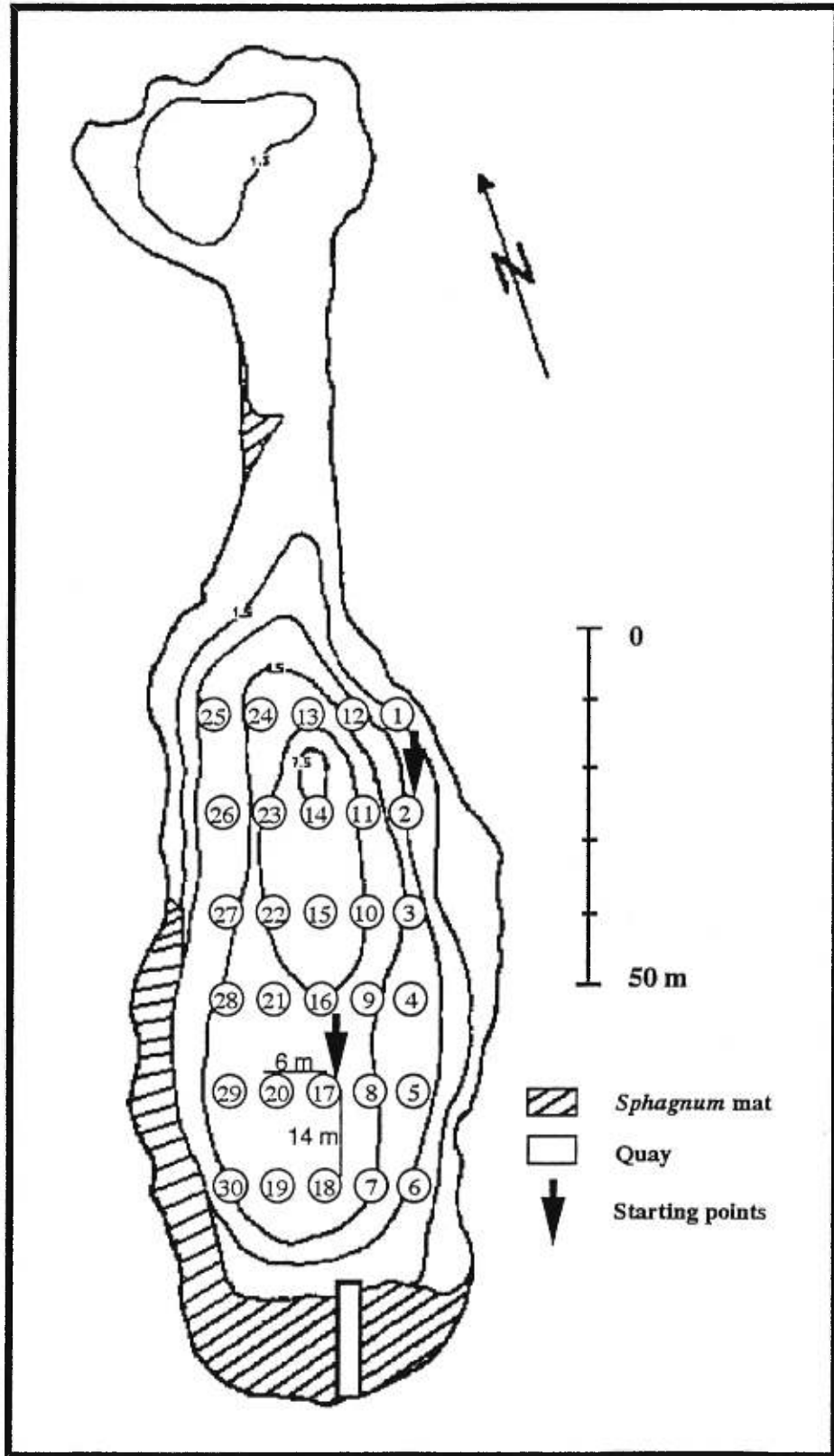
### 1.2.2 Sampling design and water analysis

Sampling took place during the daylight hours of August 3<sup>rd</sup> 1993 (7.30 AM to 7.30 PM). This period corresponds to the maximum of water stability and stratification. Furthermore, this date falls during the emergence period of both chaoborid species since *Chaoborus americanus* emerges during all the summer, while the emergence of *C. trivittatus* peaks at the end of the summer. Thus, the day of sampling corresponds to a period when the physico-chemical stratification is the strongest and the chaoborid populations are the most abundant and well diversified in term of species number and size structure.

Wind conditions were quite calm during the sampling period. The wind speed and direction registered at 8.00 AM in the SBL meteorological station was 15 km.h<sup>-1</sup> and south-west, respectively. However, when exposed to wind speed less than 20 km.h<sup>-1</sup>, the surface waters of this sheltered lake are not disturbed.

A systematic survey was conducted on stations distributed on a grid (24 x 70 m = 1680 m<sup>2</sup>; see Figure 2) in the biggest part of the lake. The stations were positioned at equal distances using ropes and floats (6 m wide, 14 m long). Pelagic and littoral areas were sampled simultaneously by starting from station 1 to station 15 on one side, and from station 16 to station 30 on the other side (starting points; Figure 2). Thirty stations were sampled in the epilimnion (0-1.5 m), 22 stations in the metalimnion (1.5-3 m), and 14 stations in the hypolimnion (3-7.5 m). Water temperature and dissolved oxygen were measured on 0.5 m intervals at each station from the surface to the bottom with an electronic temperature/oxygen meter (YSI model 51B). Duplicate water samples were collected in each strata with a 6 L Van Dorn bottle and homogenized in a bucket (25 L). Afterwards, polyethylene brown bottles were immersed in the bucket and filled to the top to avoid gases exchange between the time of sampling and laboratory analysis. These water samples were used for all physico-chemical and chlorophyll *a* analyses. Nutrients concentrations were measured to evaluate chemical characteristics of each water layer. An

Figure 2 : Map of Lake Geai showing locations of the epilimnetic zooplankton sampling stations; bathymetric contours are in meters.



additional water sample was also collected with the Van Dorn bottle, 1 m above sediments to evaluate density of chaoborids at the sediment-water interface.

Two size fractions ( $< 20$  and  $> 20 \mu\text{m}$ ) of chlorophyll *a* were measured. Since the dynamics of energy flow are reflected by the size of the organisms and the size structure of communities, the use of two size fractions of chlorophyll *a* to explain spatial variations of zooplankton size structure can provide a more useful characterization of phytoplankton associations than taxonomic information (Sprules and Holtby 1979). Based on the two size fractions, we found that microphytoplankton ( $> 20 \mu\text{m}$ ) was mainly dominated by Euglenophyceae (*Euglena texta*, *Lepocinclis fusiformis*, *Phacus caudatus*, *Phacus tortus*, and *Trachelomonas bacillifera*). No filamentous species was observed in Lake Geai at the period of study (Pinel-Alloul, unpublished data). The nanoplankton ( $< 20 \mu\text{m}$ ) was dominated by some Cyanophyceae (*Anabaena solitaria*, *Aphanocapsa elachista* and *Merismopedia glauca*) and Chlorophyceae (*Chlamydomonas* sp., *Eudorina elegans*, *Gloeocystis planctonica*, *Planctonema lauterborni*, and *Quadrigula chodatii*).

The fractionation was performed with a  $20 \mu\text{m}$  Nitex net. All water samples (200 ml) were filtered in subdued light on  $0.45 \mu\text{m}$  cellulose membranes.  $\text{MgCO}_3$  was added at the end of the filtration to avoid chlorophyll degradation before extraction. The filters were wrapped in aluminium foil, and kept at  $-20^\circ\text{C}$  until extracted in 90% acetone. Chlorophyll *a* concentration was measured by fluorometry with a Turner 10-AU model ( $\pm 0.11 \mu\text{g Chl } a \cdot \text{L}^{-1}$ ), after calibration with a spectrophotometer (Strickland and Parsons 1968). Turbidity, pH and conductivity were measured in the laboratory using a Nephelometer (Hach model 18900-00), a pH-meter (Fisher Acumet model 620) and a conductivity meter (Cole Parmer model 1484). Measures of pH were determined on non-degassed samples. Alkalinity was evaluated by titration using 0.06 M HCl until pH reached 4.5 (APHA 1989). This method has been preferred to Gran alkalinity titration because the high number of samples (66) to analyse in a short time. The Gran titration is much slower. However, this method can lead to some overestimations of the alkalinity, since Gran alkalinity of soft water with pH below 5 is generally negative (e.g. Neary et al. 1990).

Afterwards, water samples were filtered ( $0.45 \mu\text{m}$  cellulose membranes) for dissolved nutrient analysis and kept at  $4^\circ\text{C}$  in sterilized 30 ml tubes until analysis (24 h). All nutrients were analysed with an Alpkem autoanalyzer (model RFA 300). TDP (total dissolved phosphorus) was measured using the molybdenum blue method after persulfate

digestion (Murphy and Riley 1962).  $\text{NH}_4$  and  $\text{NO}_3$  were analysed following the indophenol blue and cadmium reduction technique (Armstrong et al 1967) using 2 or 5-cm flow cells. Dissolved silica concentration was measured by the acidic ammonium molybdate method after reduction with  $\text{SnCl}_2$  (Golterman and Clymo 1969). Water samples for DOC (dissolved organic carbon) analysis were obtained by filtering samples through Whatmann GFF filters, precombusted at  $500^\circ\text{C}$ . Samples were kept at  $4^\circ\text{C}$  in 60 ml polyethylene bottles and read within 48 hours. Concentration was determined by conductimetry after persulfate-UV oxidation (Kaplan 1992).

### 1.2.3 Zooplankton analysis

Zooplankton was collected as separate integrated samples through the epi-, meta-, and hypolimnion using a cantilevering towed net ( $53\ \mu\text{m}$  mesh size) modified from Filion et al. (1993) by adding a second line close to the counterweight. Sampling was performed by using this second line to close the net at the top of each water layer. After collection, organisms were immediately narcotized in carbonated water, and preserved in 4% formaldehyde solution with sugar (Prepas 1978). Zooplankton samples were split in two equivalent fractions with a Folsom splitter, and one half was used for biomass determination. Ash-free dry weight was preferred to dry weight because losses of filter pieces during the drying procedure could cause an underestimation of the zooplankton biomass. To estimate the zooplankton biomass, samples were filtered through Nitex sieves of 500, 202, 100 and  $53\ \mu\text{m}$  mesh size in order to obtain four size fractions :  $53$  to  $100\ \mu\text{m}$ ,  $100$  to  $202\ \mu\text{m}$ ,  $202$  to  $500\ \mu\text{m}$  and  $> 500\ \mu\text{m}$ . Zooplankton in each sieve was back-washed, filtered onto precombusted ( $500^\circ\text{C}$ , 24 h) 25 mm Whatmann GFC glass fiber filters, dried at  $60^\circ\text{C}$  for 24 hours, and weighted using a Cahn microbalance ( $x \pm 0.1\ \mu\text{g}$ ) to obtain dry-weight estimates. Finally, dry samples on filters were burned at  $500^\circ\text{C}$  for 24 hours and weighted again to obtain ash weights. Zooplankton biomass in each size fraction (organic carbon biomass:  $\mu\text{g.C}$  weight) was obtained by subtracting ash weights from dry weights. Zooplankton biomass did not include chaoborids which were removed individually before drying. All chaoborids collected in samples were counted and measured. No correction was applied on body dimension for shrinkage in formalin. Based on size of species, we found that size fraction  $> 500\ \mu\text{m}$  was mainly composed by the cladocerans *Holopedium gibberum*, the calanoid *Aglaodiaptomus leptopus* and the cyclopoid *Orthocyclops modestus*; the 202-500  $\mu\text{m}$  size fraction by the cladocerans *Diaphanosoma brachyurum* and *Bosmina* spp., the cyclopoid *Tropocyclops prasinus*, and instars of calanoids and cyclopoids; the 100-202  $\mu\text{m}$  size fraction by the nauplii of

calanoids and cyclopoids and the rotifer *Trichocerca* spp.; and the 53-100  $\mu\text{m}$  size fraction by the rotifers *Conochilus* spp., *Keratella cochlearis* and *K. taurocephala*. For small fractions ( $< 202 \mu\text{m}$ ), organic carbon weights included particulate organic matter such as net phytoplankton and detritus observed in the samples. However, algae and detritus contamination was mainly apparent in the 53-100  $\mu\text{m}$  size fraction.

#### 1.2.4 Statistical treatments

To describe vertical and horizontal spatial patterns in water chemistry, size and density of invertebrate predators, chlorophyll *a* size fractions, and zooplankton biomass of each size fraction, we computed their means and standard deviations for each water layer (epi-, meta-, and hypolimnion). Differences among layers on the vertical axis were tested for significance using nonparametric ANOVA (Kruskal-Wallis tests) and multiple comparisons tests (Mann-Whitney tests) (Zar 1984). Multivariate analyses were performed to identify clusters of stations with similar abiotic and biotic conditions for the whole lake and each limnetic layer. Nine abiotic variables (temperature, oxygen, alkalinity, conductivity and turbidity, DOC and silica,  $\text{NH}_4$  and SRP) were used in the analyses while pH,  $\text{NO}_3$  and TDP were not retained because they were highly correlated with alkalinity,  $\text{NH}_4$  and SRP respectively ( $r > 0.5$ ;  $P < 0.05$ ). For the biotic variables, we considered zooplankton biomass of each size fraction, chlorophyll *a* fractions, abundance and mean size of chaoborids. Gower's coefficient (S15) was used to construct the similarity matrices independently for abiotic and biotic factors. This coefficient has been chosen for two reasons : (1) it considers double zeros as an indication of resemblance, (2) because it permits the combinaison of different types of descriptors after having processed each of them according to its own mathematical type (Legendre and Legendre 1984). Thereafter, a hierarchical agglomerative clustering model, based on proportional link with 75% connectedness, was carried out to form homogeneous clusters of stations (running biotic and abiotic variables separately). Following the cluster analyses the data sets were further subjected to Principal Coordinates Analysis (PCoA). This analysis provided a view of the sampling site similarities in 2-, or more- dimensional space, when the cluster analysis dendrogram is fundamentally 1-dimensional.

In attempt to identify the important factors explaining zooplankton biomass distribution either on the whole lake or in each water layer, we computed nonparametric correlations (Kendall's tau : Conover 1980) between abiotic variables and the two PCoA axes coordinates. The same approach was applied (correlations between biotic variables

and axes coordinates) to show how biotic variables were distributed among station clusters based on the abiotic variables. The significance of the differences between clusters of stations based on abiotic (or biotic) factors was tested using nonparametric ANOVA.

We used stepwise multiple regressions to identify the main abiotic and biotic factors influencing the total zooplankton biomass and that of each size fraction (Neter et al. 1990). In these statistical analyses, we preferred pH to alkalinity because it explained a larger variation of zooplankton biomass. Normality of data was verified using Kolmogorov Smirnov tests. Statistical analyses were performed with SPSS 4.0 and R software package (Legendre and Vaudor 1991) for Macintosh computers.

## 1.3 RESULTS

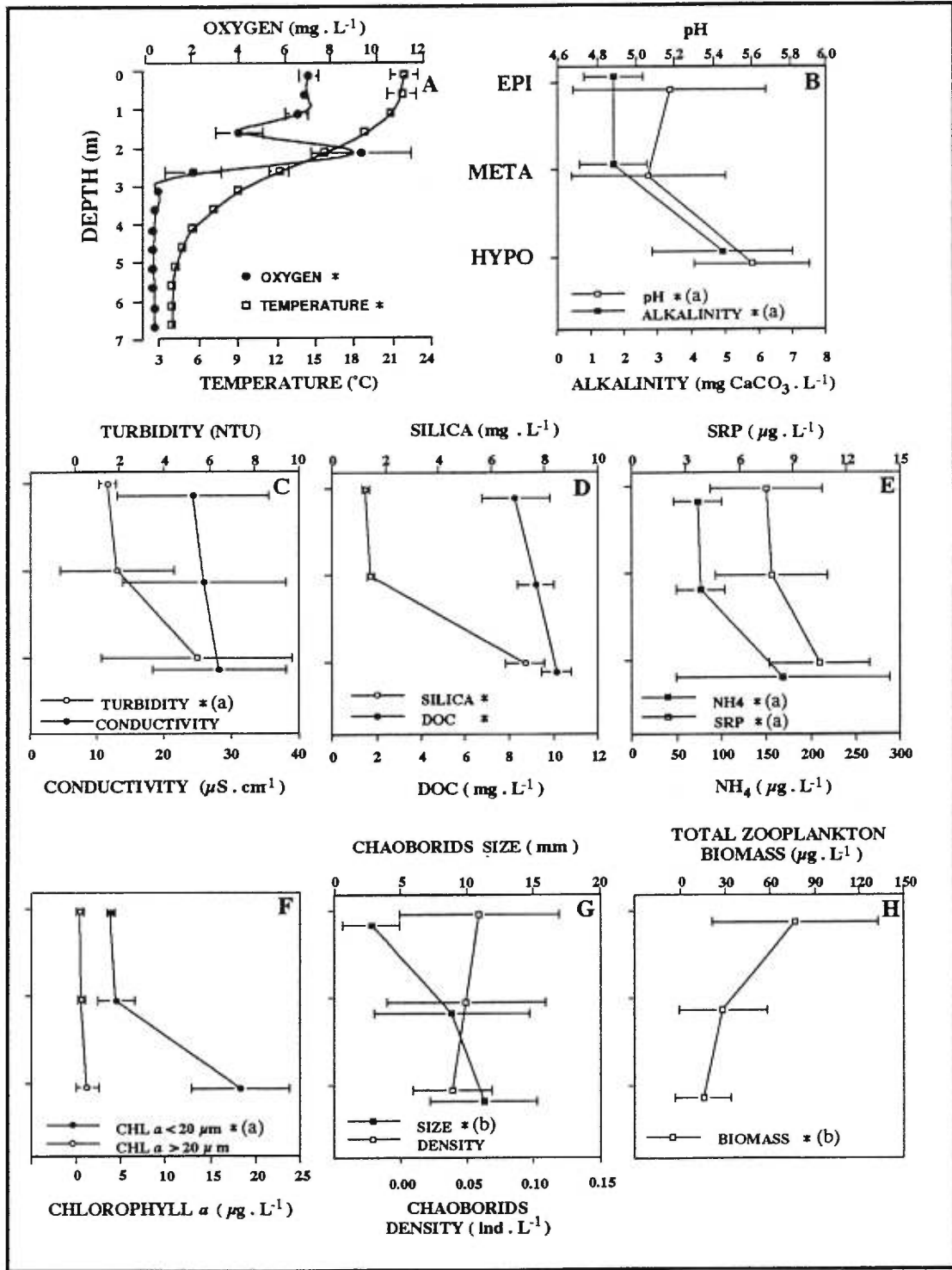
### 1.3.1 Vertical profiles of abiotic and biotic variables

At the time of sampling, Lake Geai was well stratified (Figure 3A). Water temperature reached 22 °C in the epilimnion (0 - 1.5 m), decreased rapidly from 21 to 9 °C in the metalimnion (1.5 - 3 m), and more slowly from 9 to 4 °C in the hypolimnion (3 - 7 m). The oxygen profile followed a positive heterograde curve (Figure 3A), with a maximum of 14 mg.L<sup>-1</sup> in the metalimnion. Oxygen concentrations at the surface were about 7 mg.L<sup>-1</sup>, while hypolimnetic waters were anoxic. pH and alkalinity profiles were similar (Figure 3B) with maximum values in the hypolimnion (mean of 5.6 and 5.0 mg CaCO<sub>3</sub>.L<sup>-1</sup> respectively). The alkalinity of Lake Geai was very low with a maximum of 8.8 mg CaCO<sub>3</sub>.L<sup>-1</sup>; pH ranged from 3.95 to 6.08. Significant differences were observed in pH and alkalinity between the two surface layers and the hypolimnion ( $P \leq 0.003$ ) but no significant variations occurred between epi- and metalimnion ( $P = 0.16$  and  $0.84$ ). Turbidity and conductivity tended to increase from the epilimnion to the hypolimnion (Figure 3C), but these variations were not significant for conductivity ( $P \geq 0.26$ ) and between the epi- and metalimnion strata for turbidity ( $P = 0.37$ ). Conductivity varied greatly in the horizontal plane, from 16.5 to 65  $\mu\text{S}\cdot\text{cm}^{-1}$ .

All nutrients (DOC, silica, SRP, NH<sub>4</sub>) concentrations increased with depth (Figures 3D and E). Mean values were significantly different among layers ( $P \leq 0.02$ ), except between the epi- and metalimnion for SRP ( $P = 0.90$ ) and NH<sub>4</sub> ( $P = 0.36$ ). Mean concentrations of silica in the hypolimnion were six times higher than those in the



Figure 3 : Values (means and standard deviation) of main abiotic and biotic variables in the three limnetic layers, epi-, meta-, and hypolimnion. Variables that showed significant differences between all layers are marked with an asterisk; variables that showed nonsignificant differences between the epi- and metalimnion are marked "a", between the epi- and hypolimnion are marked "b", and between the meta- and hypolimnion "c".



epilimnion (7.27 vs 1.20 mg.L<sup>-1</sup>), and there was no difference in mean silica concentration between epi- and metalimnion. Concentrations of dissolved organic carbon (DOC), soluble reactive phosphorus (SRP) and ammonia (NH<sub>4</sub>) ranged between 7.3 - 16.2 mg.L<sup>-1</sup>, 1.3 - 17.3 µg.L<sup>-1</sup>, and 3.4 - 390 µg.L<sup>-1</sup> respectively.

Algae < 20 µm accounted for most of the total chlorophyll *a* and the highest concentration was 28 µg.L<sup>-1</sup> in the hypolimnion (Figure 3F). Concentrations differed among layers ( $P \leq 0.001$ ) except between epi- and metalimnion ( $P = 0.10$ ) where the lowest concentrations occurred (< 5 µg.L<sup>-1</sup>). Chlorophyll *a* concentrations were low for the size fraction > 20 µm ( $\approx 0.7$  µg.L<sup>-1</sup>) and did not differ among layers ( $P \geq 0.23$ ).

The mean abundance of chaoborids varied between 0.03 and 0.06 ind.L<sup>-1</sup> into the three limnetic strata (Figure 3G), but did not differ among layers ( $P \geq 0.13$ ). We found the highest densities of chaoborids (3.67 ind.L<sup>-1</sup>; data not included) at the water-sediment interface (last 1 m above the sediment). A maximum of 0.28 ind.L<sup>-1</sup> was observed in the epilimnion where the larvae were of small size ( $P \leq 0.004$ ) compared with those in the deeper strata (2.6 vs 11.1 mm). No change in mean size was noted between meta- and hypolimnion ( $P = 0.62$ ; Figure 3G).

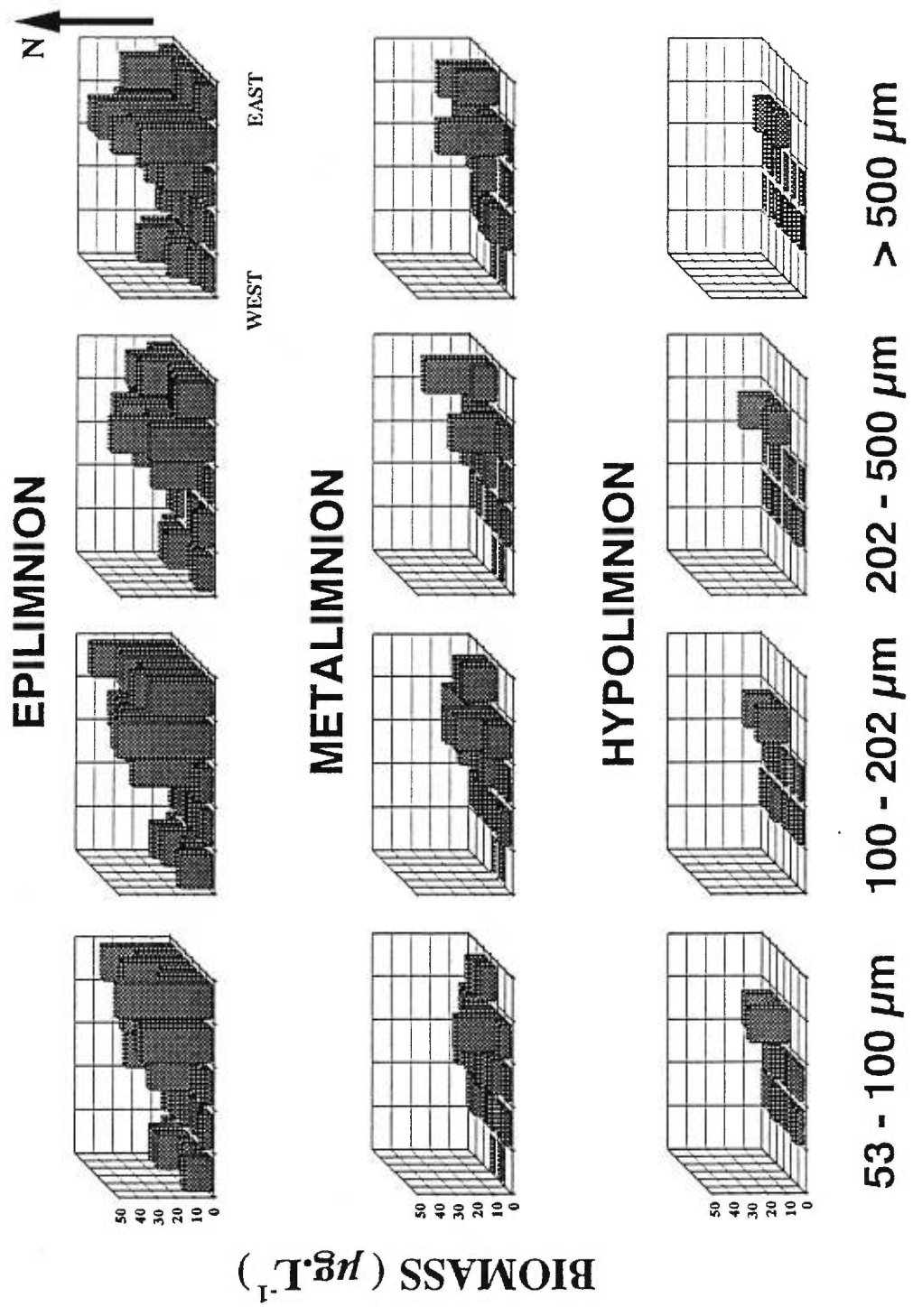
A 24h diel cycle study was carried out the day following the sampling to detect diel vertical migration of the chaoborids. We observed a night-time ascent and a day-time descent indicating a consistent pattern of vertical migration despite the absence of fish. The highest densities (0.75 ind.L<sup>-1</sup>) were detected in the epilimnion at 11h pm while in this stratum, chaoborids densities remained lower than 0.10 ind.L<sup>-1</sup> during the daylight period. During the day, maximum densities were observed in the hypolimnion at 11 AM (0.33 ind.L<sup>-1</sup>).

Total zooplankton biomass decreased with increasing depth ( $P \leq 0.002$ ; Figure 3H), but no significant difference was observed between meta- and hypolimnetic layers ( $P \geq 0.11$ ). Mean biomass declined from 76.9 to 15.1 µg.L<sup>-1</sup> from the epilimnion to the hypolimnion, while 207 µg.L<sup>-1</sup> was the highest biomass observed in the epilimnion.

### 1.3.2 Zooplankton spatial patterns

Figure 4 illustrates the spatial distribution of zooplankton of each size fraction in each water layer. The vertical and horizontal patterns were quite similar for each size

Figure 4 : Horizontal distribution of the four size classes zooplankton biomass in each limnetic layer.



fractions. The distribution of the biomass of each size fraction was positively correlated to those of other size fractions ( $r \geq 0.43$  ;  $P \leq 0.001$ ). On the vertical axis, the highest biomasses of each size fraction were observed in the epilimnion and they progressively decreased with increasing depth as shown for total zooplankton biomass (Figure 3H). Strong spatial heterogeneity occurred on the horizontal axis, particularly in the epilimnion; biomasses were higher in the east part of the lake.

### 1.3.3 Vertical distribution patterns of abiotic and biotic variables

The physico-chemical stratification is more accentuated in the vertical axis (Figure 5A). PCoA clustered the stations in 2 main groups; one included the hypolimnetic stations (group 1) and the other the epi- and metalimnion stations (group 2). The first axis mainly represented an increasing gradient of alkalinity ( $r = - 0.63$  ;  $P = 0.001$ ) and DOC concentration ( $r = - 0.43$  ;  $P = 0.001$ ) with depth, and a decreasing gradient of temperature ( $r = 0.53$  ;  $P = 0.01$ ) from epi- and metalimnion to the hypolimnion. Total zooplankton biomass and all size fractions were significantly greater in group 2 ( $P \leq 0.006$ ; Table I). On the other hand, stations in the hypolimnion were characterized by larger chaoborids (11.12 vs 5.19 mm;  $P = 0.001$ ) and higher total chlorophyll *a* and algae  $< 20 \mu\text{m}$  concentrations ( $P = 0.001$ ) than in the epi- and metalimnion stations (Table I).

Based on biotic variables (Figure 5B), stations were also classified on the first axis in 2 groups, where group 1 (including hypolimnion stations) was defined by the highest chlorophyll *a*  $< 20 \mu\text{m}$  concentrations ( $r = - 0.32$ ;  $P = 0.001$ ) and the lowest zooplankton biomass (all size fractions,  $r \geq 0.63$ ;  $P = 0.001$ ). This group showed significant differences in water alkalinity ( $P = 0.003$ ), temperature ( $P = 0.009$ ), silica ( $P = 0.004$ ) and DOC concentrations ( $P = 0.001$ ) (Table I). The second axis of this analysis contributed to separate stations (groups 1b and 2b) characterized by higher chaoborid size ( $r = - 0.69$ ;  $P = 0.001$ ) and density ( $r = - 0.37$ ;  $P = 0.001$ ) and higher chlorophyll *a*  $< 20 \mu\text{m}$  concentrations ( $r = - 0.34$ ;  $P = 0.001$ ) than the other stations (groups 1a and 2a) generally located in the epi- and metalimnion.

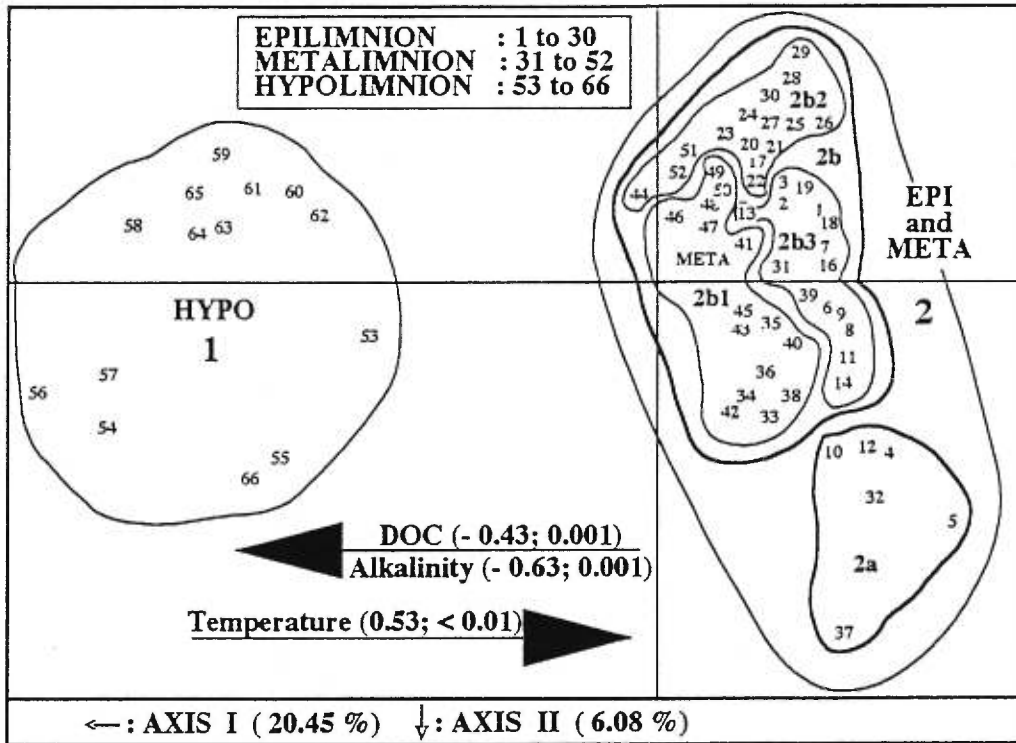
### 1.3.4 Horizontal distribution patterns of abiotic and biotic variables

For each water layer, the west side and east side stations of the lake were clustered in separate groups (Figures 6A, 7A and 8A). Group 2 (east side stations) showed higher

Figure 5 : PCoA for the whole lake based on water chemistry (A), and biotic variables (B). The direction of the arrows indicates the highest values of variables; Values in parentheses are Kendall correlations and probabilities.

# WHOLE LAKE

## 5A : ABIOTIC FACTORS



## 5B : BIOTIC FACTORS

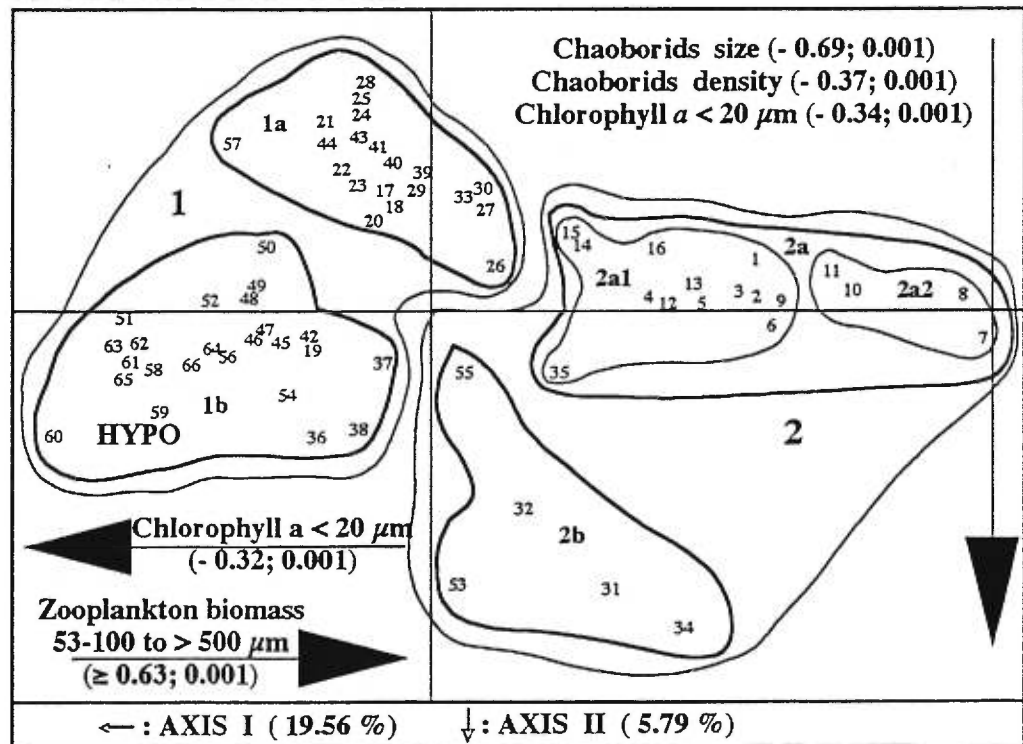




Table I : Values of biotic and abiotic variables of groups of stations defined by PCoA analyses based on the spatial distribution of abiotic (Fig. 5A) and biotic (Fig. 5B) variables in the whole lake.

Biotic variable	GROUP 1		GROUP 2		P	Abiotic variable	GROUP 1		GROUP 2		P
	(n = 14)	(n = 52)	(n = 14)	(n = 52)			(n = 44)	(n = 22)			
<b>Zooplankton</b>											
Total ( $\mu\text{g.L}^{-1}$ )	15.07 (18.34)	56.37 (51.97)	0.001	Conductivity ( $\mu\text{S.cm}^{-1}$ )	23.2 (8.80)	29.2 (14.2)	0.092				
53-100 $\mu\text{m}$	5.43 (5.88)	13.42 (12.22)	0.006	Alkalinity ( $\text{mg.L}^{-1}$ )	2.93 (1.99)	1.56 (0.99)	0.003				
100-202 $\mu\text{m}$	3.93 (4.98)	15.79 (14.75)	0.001	Temperature ( $^{\circ}\text{C}$ )	15.5 (6.13)	19.5 (4.58)	0.009				
202-500 $\mu\text{m}$	3.57 (5.26)	12.27 (12.22)	0.002	Oxygen ( $\text{mg.L}^{-1}$ )	5.97 (4.23)	6.05 (2.02)	0.828				
> 500 $\mu\text{m}$	2.14 (3.03)	14.94 (18.04)	0.001	Turbidity (NTU)	2.93 (3.30)	1.73 (1.47)	0.466				
<b>Chaoborids</b>											
size (mm)	11.12 (4.03)	5.19 (5.09)	0.001	NH4 ( $\mu\text{g.L}^{-1}$ )	103 (81.7)	76.5 (28.9)	0.170				
density (individuals/L)	0.04 (0.03)	0.06 (0.06)	0.618	SRP ( $\mu\text{g.L}^{-1}$ )	8.10 (3.36)	8.43 (3.11)	0.596				
<b>Chlorophyll <i>a</i></b>											
Total ( $\mu\text{g.L}^{-1}$ )	16.45 (5.35)	2.48 (0.96)	0.001	Silica ( $\text{mg.L}^{-1}$ )	2.97 (2.73)	1.74 (1.66)	0.004				
> 20 $\mu\text{m}$	1.27 (1.28)	0.49 (0.52)	0.209	DOC ( $\text{mg.L}^{-1}$ )	9.32 (1.49)	8.29 (0.78)	0.001				
< 20 $\mu\text{m}$	16.22 (5.42)	2.14 (1.33)	0.001								

Note: Values are given as the mean with the standard deviation in parentheses. Values in boldface type are significantly different according to Mann-Whitney tests.

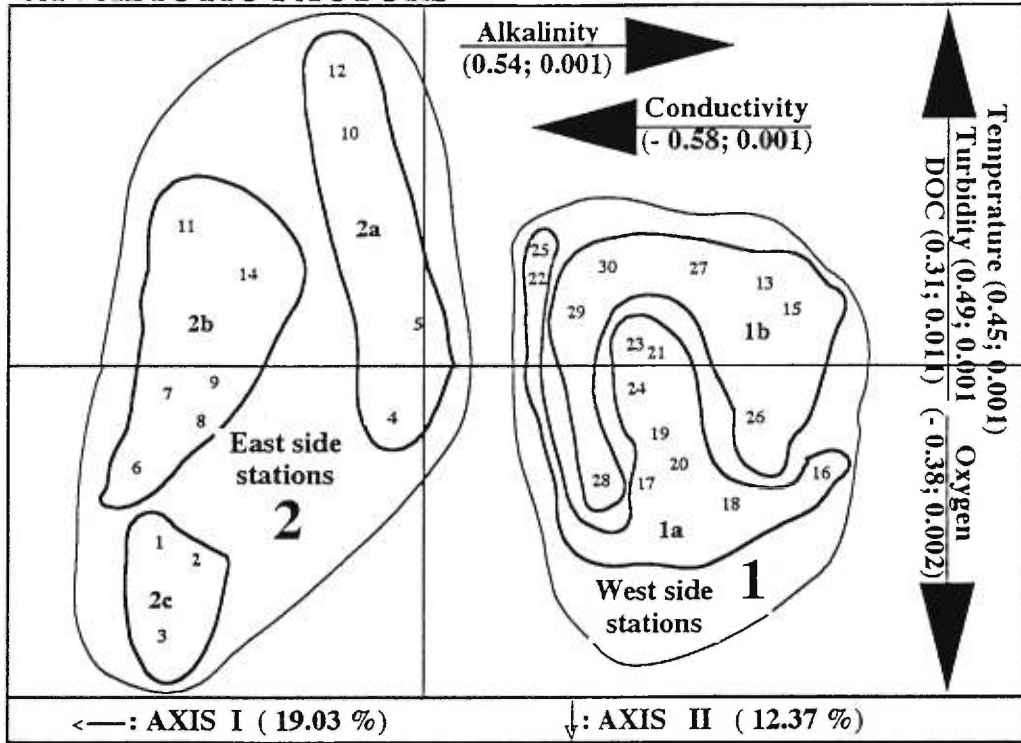
conductivity ( $r \geq -0.42$ ;  $P \leq 0.022$ ) and lower alkalinity ( $r \geq 0.54$ ;  $P \leq 0.001$ ; except for the hypolimnion) than group 1 (west side stations). Total zooplankton biomass and biomasses of the size fractions were significantly higher in the east side stations in the epilimnetic waters ( $P \leq 0.044$ ; Table II). In the metalimnetic layer, the zooplankton biomass of fraction  $< 500 \mu\text{m}$  were significantly greater in east side stations ( $P \leq 0.028$ ; Table III), while only one size fraction (53-100  $\mu\text{m}$ ) was significantly different between groups in the hypolimnion ( $P = 0.044$ ; Table IV). Chaoborid density was also significantly higher in the east side stations (group 2) of the epilimnion ( $P = 0.012$ ; Table II), while higher chaoborids size and density were observed in the hypolimnetic stations on the west side ( $P \leq 0.026$ ; Table IV). On the second PCoA axis (Figure 6A), epilimnetic west side stations were differentiated by a positive gradient of DOC ( $r = 0.31$ ;  $P = 0.011$ ), temperature ( $r = 0.45$ ;  $P = 0.001$ ) and turbidity ( $r = 0.49$ ;  $P = 0.001$ ) and a negative one of oxygen ( $r = -0.38$ ;  $P = 0.002$ ) from subgroups 1a and 1b. Subgroup 1b presented significant ( $P \leq 0.047$ ; data not included) higher zooplankton biomass (57 vs 27  $\mu\text{g.L}^{-1}$ ), chlorophyll *a* (2.49 vs 2.09  $\mu\text{g.L}^{-1}$ ) and lower density of chaoborids (0.02 vs 0.08  $\text{ind.L}^{-1}$ ). For the meta- and hypolimnetic layers (Figures 7A and 8A), no significant difference in the zooplankton biomass was observed between subgroups.

PCoA based on biotic variables clustered west side (group 1) and east side (group 2) stations in two groups only in the epilimnetic waters (Figures 6B, 7B, and 8B). There was a positive gradient of all size classes of zooplankton biomass ( $r \leq 0.46$ ;  $P = 0.001$ ), chaoborids density ( $r = 0.55$ ;  $P = 0.001$ ) and size ( $r = 0.41$ ;  $P = 0.001$ ) and a negative one for chlorophyll *a* ( $r = -0.30$ ;  $P = 0.011$ ) from group 1 (west side) to group 2 (east side; Figure 6B). East side stations were characterised by significant higher conductivity ( $P = 0.001$ ) and lower alkalinity ( $P = 0.01$ ; Table II). Although differentiated by their zooplanktonic biomass, stations in meta- and hypolimnion did not present significant difference in abiotic conditions (Tables III and IV). However, sub-group 1b of the metalimnion (Figure 7B) presented greater chaoborid size (11.55 vs 5.29 mm) and chlorophyll *a*  $< 20 \mu\text{m}$  concentration (3.43 vs 1.98  $\mu\text{g.L}^{-1}$ ) than sub-group 1a. Group 1a had the highest zooplankton biomass ( $> 500 \mu\text{m}$ : 4.73 vs 3.25  $\mu\text{g.L}^{-1}$ ; 202-500  $\mu\text{m}$ : 5.82 vs 1.25  $\mu\text{g.L}^{-1}$ ; 100-202  $\mu\text{m}$ : 8.73 vs 1.38  $\mu\text{g.L}^{-1}$ ; 53-100  $\mu\text{m}$ : 8 vs 2  $\mu\text{g.L}^{-1}$ ). Higher conductivity characterized also group 1a stations (26.95 vs 19.25  $\mu\text{S.cm}^{-1}$ ;  $P = 0.036$ ; data not included).

Figure 6 : PCoA for the epilimnion based on water chemistry (A), and biotic variables (B). For details see Fig. 5.

# EPILIMNION

## 6A : ABIOTIC FACTORS



## 6B : BIOTIC FACTORS

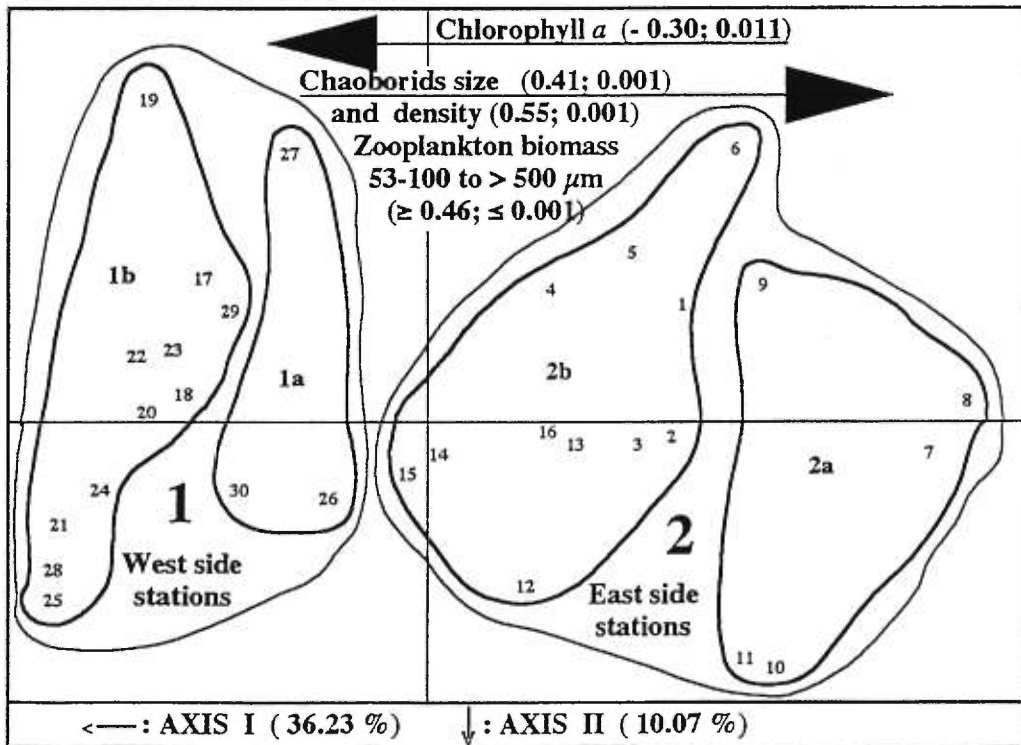


Table II : Values of biotic and abiotic variables of groups of stations defined by PCoA analyses based on the spatial distribution of abiotic (Fig. 6A) and biotic (Fig. 6B) variables in epilimnetic waters.

Biotic variable	GROUP 1		GROUP 2		P	Abiotic variable		GROUP 1		GROUP 2		P
	West side (n = 17)	East side (n = 13)	West side (n = 14)	East side (n = 16)		West side (n = 14)	East side (n = 16)					
<b>Zooplankton</b>												
Total ( $\mu\text{g.L}^{-1}$ )	39.8 (29.4)	125 (43.2)	0.001	0.001	Conductivity ( $\mu\text{S.cm}^{-1}$ )	17.9 (0.76)	29.1 (13.4)	0.001				
53-100 $\mu\text{m}$	9.71 (7.84)	29.7 (10.4)	0.001	0.001	Alkalinity ( $\text{mg.L}^{-1}$ )	2.28 (0.31)	1.35 (0.98)	0.010				
100-202 $\mu\text{m}$	10.6 (9.04)	36.5 (8.84)	0.001	0.001	Temperature ( $^{\circ}\text{C}$ )	21.9 (0.40)	21.8 (0.31)	0.325				
202-500 $\mu\text{m}$	8.29 (7.45)	26.9 (10.9)	0.001	0.001	Oxygen ( $\text{mg.L}^{-1}$ )	6.14 (0.56)	6.37 (0.33)	0.492				
> 500 $\mu\text{m}$	11.4 (7.48)	32.5 (26.4)	0.008	0.008	Turbidity (NTU)	1.65 (0.49)	1.46 (0.27)	0.441				
<b>Chaoborids</b>												
size (mm)	2.57 (2.86)	2.73 (0.39)	0.106	0.106	NH4 ( $\mu\text{g.L}^{-1}$ )	69.1 (22.7)	76.8 (30.1)	0.740				
density (individuals/L)	0.05 (0.05)	0.09 (0.06)	0.012	0.012	SRP ( $\mu\text{g.L}^{-1}$ )	6.51 (2.78)	8.33 (3.29)	0.124				
<b>Chlorophyll a</b>												
Total ( $\mu\text{g.L}^{-1}$ )	2.33 (0.35)	2.20 (0.14)	0.325	0.325	Silica ( $\text{mg.L}^{-1}$ )	1.20 (0.06)	1.21 (0.06)	0.394				
> 20 $\mu\text{m}$	0.51 (0.29)	0.33 (0.23)	0.098	0.098	DOC ( $\text{mg.L}^{-1}$ )	8.56 (2.21)	8.03 (0.54)	0.660				
< 20 $\mu\text{m}$	1.88 (0.47)	1.88 (0.24)	0.630	0.630								

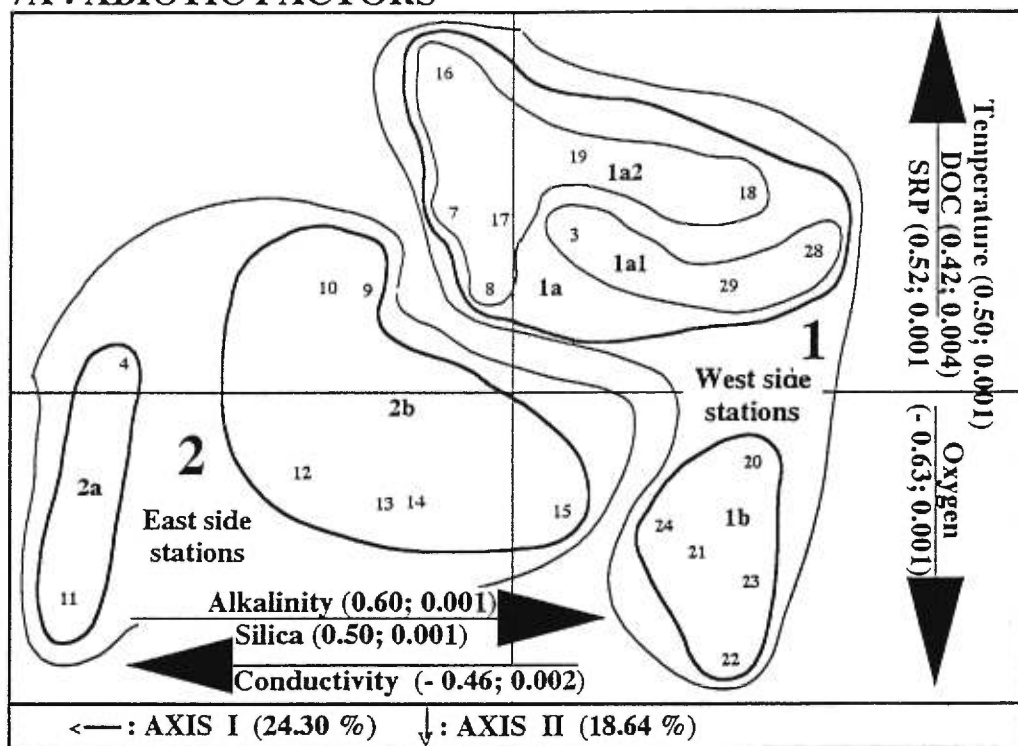
Note: Values are given as the mean with the standard deviation in parentheses. Values in boldface type are significantly different according to Mann-Whitney tests.

Figure 7 : PCoA for the metalimnion based on water chemistry (A), and biotic variables (B). For details see Fig. 5.



# METALIMNION

## 7A : ABIOTIC FACTORS



## 7B : BIOTIC FACTORS

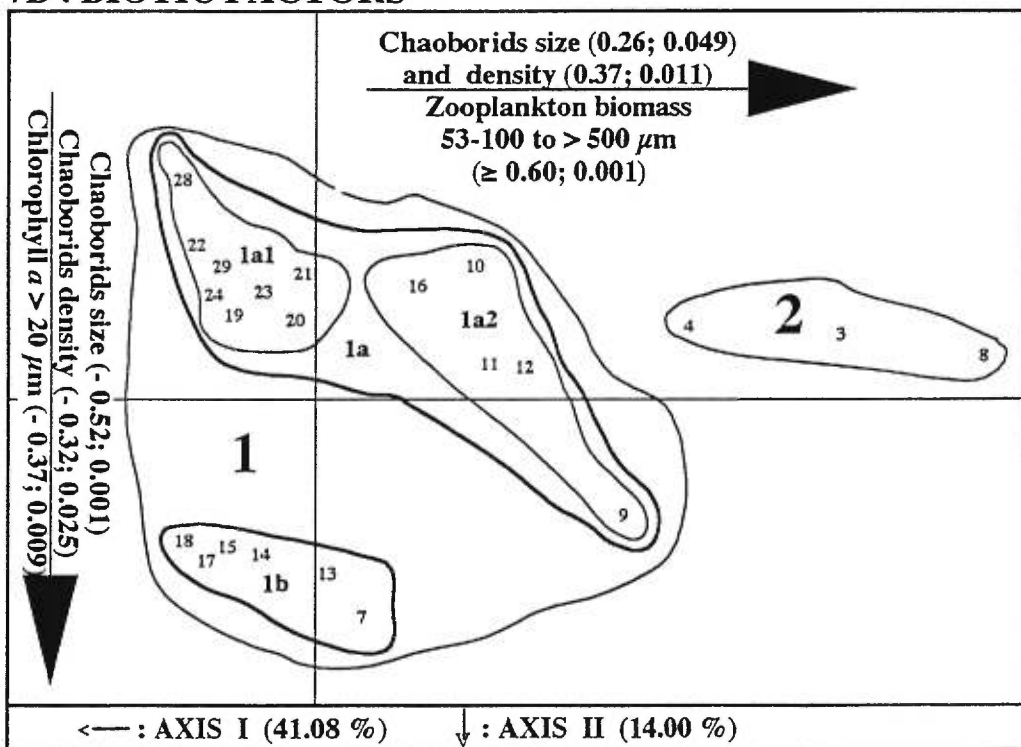


Table III : Values of biotic and abiotic variables of groups of stations defined by PCoA analyses based on the spatial distribution of abiotic (Fig. 7A) and biotic (Fig. 7B) variables in metalimnetic waters.

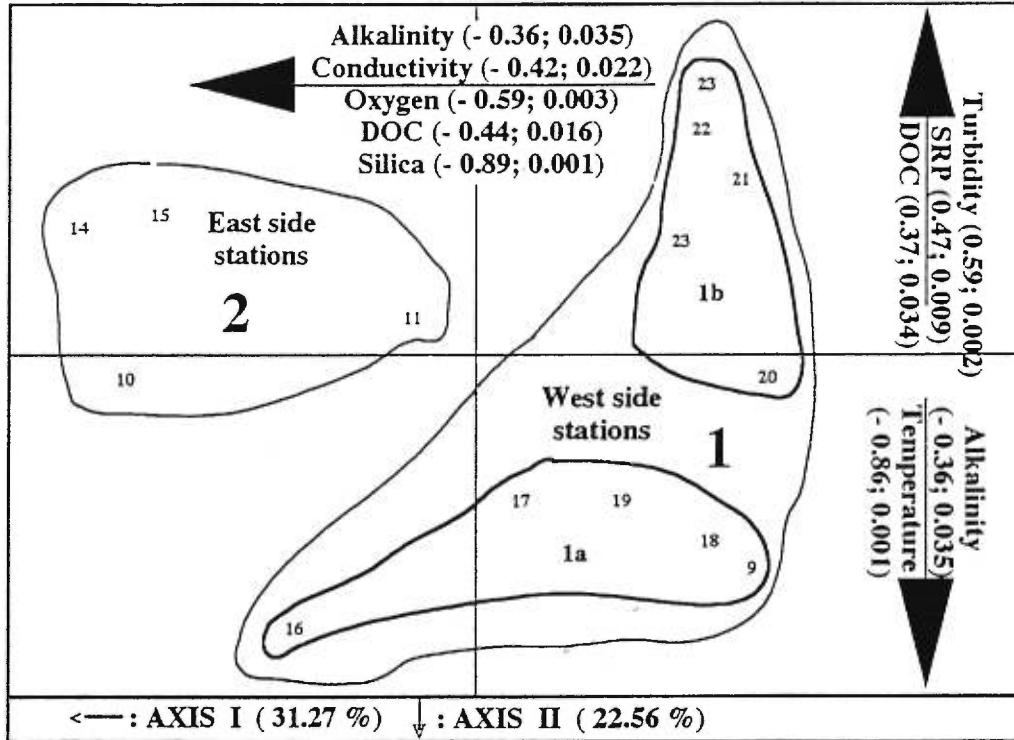
Biotic variable	GROUP 1		GROUP 2		P	Abiotic variable	GROUP 1		GROUP 2		P
	West side (n = 14)	East side (n = 8)	West side (n = 19)	East side (n = 3)			West side (n = 19)	East side (n = 3)			
<b>Zooplankton</b>											
Total ( $\mu\text{g.L}^{-1}$ )	24.5 (33.6)	32.3 (18.6)	0.101	0.101	Conductivity ( $\mu\text{S.cm}^{-1}$ )	23.7 (8.79)	37.0 (24.8)	0.532			
53-100 $\mu\text{m}$	<b>5.29 (6.14)</b>	<b>9.13 (3.31)</b>	<b>0.013</b>	<b>0.013</b>	Alkalinity ( $\text{mg.L}^{-1}$ )	1.79 (1.05)	1.65 (0.61)	0.667			
100-202 $\mu\text{m}$	<b>5.50 (7.60)</b>	<b>11.3 (7.89)</b>	<b>0.024</b>	<b>0.024</b>	Temperature ( $^{\circ}\text{C}$ )	16.4 (0.61)	16.7 (0.29)	0.921			
202-500 $\mu\text{m}$	<b>6.29 (10.7)</b>	<b>7.50 (3.85)</b>	<b>0.028</b>	<b>0.028</b>	Oxygen ( $\text{mg.L}^{-1}$ )	9.58 (2.49)	8.00 (0.53)	0.416			
> 500 $\mu\text{m}$	7.36 (10.7)	7.25 (7.03)	0.391	0.391	Turbidity (NTU)	2.08 (2.71)	1.26 (0.20)	0.165			
<b>Chaoborids</b>											
size (mm)	9.40 (5.43)	7.42 (6.76)	0.558	0.558	$\text{NH}_4$ ( $\mu\text{g.L}^{-1}$ )	79.1 (27.6)	58.5 (12.2)	0.094			
density (individuals/L)	0.05 (0.06)	0.05 (0.07)	0.972	0.972	SRP ( $\mu\text{g.L}^{-1}$ )	7.67 (3.13)	8.41 (3.81)	0.599			
<b>Chlorophyll <i>a</i></b>											
Total ( $\mu\text{g.L}^{-1}$ )	2.91 (1.74)	2.54 (0.50)	0.453	0.453	Silica ( $\text{mg.L}^{-1}$ )	1.44 (0.11)	1.34 (0.25)	0.473			
> 20 $\mu\text{m}$	0.51 (0.73)	0.65 (0.78)	0.373	0.373	DOC ( $\text{mg.L}^{-1}$ )	9.27 (0.79)	8.70 (1.10)	0.412			
< 20 $\mu\text{m}$	<b>2.82 (2.42)</b>	<b>1.92 (0.37)</b>	<b>0.838</b>	<b>0.838</b>							

Note: Values are given as the mean with the standard deviation in parentheses. Values in boldface type are significantly different according to Mann-Whitney tests.

Figure 8 : PCoA for the hypolimnion based on water chemistry (A), and biotic variables (B). For details see Fig. 5.

# HYPOLIMNION

## 8A : ABIOTIC FACTORS



## 8B : BIOTIC FACTORS

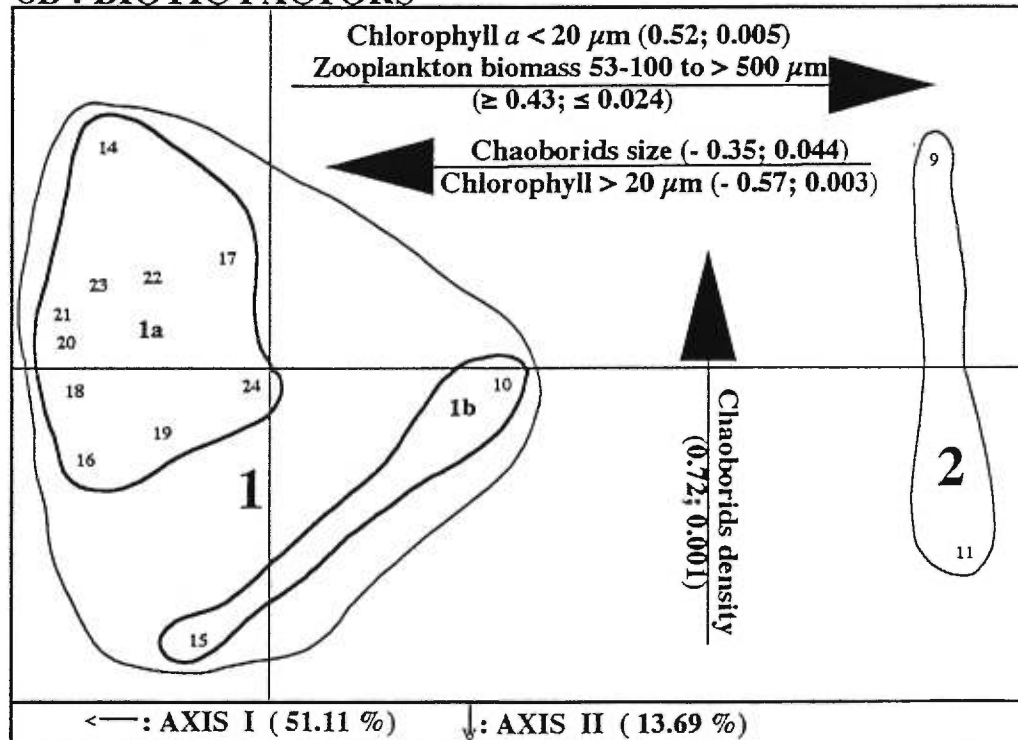


Table IV : Values of biotic and abiotic variables of groups of stations defined by PCoA analyses based on the spatial distribution of abiotic (Fig. 8A) and biotic (Fig. 8B) variables in hypolimnetic waters.

Biotic variable	GROUP 1		GROUP 2		P	Abiotic variable	GROUP 1		GROUP 2		P
	West side (n = 10)	East side (n = 4)	West side (n = 12)	East side (n = 2)							
<b>Zooplankton</b>											
Total ( $\mu\text{g.L}^{-1}$ )	11.5 (15.8)	24.0 (23.6)	28.3 (10.6)	24.0 (1.41)	0.087	Conductivity ( $\mu\text{S.cm}^{-1}$ )	28.3 (10.6)	24.0 (1.41)	0.659		
53-100 $\mu\text{m}$	<b>4.40 (5.93)</b>	<b>8.00 (5.66)</b>	5.33 (2.10)	3.11 (0.06)	<b>0.044</b>	Alkalinity ( $\text{mg.L}^{-1}$ )	5.33 (2.10)	3.11 (0.06)	0.198		
100-202 $\mu\text{m}$	3.30 (4.57)	5.50 (6.35)	6.33 (0.37)	6.75 (0.35)	0.272	Temperature ( $^{\circ}\text{C}$ )	6.33 (0.37)	6.75 (0.35)	0.198		
202-500 $\mu\text{m}$	2.40 (3.60)	6.50 (8.06)	0.14 (0.04)	0.15 (0.07)	0.311	Oxygen ( $\text{mg.L}^{-1}$ )	0.14 (0.04)	0.15 (0.07)	0.923		
> 500 $\mu\text{m}$	1.30 (2.11)	4.25 (4.27)	5.66 (4.34)	4.60 (5.09)	0.101	Turbidity (NTU)	5.66 (4.34)	4.60 (5.09)	0.791		
<b>Chaoborids</b>											
size (mm)	<b>13.0 (1.32)</b>	<b>6.46 (4.94)</b>	182.3 (122.3)	81.3 (33.1)	<b>0.005</b>	NH4 ( $\mu\text{g.L}^{-1}$ )	182.3 (122.3)	81.3 (33.1)	0.264		
density (individuals/L)	<b>0.05 (0.03)</b>	<b>0.02 (0.01)</b>	10.6 (2.97)	9.87 (2.40)	<b>0.026</b>	SRP ( $\mu\text{g.L}^{-1}$ )	10.6 (2.97)	9.87 (2.40)	0.923		
<b>Chlorophyll <math>\alpha</math></b>											
Total ( $\mu\text{g.L}^{-1}$ )	15.5 (4.30)	19.0 (7.55)	7.34 (0.75)	6.85 (0.46)	0.322	Silica ( $\text{mg.L}^{-1}$ )	7.34 (0.75)	6.85 (0.46)	0.659		
> 20 $\mu\text{m}$	1.49 (1.41)	0.73 (0.78)	10.2 (0.68)	9.75 (0.49)	0.390	DOC ( $\text{mg.L}^{-1}$ )	10.2 (0.68)	9.75 (0.49)	0.352		
< 20 $\mu\text{m}$	14.6 (4.84)	20.2 (5.25)			0.120						

Note: Values are given as the mean with the standard deviation in parentheses. Values in boldface type are significantly different according to Mann-Whitney tests.

### 1.3.5 Multiple-regression models of vertical and horizontal zooplankton biomass distributions

Chaoborid density and size and vertical depth profiles of temperature, oxygen and pH explained together between 30 to 55% of the spatial variation of total zooplankton biomass and biomasses of the size fractions (Table V).

Table V. Best models predicting total zooplankton biomass and biomasses of each size fraction ( $\mu\text{g}\cdot\text{L}^{-1}$ ) in the whole lake ( $n = 66$ ).

Equation	Model		$r^2$	SE
1 A	Total zooplankton =	+ 124.02		
		+ 374.46 chaoborid density	<b>0.30</b>	42.19
		+ 4.49 temperature	<b>0.46</b>	37.29
		- 4.46 O <sub>2</sub>	<b>0.50</b>	36.25
		- 27.55 pH	<b>0.55</b>	34.57
1 B	Zooplankton > 500 $\mu\text{m}$ =	- 11.20		
		+ 1.05 temperature	<b>0.18</b>	15.48
		+ 109.89 chaoborid density	<b>0.30</b>	14.43
1 C	Zooplankton 202-500 $\mu\text{m}$ =	- 6.82		
		+ 105.92 chaoborid density	<b>0.29</b>	9.94
		+ 0.702 temperature	<b>0.42</b>	9.10
1 D	Zooplankton 100-202 $\mu\text{m}$ =	+ 51.17		
		+ 148.83 chaoborid density	<b>0.32</b>	11.80
		- 0.99 chaoborid size	<b>0.50</b>	10.23
		- 7.47 pH	<b>0.55</b>	9.72
1 E	Zooplankton 53-100 $\mu\text{m}$ =	+ 10.97		
		+ 126.99 chaoborid density	<b>0.27</b>	10.05
		- 0.90 chaoborid size	<b>0.45</b>	8.83

Note: The coefficient of determination ( $r^2$ ) of the model as well as the partial  $r^2$  of the coefficients, and the standard error of the coefficients (SE) are listed. Chaoborid density is given in individual/L, chaoborid size in millimetres, temperature in degrees Celcius, and oxygen concentration in milligrams per litre.



Positive relationships were observed with density of chaoborids and temperature since these variables showed higher values in the epilimnetic layer where zooplankton biomasses were greater (Table V). Although no significant variations in chaoborids density were depicted on the vertical axis (Figure 3G), the relationship could also be caused by similar distribution patterns of chaoborids and zooplankton in the horizontal axis. The fact that the density of chaoborids is a primary factor determining zooplankton biomass in the whole lake suggests that horizontal heterogeneity is as important as the vertical one. This result is opposed to the PCoA also applied on the whole lake data (Figure 5A). The negative relationships with chaoborids size and pH reflect the lower biomass of zooplankton in hypolimnetic water and could indicate the effect of predation of larger chaoborids on small zooplankters (Equations 1D and 1E in Table V). In these relationships, pH represented the alkalinity level ( $r = 0.80$  with pH) in the water column that increased with depth.

Chaoborid density, pH, and  $\text{NH}_4$  concentration accounted for 17 to 74% of the horizontal variation in zooplankton biomass in the epi- and metalimnetic layers (Tables VI and VII). Higher density of chaoborids and higher  $\text{NH}_4$  concentrations as well as higher zooplankton biomass occurred in the east side of the lake, where the highest conductivity was observed (lowest pH). In the hypolimnetic waters, the small algae ( $< 20 \mu\text{m}$ ) was the only variable explaining zooplankton biomass distribution of all size fractions (Table VIII).

Table VI. Best models predicting horizontal variation of total zooplankton biomass and biomasses of each size fraction ( $\mu\text{g.L}^{-1}$ ) in the epilimnetic waters ( $n = 30$ ).

Equation	Model	$r^2$	SE
<b>1 A</b>	Total zooplankton =	+ 219.05	
		+ 549.32 chaoborid density	<b>0.28</b> 49.13
		- 45.94 pH	<b>0.40</b> 45.78
		+ 0.878 $\text{NH}_4$	<b>0.54</b> 40.93
<b>1 B</b>	Zooplankton > 500 $\mu\text{m}$ =	+ 38.10	
		- 9.99 pH	<b>0.17</b> 19.60
<b>1 C</b>	Zooplankton 202-500 $\mu\text{m}$ =	+ 50.46	
		+ 112.41 chaoborid density	<b>0.22</b> 11.85
		- 10.60 pH	<b>0.34</b> 11.12
		+ 0.20 $\text{NH}_4$	<b>0.47</b> 10.16
<b>1 D</b>	Zooplankton 100-202 $\mu\text{m}$ =	+ 57.79	
		+ 181.64 chaoborid density	<b>0.38</b> 12.81
		+ 0.26 $\text{NH}_4$	<b>0.50</b> 11.71
		- 12.63 pH	<b>0.65</b> 10.07
<b>1 E</b>	Zooplankton 53-100 $\mu\text{m}$ =	+ 2.19	
		+ 145.79 chaoborid density	<b>0.36</b> 11.09
		+ 0.20 $\text{NH}_4$	<b>0.48</b> 10.24

Note: The coefficient of determination ( $r^2$ ) of the model as well as the partial  $r^2$  of the coefficients, and the standard error of the coefficients (SE) are listed. See Table V for units of measurement of independent variables. The  $\text{NH}_4$  concentration is given in micrograms per litre.

Table VII. Best models predicting horizontal variation of total zooplankton biomass and biomasses of each size fraction ( $\mu\text{g.L}^{-1}$ ) in the metalimnetic waters ( $n = 22$ ).

Equation	Model	$r^2$	SE
1 A	Total zooplankton = + 10.34 + 382.18 chaoborid density	<b>0.62</b>	18.39
1 B	Zooplankton > 500 $\mu\text{m}$ = + 0.953 + 134.64 chaoborid density	<b>0.74</b>	4.87
1 C	Zooplankton 202-500 $\mu\text{m}$ = + 1.39 + 112.86 chaoborid density	<b>0.60</b>	5.68
1 D	Zooplankton 100-202 $\mu\text{m}$ = + 39.44 + 81.53 chaoborid density - 7.02 pH	<b>0.43</b> <b>0.55</b>	6.20 5.64
1 E	Zooplankton 53-100 $\mu\text{m}$ = + 33.87 + 40.31 chaoborid density - 5.72 pH	<b>0.25</b> <b>0.42</b>	4.92 4.44

Note: See Table V and VI for details and units of measurement of independent variables.

Table VIII. Best models predicting horizontal variation of total zooplankton biomass and biomasses of each size fraction ( $\mu\text{g.L}^{-1}$ ) in the hypolimnetic waters ( $n = 14$ ).

Equation	Model	$r^2$	SE
1 A	Total zooplankton = - 20.22 + 2.18 CHL < 20 $\mu\text{m}$	<b>0.41</b>	14.62
1 B	Zooplankton > 500 $\mu\text{m}$ = - 3.31 + 0.34 CHL < 20 $\mu\text{m}$	<b>0.36</b>	2.53
1 C	Zooplankton 202-500 $\mu\text{m}$ = - 7.21 + 0.66 CHL < 20 $\mu\text{m}$	<b>0.47</b>	3.99
1 D	Zooplankton 100-202 $\mu\text{m}$ = - 4.83 + 0.54 CHL < 20 $\mu\text{m}$	<b>0.35</b>	4.20
1 E	Zooplankton 53-100 $\mu\text{m}$ = - 4.91 + 0.64 CHL < 20 $\mu\text{m}$	<b>0.35</b>	4.95

Note: CHL < 20  $\mu\text{m}$  denotes Chlorophyll *a* of algae < 20  $\mu\text{m}$  ( $\mu\text{g.L}^{-1}$ ).

## **1.4 DISCUSSION**

### **1.4.1 Spatial heterogeneity of zooplankton in the whole lake**

Zooplankton biomass was clearly heterogeneously distributed in both horizontal and vertical axes of Lake Geai. Although Pinel-Alloul et al. (1988) and Pinel-Alloul and Pont (1991) established that the maximum zooplankton spatial heterogeneity occurred on the vertical axis (depth), heterogeneity can be as important as on the horizontal axis as we observed in this study. Urabe (1989) indicated that contribution of horizontal axis to total variance of individuals density could be very important and exceed vertical axis variance. This strong horizontal heterogeneity has been detected because the study was carried out at large scale. Furthermore, the majority of the horizontal heterogeneity was mainly observed in the epilimnetic stratum. This can be easily explained by the exposure of this stratum to external factors which cannot directly affect underlying strata without passing through the thermocline barrier. Thus, horizontal axis should not be neglected in zooplankton community studies since responses of these organisms to environmental factors depend on the scale of observation (Malone and McQueen 1983; Pinel-Alloul 1995).

### **1.4.2 Vertical versus horizontal heterogeneity of zooplankton biomass**

#### **1.4.2.1 Vertical heterogeneity**

As observed by Salonen and Lehtovaara (1992) in a highly humic Finnish lake, zooplankton vertical distribution in Lake Geai was regulated by water temperature, oxygen level, and by density and size of chaoborids. The coldest temperature and lowest oxygen concentration in the hypolimnion could together explain the lowest biomass of zooplankton in this layer, whereas better conditions occurred in the surface waters. Because the water below 3 m depth is anoxic, the hypolimnetic zone is potentially lethal environment for any organism that lacks the ability to migrate vertically (Salonen and Lehtovaara 1992). According to Gliwicz (1979), maximum zooplankton biomass is often detected above the thermocline where thermal and density discontinuities are established. However, this effect could be reinforced by an oxycline as observed in Lake Geai. These abiotic factors affect vertical distribution of zooplankton in various type of lakes (acidic to alkaline, oligotrophic to eutrophic, and clear to brownwaters lakes), bog lakes are not

ruled out. Although the pH level and DOC concentration were also detected as potential variables affecting vertical distribution of zooplankton biomass, their negative relationship with zooplankton reflected much more the chemical conditions in the hypolimnetic layer, where lower biomass was detected.

Predation seemed the most important factor controlling zooplankton biomass distribution in Lake Geai. Although the density of chaoborids was recognized as the primarily factor, their effects on vertical distribution zooplankton was rather related either to their size or to the highest abundance registered in the last meter above the bottom (not considered in the regression models). The size of *Chaoborus* sp. significantly increased from the epilimnion to the deepest waters. Small *Chaoborus* are recognized to be less efficient predator of zooplankton (Neill and Peacock 1980) allowing the highest zooplankton biomass in the epilimnion. The presence of smallest chaoborids in the epilimnion can be attributed to the mobility of *Chaoborus* larvae which move deeper with age (Parma 1971, Franke 1983) reducing the risk of predation by their larger congeners (Tsalkitzis et al. 1994). The effect of chaoborids size on zooplankton is directly observed by a negative relationship with smaller fractions of zooplankton biomass. Thus, the positive relation between density of chaoborids and zooplankton biomass suggests a sort of common avoidance of larger chaoborids and a possible source of prey for smaller chaoborids. These results are similar to those of Fedorenko (1975) who argued that *Chaoborus* predation on zooplankton appears to be reduced by spatial aggregation of predator and prey and by size incompatibility.

On the other hand, we can hypothesize that zooplankters prefer to stay in the upper layers during the day because of the vertical migration of chaoborids at night. Zooplankton community could both limit their vertical movements to avoid invertebrate predators (Zaret and Suffern 1976) and adopt a flocking behaviour (Kvam and Kleiven 1995) to counteract the diel vertical migration of chaoborids. In the absence of fish predation, invertebrate predators such as *Chaoborus* (a midge larvae) can reach high densities (Von Ende 1979) and can have an enormous impact on populations of small zooplankton (Fedorenko 1975). Besides, the highest densities of chaoborids (3.67 ind.L<sup>-1</sup>) were observed in the bottom water layer (1 m above sediments) during the study. Thus, the highest zooplankton biomass in upper layers reflected an avoidance of the largest and highest density of invertebrate predators.

### 1.4.2.2 Horizontal heterogeneity

On the horizontal axis, an important peak of zooplankton biomass (for all size fractions) has been observed in the east part of the lake and more surprisingly, this occurred in all three limnetic layers. We can hypothesize that, logically, wind action could be the logical factor causing such spatial aggregation as mentioned in numerous studies (e.g. : Langford and Jermolajev 1966; Malone and McQueen 1983; Patalas and Salki 1992). Based on the wind speeds registered the evening (18 km.h<sup>-1</sup>) and the morning (15 km.h<sup>-1</sup>) previous the sampling day, it is unlikely that the wind had influenced surface waters of Lake Geai, since this lake is well sheltered from the wind effect under 20 km . h<sup>-1</sup>. However, the winds occurred the night previous to the sampling day could be at the origin of this aggregation, but no information was available for this period. Bowling (1990) indicated that in brown water lakes the incoming solar radiation is rapidly absorbed by the surface waters and strong thermal gradients can potentially arise rather rapidly with correspondingly greater thermal stability and resistance to wind mixing. This effect is readily apparent in small and sheltered forest lakes as Lake Geai. Thus, although we cannot reject the hypothesis of the wind effects because we did not have any information on wind conditions during the night previous the sampling day, all arguments seem to indicate that the aggregation of zooplankton in the eastern part of the lake is not related to wind effects.

The water conductivity was the most important abiotic factor explaining horizontal distribution of zooplankton biomass in the three limnetic zones of the Lake Geai. The highest conductivity was associated with the weakest alkalinity and the strongest acidity (alkalinity was highly correlated with pH;  $r = 0.96$ ). That means that the maximum biomass of zooplankton occurred where the water acidity and conductivity levels were higher. In order to interpret such result, it is important to understand the mechanisms regulating the water chemistry in a bog lake. On the one hand, the negative relationship between pH and conductivity is unusual, because positive relationship is observed between specific conductance and pH in the common bicarbonate-type of lake water (Wetzel 1983). However, this relationship deteriorates among lakes of low salinity and high dissolved organic matter content (Strom 1947), that explains the phenomena observed in Lake Geai. On the other hand, the *Sphagnum* floating bed located at the south and southwest littoral parts of Lake Geai (Figure 2), could continuously change the chemical quality of the water by liberating organic acids, thus affecting its ionic composition (Wetzel 1983). The low pH values of colored waters largely results from

dissociation of humic acids. *Sphagnum* sp. absorb cations and exchange them for  $H^+$  on new exchange sites in the plants (Clymo 1963). This process can regulate cation concentration in the water and alter its conductivity. Thus, this mechanism could explain the lowest water conductivity where the lowest zooplankton biomass was observed. However, we did not detect lower pH in the area of *Sphagnum* and this could be related to the time scale of the study. Water chemistry of bog lakes are not simple and further investigations should be carried out at larger time scale on *Sphagnum* and its relationship with water chemistry in Lake Geai. This study was conducted during only one day.

The ionic composition of the water is very important physiologically for the zooplankton especially in acidic water bodies as Lake Geai. Jones (1992), indicated that humic substances might influence planktonic organisms in lakes by altering the physical or chemical environment. The interaction between  $H^+$  and other water chemistry variables (e.g. Al, humic substances, etc.) could also enhance their toxicity and increase membrane permeability, including swelling of the heart muscle, rapid fading of haemoglobin, and a net loss of Na and Cl (see Locke 1991 for a review). There is a great energetic cost to maintain internal environment when internal and external media are not isotonic (Robertson 1949). Some taxa are more sensitive to ionic environment and Nilssen et al. (1984) suggest that water permeability may be a key factor. Therefore, zooplankters must migrate to the area (for instance : east part of the Lake Geai) where they can growth, reproduce and feed more efficiently in term of energetic cost. Based on spatial differences in conductivity, the ion concentrations were not spatially well distributed in Lake Geai. Thus the higher zooplankton biomass observed in the area of higher conductivity could be explained in term of zooplankters meeting their physiological needs.

Regression models also allowed to relate zooplankton biomass distribution to  $NH_4$  concentrations.  $NH_4$  is one of the most important excretion product from zooplankters (Ejsmont-Karabin 1984). This spatial relationship was also observed for *Lepdotora kindtii* (Forke) in 15 Newfoundland lakes (Campbell and Knoechel 1990) and for many taxa in Lake Léman (Guay, C., pers. comm.). This relationship was probably attenuated in metalimnion and hypolimnion by the decrease of the zooplankton biomass with increasing depth. Thus, the relationship of  $NH_4$  with zooplankton reflects the highest biomass observed in the epilimnion and could also be perceived as a possible grazing impact on algal population, since opposite distributions were observed between zooplankton and algae  $< 20 \mu m$  in epilimnetic waters.

The chlorophyll *a* did not seem to play an important role in structuring zooplankton biomass distribution. Nevertheless, some positive and negative relationships were observed in different area of the Lake Geai. Chlorophyll *a* concentrations were weak at the surface, while they strongly increased in the hypolimnetic waters. It is possible that the low levels of chlorophyll *a* in the surface waters represent actively reproducing algae that are rapidly cropped by grazers, while large pool of chlorophyll at the hypolimnion could be due to an aggregation of relatively unproductive algal and bacterial cells which sank during summer (Murtaugh 1985). The high level of dissolved silica in the hypolimnetic waters could indicate that the strong chlorophyll *a* concentration could be the result of degradation of diatoms. In such environment, zooplankton has to diversify its feeding, since Salonen and Hammar (1986) claimed less than 20% of zooplankton carbon in humic lakes to be of algal origin, while more than 80% came from DOC, bacteria and protozoa. This is probably a situation most common in humic lakes with a high fraction of allochthonous DOC, resulting in relatively large quantities of low-quality food (Hessen 1990).

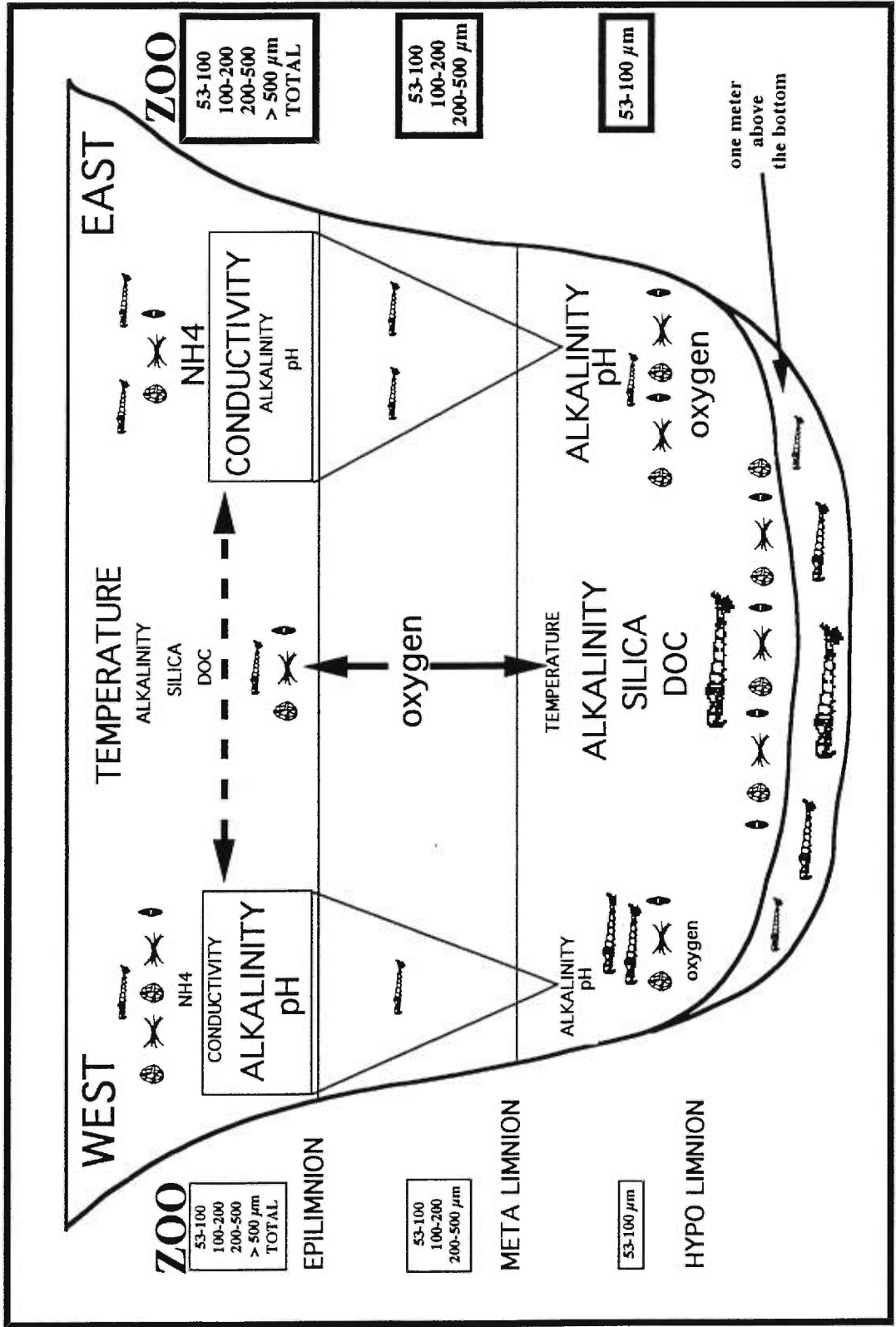
As observed on the vertical axis, the density of chaoborids was positively related to zooplankton biomass, especially in the epilimnion and metalimnion. It is only in the hypolimnion where we detected a negative correlation between size and density of chaoborids and zooplankton biomass ( $< 53 \mu\text{m}$ ). The biomass of small zooplankters in the other limnetic layers did not respond negatively to the highest densities of predator and this is likely related to the size of the larvae which were smaller in the epi- and metalimnetic layers. As mentioned by Swift and Federenko (1975), there is a strong relationship between the size of Chaoborid larva and the size of their potential prey.

### **1.4.3 Environmental control of zooplankton biomass distribution in Lake Geai**

The spatial distribution of zooplankton biomass and biotic and abiotic factors influencing their distribution in both axes of Lake Geai are presented in Figure 9. The largest part of the zooplankton biomass was located in the east part of the lake and it decreased with depth. The zooplankton seems located in the best physico-chemical environment (high temperature, oxygen and conductivity levels) in spite of the high density of the invertebrate predators in this area (chaoborids larvae). However, the spatial overlap between zooplankters and their potential predators have probably no impact on large zooplankters because of the small size of the chaoborids in this region of the lake.



Figure 9 : Synthesis of the biotic and abiotic factors affecting zooplankton biomass of Lake Geai according to the results of Mann-Whitney tests and regression models



Water conductivity and chaoborids size structure affected horizontal distribution of zooplankton biomass, while water temperature, oxygen level, density and size of the predators seemed to control their vertical distribution. Higher chaoborids density in the profundal zone was likely influencing the vertical distribution of zooplankton biomass but not as much as the size structure did spatially. Thus, the duality of the abiotic and biotic forces in the control of the zooplankton distribution in both axes of Lake Geai agreed with the Arnott and Vanni's model (1993). In a harsh environment (an acidic bog lake), predation by invertebrates (density and size of chaoborids) and the abiotic stress (water temperature, conductivity, and oxygen level) are of high relative importance, whereas the significance of competition has declined. This is confirmed by the strong aggregation of all fractions of zooplankton biomass in the whole lake. Hessen (1990) indicated that disruptive behaviours were weak in a humic lake, and the narrow environmental frames leaves very limited space for niche segregations. By considering the dimensional aspect in the variability of abiotic and biotic factors affecting zooplankton assemblage structure in a bog lake, this study allows us to apply the Arnott and Vanni's model in a different perspective. In spite of the strong spatial horizontal and vertical variabilities of abiotic factors in Lake Geai, the biotic factors (chaoborids size structure and density) are more important in structuring zooplankton assemblage in the three limnetic layers.

In limnology, it has been common practice to regard humic lakes as unproductive system (De Hann 1992). Nevertheless, these small lakes are well suited to study the behaviour of a wide variety of organisms exposed to different stresses (biotic and abiotic factors). As argued by Arnott and Vanni (1993), the strength of biotic interactions and energy flow within a food web may be altered by differential effects of water quality (e.g., ion content, nutrient levels, light intensity, toxins) on zooplankton. In this study, water chemistry modulated the interactions between predators and prey because of the harsh physico-chemical conditions of its waters (Locke 1991). However, the weak relationships between algae  $< 20 \mu\text{m}$  and zooplankton biomass observed in this study imply that we need more accurate information on algae species in such environment which could modulate spatial distribution of zooplankters. Further investigations should also evaluate the impact of bacteria and protozoa, since these organisms may significantly affect energy transferred to the higher levels in the food web and could be probably the main source of food of zooplankton in bog lakes (Salonen and Hammar 1986).

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## CHAPITRE 2

### DIEL VERTICAL AND HORIZONTAL DISTRIBUTION OF CRUSTACEAN ZOOPLANKTON AND YOY FISH IN A SUB ALPINE LAKE: AN APPROACH BASED ON HIGH FREQUENCY SAMPLING

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## RÉSUMÉ

La compréhension des relations dynamiques dans la répartition spatiale des prédateurs et de leurs proies est un des importants buts en écologie aquatique. Dans ce travail, nous étudions, sur un gradient rive-large dans le lac Annecy, les patrons de répartition spatiale et temporelle de jeunes perches de l'année (*Perca fluviatilis*) et des crustacés zooplanctoniques (*Daphnia hyalina*, *Cyclops prealpinus*). La biomasse et la structure en taille des poissons ont été estimées par échosondage et par chalutage, tandis que les abondances de daphnies et de copépodes ont été évaluées en utilisant un échantillonneur modifié de type "Longhurst-Hardy's continuous plankton recorder". C'est un des premier travail qui aborde l'étude des répartitions spatiales des poissons et de leurs proies à grandes échelles en utilisant simultanément les techniques d'échosondage des poissons et l'estimation à haute fréquence du zooplancton. Les patrons des répartitions horizontale et verticale des poissons et du zooplancton ont été déterminés à trois périodes du cycle journalier (l'après-midi, le soir, et le milieu de la nuit). Nous avons évalué, d'une part les changements temporels sur une journée de la distribution des poissons et du zooplancton, et d'autre part le chevauchement qui existait entre leur répartition. La biomasse ichthyenne était dominée par les perches d'âge 0+ (*Perca fluviatilis*). Les jeunes de l'année (YOY) formaient des bancs dans les eaux épilimnétiques, mais ces bancs éclataient au cours de la nuit. Les daphnies et les cyclopoïdes effectuaient une migration verticale de grande amplitude au cours du cycle diurne. Le zooplancton présentait un gradient horizontal de répartition avec de plus fortes densités en zone littorale à l'opposé des jeunes perches de l'année qui étaient plutôt pélagiques. La distribution spatiale du zooplancton pourrait être reliée à l'évitement des prédateurs se traduisant par un comportement d'anti-prédation (DVM et DHM). La nuit, les cyclopoïdes, qui représentaient le principal item du régime alimentaire des perches, étaient plus abondants dans les eaux métalimnetiques plus froides qui étaient évitées par les jeunes perches.

## ABSTRACT

Understanding the spatial dynamics of predators and their prey is one important goal in aquatic ecology. We studied spatial and temporal distribution patterns of age 0+ perch (*Perca fluviatilis*) and crustacean zooplankton (*Daphnia hyalina*, *Cyclops prealpinus*) along the offshore-onshore gradient in Lake Annecy. Fish biomass and size structure were assessed using both a 70 kHz split-beam transducer and trawling, whereas daphnid and cyclopoid abundances were estimated with a small-sized king of Longhurst-Hardy's continuous plankton recorder. Our study represents a first attempt at coupling acoustic fish survey data and high frequency zooplankton recording to assess the large scale simultaneous distribution patterns of young fish and their zooplankton prey. This approach was completed by an examination of the diet of juveniles. Horizontal and vertical distribution patterns of fish and zooplankton were evaluated at three segments of a diel cycle (mid-day, dusk and mid-night). We evaluated the diel changes in the spatial distribution patterns of fish and zooplankton and determined the overlap between their distribution. The fish biomass was dominated by 0+ perch (*Perca fluviatilis*). Young of the year (YOY) were aggregated in dense schools in the epilimnion at daytime; then, they dispersed during the night. A strong diel vertical migration was observed for daphnids and cyclopoid copepods. Zooplankton also presented an horizontal spatial gradient with highest density in the nearshore zone contrary to the distribution of YOY. The spatial distribution of zooplankton could be linked to the avoidance of the predators which is traducts by antipredator behaviours (DVM and DHM). At night, the cyclopoids, that represented the main food item of the perch, were more abundant in the coldest metalimnetic waters avoided by 0+ perch.

*Key words:* Daphnids; cyclopoids; *Perca fluviatilis*; acoustic; high frequency sampling; horizontal/vertical distribution; DVM; DHM; alpine lake.

## 2.1 INTRODUCTION

The spatial distribution of crustacean zooplankton in lacustrine environments is affected by multiple physico-chemical and biological processes, the nature and relative importance of which vary among ecosystems and at different spatial and temporal scales (Lampert, 1992, 1993; Angeli et al., 1995a; Pinel-Alloul 1995). Fish predation has been cited as one of the most important factors influencing zooplankton community structure (Brooks and Dodson, 1965; Kerfoot, 1987) and distribution over space and time (Urabe, 1990; Gliwick and Rybowska, 1992). To counteract fish predation, zooplankton have developed avoidance strategies such as diurnal horizontal migration (DHM) in weedy littoral zones of shallow lakes (Kairesalo, 1980; Davis, 1985) and diel vertical migration (DVM) (Zaret and Suffern, 1976; Lampert, 1993; Ringelberg, 1993).

The relative importance of zooplankton DHM and DVM as predator avoidance strategies, can better be evaluated by performing simultaneously the surveys of zooplankton and fish on both horizontal and vertical scales. Indeed, in the pelagic zone of lakes, horizontal and vertical scales are interdependent as zooplankton and fish can move in both. Relationships between predator and prey on horizontal and vertical scales of lakes leads to spatial and temporal distribution patterns of high complexity (Franke, 1987).

Given the difficulty for coupling fish and zooplankton sampling (e.g. Post and McQueen, 1988; Rudstam et al., 1993; Scheuerell, 1996), there are still few studies which evaluate the spatio-temporal distribution of both zooplankton and fish. In most of those studies, vertical and horizontal distribution patterns were confounded by using discrete and coarse sampling based on only few series of vertical hauls for zooplankton and gill nets and/or seines for fish. Moreover, studies were carried out on small scales and at few stations within a lake. Such sampling designs poorly cope with the discrimination of horizontal and vertical distribution patterns.

In this paper, we provide a more complex description of distribution patterns of prey (crustacean zooplankton) and predators (0+ perch) in Lake Annecy along the offshore-onshore gradient and over a day to night diel cycle. Horizontal and vertical distribution of daphnids, cyclopoid copepods, and age 0+ perch were studied on a daily cycle at mid-day, dusk, and mid-night, using simultaneously for the first time, both fish echosounding and zooplankton continuous sampling with a PSM (Plankton Sampling Mechanism). We tested if there is an inverse correlation between offshore-onshore

distribution patterns of fish and zooplankton and if such patterns varied over the diel cycle.

## 2.2 METHOD

### 2.2.1 Study site

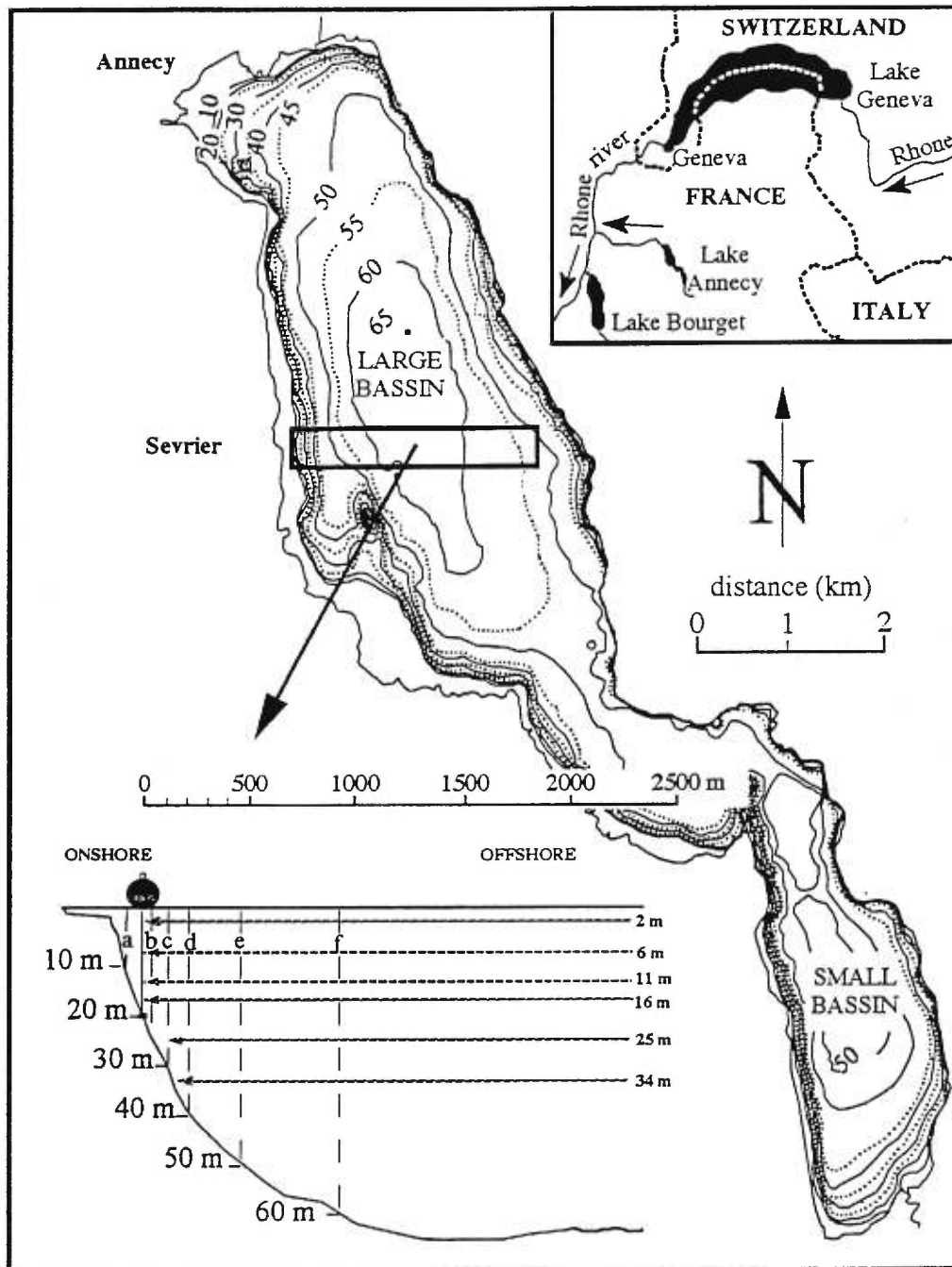
Sampling was carried out the 3<sup>rd</sup> week of June 1996 in the Sevrier area of Lake Annecy (France) (Figure 1). Climatic conditions were stable during the second and third week of June, with mean daily air temperatures ranging between 19 and 23 °C and mean wind speeds from 1.9 to 3.4 m. s<sup>-1</sup>. The study lake (max. depth 65 m, 11.5 km long, 3 km wide) is a monomictic sub-alpine lake of glacial origin, situated at an elevation of 446 m in the Northern French Alps (45° 50' N, 6° 40' E). Lake Annecy is divided into two basins of similar mean depth (42 m). The lake area is 27.04 km<sup>2</sup> (21.10 km<sup>2</sup> for the large basin) and surrounded by a watershed of 278 km<sup>2</sup>. This popular tourist site has benefited from a diversion of urban waste waters to protect its water quality. As total phosphorus never exceeded 10 µg.L<sup>-1</sup>, Lake Annecy is maintained at an oligo-mesotrophic state (Balvay and Pelletier, 1988).

Secchi disk transparency ranges from 15 m in winter to 3-4 m during the summer season. The epilimnion develops at 7-8 m in late spring reaching 12-15 m in mid-autumn. The phytoplankton community is mainly represented by diatoms (mainly *Cyclotella cyclopuncta*) and Cryptophyceae (*Rhodomonas minuta*), which are a good food for crustacean grazers. Dominant cyclopoids and cladoceran are *Cyclops prealpinus*, *Daphnia hyalina*, and occasionally, *Bosmina longirostris* (Balvay et al., 1997). Large invertebrate predators (*Chaoborus flavicans*, *Leptodora kindtii* and *Bytotrephes longimanus*) are scarce (< 100 ind.m<sup>-3</sup>). The fish community is dominated by whitefish (*Coregonus schinzi palea*) (Cretenoy and Gerdeaux, 1997) and, to a lesser extent by Arctic charr (*Salvelinus alpinus*). Both were introduced at the end of the last century with other species such as lake trout (*Salmo trutta*) and perch (*Perca fluviatilis*) (Gerdeaux, 1988).

### 2.2.2 Sampling strategies

We carried out two series of pre-sampling during the day and the night preceding the high-frequency surveys reported in detail in this paper. The depths of the epi-, meta-,

Figure 1 : Bathymetric map of the Lake Annecy, with sampling locations for both physico-chemistry (a to f) and zooplankton (2 to 34 m) surveys.



and hypolimnion were first determined from depth profiles of temperature and dissolved oxygen at 1 m intervals. Afterwards, we sampled zooplankton with a opening/closing net (433 cm<sup>2</sup> mouth area, 200  $\mu$ m mesh-size) to determine the day and night zooplankton vertical distribution. We collected zooplankton at each 5 m interval from the surface to 30 m depth, and thereafter at each 10 m intervals to the lake bottom. Finally, the horizontal and vertical spatial distributions of the fish community was studied by conducting either series of echosounding surveys on offshore-onshore transects, or one transect over the whole lake width in the Sevrier area. The regularity of the spatial distribution of observed fish was investigated by performing other echosounding transects during subsequent nights. These data showed repeatable patterns in both horizontal and vertical distribution of fish over the diel time period and the subsequent sampling protocol was determined on this analysis.

#### **2.2.2.1 *Physical and chemical stratification of the water column***

A multiparameter probe (ME, Standard-ECO-probe Version II, Serie 52) was used to determine temperature, oxygen, conductivity, light transmission (% ambient turbidity) and chlorophyll *a* fluorescence depth profiles in the water column. In order to assess both the vertical and horizontal variation in the water chemistry, recording was carried out over the water column at 6 stations along an onshore-offshore transect at depths of 15, 20, 30, 40, 50, and 60 m respectively (Figures 1a-f).

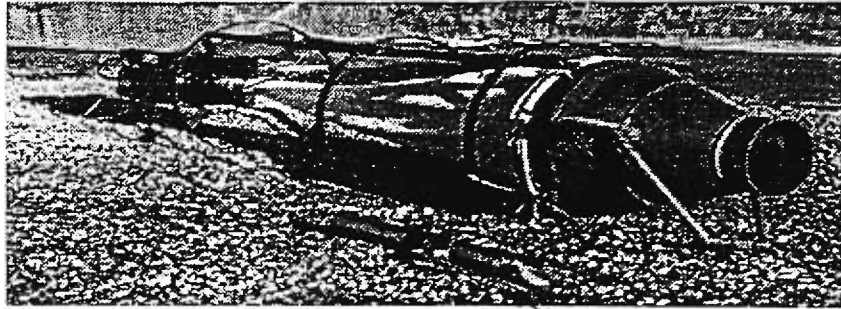
#### **2.2.2.2 *Zooplankton sampling***

During the sampling survey, we coupled a fish acoustic survey and horizontally integrated zooplankton sampling using a multiple-serial Plankton Sampling Mechanism (PSM, Figure 2a). This customer made device is a light (28 kg) transposition of the oceanographic CPR (Continuous Plankton Recorder) or LHPR (Longhurst-Hardy's Plankton Recorders) (Hardy, 1936; Longhurst et al., 1966; Longhurst and Williams, 1976). This sampler is a high speed plankton net used in oceanography (Nackthai model; Hydro-Bios, 1994) with collector modified for continuous zooplankton sampling. The prototype used in this study was 2.22 m long with a frame diameter of 46 cm, a mouth area of 238 cm<sup>2</sup>, and a net bag 1.17 m long with a 0.51 m long filter (200  $\mu$ m mesh-size) (see Figure 2b for details). The principle of this filtering system is simple: as zooplankton are collected, they are immobilized and stored between two rolls of gauze (200  $\mu$ m mesh-size) enrolled at regular intervals in a storage compartment (Figure 2c).

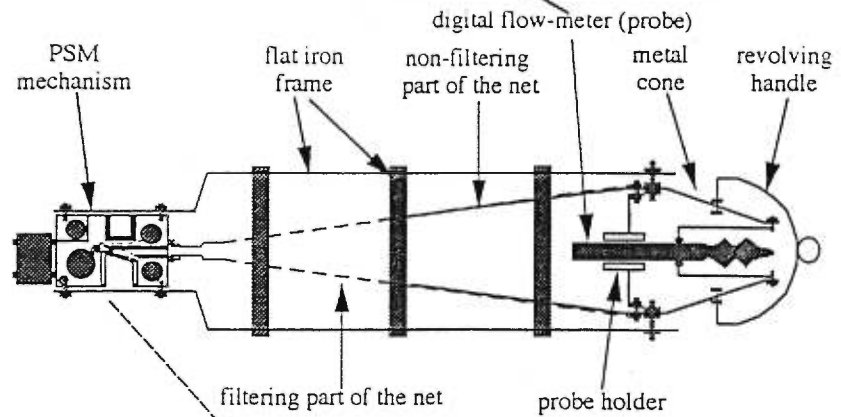
Figure 2 : Descriptive characteristics of the continuous plankton recorder: a) photography;  
b) general characteristics; c) Plankton Sampling Mechanism (PSM); d)  
zooplankton extractor.



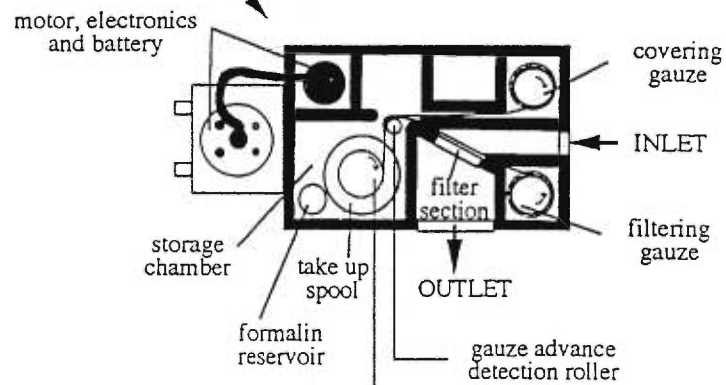
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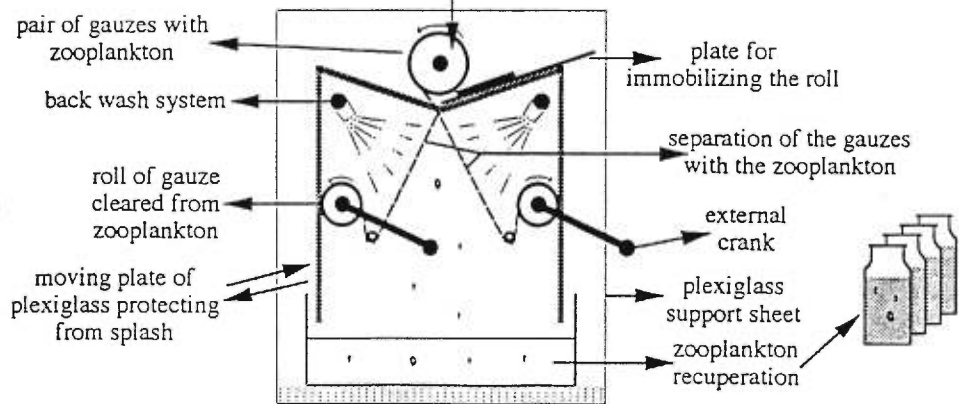
b



c



d



Sampling frequency and gap between each zooplankton sample are controlled by the gauze advance which is turned on by water contact and programmed by an electronic card. This PSM device provides sample series along large-scale distances, and is well adapted for the fine resolution measurement of zooplankton spatial aggregation and gradients. A digital flow-meter (Valport U.K.: self recording model number 104-1, see Figures 2a and 2b, turned on by water contact) equipped with a temperature and a pressure probe, is fixed in the mouth of the net, for *a posteriori* estimation of the volume of water filtered per sample, water temperature, and sampling depth. For a better control of the digital flow-meter and a rapid stabilization of the PSM at the chosen sampling depth, a 17 kg depressor has been fixed under the mouth of the PSM, via a 2.5 m cable.

Daylight horizontal and vertical patterns of zooplankton distribution were assessed by sampling 6 transects at successive discrete depths of 2, 6, 11, 16, 25, and 34 m (Figure 1). To detect diel patterns of variation in zooplankton spatial distribution, PSM sampling was repeated at only two depths (6 and 16 m) during the short twilight period and at three depths (2, 6, and 16 m) during the night. All depths sampling were chosen because of their relative importance in zooplanktonic densities previously identified during the pre-sampling surveys. Given the time (2 to 6 min) required for the device to reach a fixed sampling depth and to stabilize, the tows were always started from the pelagic area and carried out in the direction of a buoy anchored at 20 m depth (Figure 1). The exploited distances varied between 1800 and 2520 m during the day, and between 1320 and 1440 m at dusk and night. By cruising at a constant speed of 3 knots, and by setting the PSM mechanism to obtain a segmentation of the zooplankton tow at a 39 seconds interval (corresponding to spatial resolution of 60 m), each tow enabled the collection of between 21 and 42 samples. After each transect, the pair of gauzes, with the animals sandwiched in between, were individually placed in a tight bag and preserved with formaldehyde solution (4% final concentration).

In the laboratory, the pair of gauzes were unrolled. Each section corresponding to an horizontal integration of 60 m was spatially identified, according to its position in the gauze. The zooplankton was collected with a specially designed extractor (Figure 2d). The free extremities of the gauze were first introduced in the slot opened at the basis of the upper compartment. Then, the wires placed below this splash protector, separate the pair of gauzes and enable the zooplankton to be washed and retained in the lower compartment. Because few zooplankton were collected at a depth of 2 m, 3 sequential samples were pooled for analysis. In all samples, daphnid and cyclopoid copepod

densities were estimated either from the total samples or on a sub-samples (10% to 50%), depending on animal density.

### 2.2.2.3 *Fish acoustical surveys*

The hydroacoustic fish surveys were made with a Simrad EY500 split beam digital sounder. The EY500 has a frequency of 70 kHz and a pulse duration of 0.6 ms. The echosounder was equipped with a circular transducer (total beam angle of 11 degree at -3 dB), generated 5 pings per second and was utilized with two TVG (Time Varied Gain) amplification functions:  $(2\alpha R + 20 \log R)$  and  $(2\alpha R + 40 \log R)$ , where  $\alpha$  is the sound attenuation coefficient in freshwater and R is the distance in meters between the target and the transducer. According to the TVG function selected, a calculation of the biomass ( $\alpha R + 20 \log R$ ) or the size distribution of the echoes ( $\alpha R + 40 \log R$ ) can be computed (MacLennan and Simmonds, 1992). The transducer was mounted on a pipe fixed to the side of the boat and submerged at 0.5 m under the water surface.

The system was calibrated by insonifying a copper sphere (TS = -39.2 dB), attached to three thin nylon wires at a distance of 7 m from the transducer and in its acoustical axis, as defined by the EY500 sounder manual (Simrad, 1994) and recommended by Foote et al. (1987). The discrimination of single fish targets was set at a threshold of -70 dB, using the tracking menu options of the EY500 with the default settings. Data processing was carried out in the laboratory using the EP500 software (Simrad, 1994). The results obtained were reported in dB for the target strength distribution and for the acoustic biomass calculation (Area back-scattering coefficient term  $S_a$  by Simrad) in  $\text{m}^2 \cdot \text{hectare}^{-1}$ , and has not been transformed to biomass in weight units because only relative biomass was required for the purpose of this paper.

To evaluate both fish and zooplankton distribution, the echosounding survey was simultaneously performed to the PSM zooplankton sampling 3 times during the diel cycle (mid-day, dusk, and mid-night). The boat speed was maintained as constant as possible:  $1.4 (\pm 0.1) \text{ m} \cdot \text{sec}^{-1}$ . The echointegration sequences were set to cover the same distances (spatial scale of 60 m) that those of the PSM samples. Fish and zooplankton spatio-temporal distributions was compared by using fish biomass detected in depth strata 2.5 m around each PSM trawl realized above 15 m depth and in depth strata of 5 m in the deepest zones (15 m to 40 m).

In the following night of sampling survey, trawling was conducted at 1.5 and 4 m depths with an ichthyoplankton net (1.5m of cone diameter and 1 mm mesh-size) to identify the tiny epilimnetic acoustic targets. The collected fish were identified and measured, then sub-samples of 35 individuals, representative of the size structure of these samples, were used for gut content examination. All organisms found in the digestive tracts were identified and counted.

### 2.2.3 *Statistical analysis*

The spatial structure of daphnids, cyclopoids and fish were first described by maps of the density of each at different depths during the day, dusk, and night periods. Afterwards, normality of these variables were verified using Kolmogorov-Smirnov tests. To reduce asymmetry and to increase the linearity of the product moment correlation analyses (Legendre and Troussellier, 1988), a  $\text{Log}_{10}(x + 1)$  transformation was applied to the variables. Normalization tests and transformations were performed using SPSS 4.0 (Nie et al., 1984).

To detect spatial structures in the distribution of fish and zooplankton, spatial correlograms were computed for each sampling depth and period. In correlogram analysis, one value is computed for all pairs of points located within each given distance class, after which the values computed for all distance classes are assembled (Legendre and Fortin, 1989). A geographic coordinates matrix is transformed into a distance matrix using the Euclidean distance. Moran's index (1950) was used as spatial autocorrelation coefficient because it behaves mainly like Pearson's correlation coefficient and it is sensitive to extreme values (Legendre and Fortin, 1989). Given that in constructing correlograms several tests were carried out simultaneously, Bonferroni correction ( $\alpha' = \alpha / \text{distance classes number}$ ) (Hochberg, 1988) was applied to each distance class to test significance. Only interpretable distance classes were presented in correlograms.

Standard correlational methods are inefficient at resolving spatial phenomena in studies of predator-prey distribution (e.g. Ord, 1979). So, Mantel tests (1967) were used to express the spatio-temporal relationships between zooplankton density and fish biomass. These tests were performed to determine the spatial association between daphnids, cyclopoids, and fish at 6 and 16 m depths at day, dusk, and night for the whole transects. Three reasons have guided our choice: (1) because the general patterns of zooplankton and fish distributions were clearly identified on the transects for the three

periods of the study; (2) because the interactions between zooplankton and juvenile perch can only develop in the warmer layers (epi- and metalimnion); (3) because these two depths were commonly sampled during on three periods of the day. Mantel tests use 2 independently obtained distance matrices to describe the relationships among the same sampling stations by evaluating the sum of the cross-products of these two matrices (Legendre and Fortin, 1989). Similarity matrices were computed using Gower's asymmetric coefficient for the three biotic variables. This coefficient was chosen for three reasons: (1) being an asymmetrical coefficient, it does not consider double zeros as an indication of resemblance, (2) it is well adapted to normalized abundance data, (3) because the differences between the highest densities further contribute to the similarity (Legendre and Legendre, 1998). Since Mantel tests require that both matrices be of the same type, and because the spatial matrix consisted of geographic distances, Gower's coefficient was transformed into a similarity matrix.

Partial Mantel tests (Smouse et al., 1986) were performed to determine if the observed correlations between organisms were spurious, resulting from the fact that daphnids, cyclopoids and fish follow either a common or an opposed spatial structure as a result of some unknown factor. As suggested by Legendre and Fortin (1989), to decide among the possible models of interrelations among these three groups of variables, in the interpretation of the results we will refer to these three possibilities :

- (1) the zooplankton spatial structure is linked by the spatial structure of the fish; to retain this option, the relationship between space and zooplankton when removing the effect of fish should not to be significantly different from zero;
- (2) the spatial component in the zooplankton data is independent from the spatial structure of the fish; if this model is support by the data, we expect that the relationship between fish and zooplankton when removing the effect of space should not to be significantly different from zero;
- (3) the spatial structure in the zooplankton data is partly determined by the spatial gradient of the fish, and partly by other factors not explicitly identified in this study; if this option is support by the data, we expect that the relationship between fish and zooplankton when removing the effect of space should be significantly different from zero;

The method of Smouse et al., (1986) is well explained in Legendre and Fortin (1989). Each simple and partial Mantel statistic was tested for significance by performing

a *z-test*. For these tests, Bonferroni correction were applied to test significance as  $\alpha' = (\alpha / \text{comparisons number})$  because several tests were carried out simultaneously. All statistics of this section were realized using R progiciel package including following programs: Convert, Autocor, simple and partial Mantel tests (Legendre and Vaudor, 1991) for Macintosh computers.

Finally, we performed a Principal Component Analysis (PCA) to obtain a fine resolution of the relationships among zooplankton and fish revealed using the Mantel tests applied to samples at 6 m and 16 m depths. This analysis allowed us to define the evolution of the interactions between horizontal and vertical spatial structures of zooplankton and fish during a diel cycle. Principal Components Analysis (PCA) describes the dispersion of an array of  $n$  points in  $p$ -dimensional space by introducing a new set of orthogonal linear coordinates so that the sample variances of the given points with respect to these derived coordinates are in decreasing order of magnitude (Gnanadesikan, 1977). Interest lies in the coordinates along which the data show their greatest variability. The PCA was realized using the correlation matrix of log10-transformed  $(x + 1)$  abundances of cyclopoids and daphnids, and fish biomass. In this analysis, the angle between descriptors is related to the correlation among variables.

## 2.3 RESULTS

### 2.3.1 *Depth variations in water chemistry and phytoplankton*

Lake Annecy was stratified during the sampling period (Figure 3a). Water temperature varied from  $14.5 (\pm 0.3)$  to  $22.6 (\pm 0.2)$  °C in the epilimnion (0 - 8 m), decreased down to  $7.0 (\pm 0.3)$  °C in the metalimnion (8 - 20 m), then slowly dropped to  $5.5 (\pm 0.0)$  °C in the hypolimnion (20 - 60 m). Waters were well oxygenated over the whole water column with more than  $9.5 \text{ mg.L}^{-1}$ , and exhibited a metalimnetic peak of  $14 (\pm 0.3) \text{ mg.L}^{-1}$  (Figure 3a).

Water conductivity (standardized at 25 °C) varied slightly between  $268 (\pm 1)$  to  $273 (\pm 1) \mu\text{S.cm}^{-1}$  in the first 10 meters, increased up to around  $290 \mu\text{S.cm}^{-1}$  in the metalimnion, and stabilized at that level in the hypolimnion (Figure 3b). The turbidity profile followed a similar pattern. Turbidity was close to 40 % in the first 15 meters,

increased to 48 % in the metalimnion, slightly decreased down to 45% in the hypolimnion, and finally increased again near the bottom of the lake (Figure 3b).

These profiles suggest that during the summer season Lake Annecy undergoes a biogenic meromicticity with sharp thermocline and chemocline in the metalimnion. This hypothesis is also supported by the fluorescence profile (Figure 3c). Indeed phytoplankton biomass presented a sharp metalimnetic peak ( $5.1 \pm 0.25 \mu\text{g.L}^{-1}$ ) at around 15 m depth, near the metalimnetic oxygen peak. Irradiance was not measured. However, Secchi depth ranged between 4.0 and of 4.6 m in June 1997 (Balvay et al., 1997). Considering that 99% light attenuation corresponds to around 2 to 2.7 fold the Secchi depth (Margalef, 1983), the euphotic zone would be 10-12 m deep.

### *2.3.2 Spatio-temporal distribution of fish and zooplankton*

During the day, a marked opposition was observed between fish and zooplankton distributions (Figure 4). The larger part of the fish biomass was colonizing the warm surface layers (0 - 16 m), while the highest densities of zooplankton were recorded in the deepest and coldest waters (25 and 34 m). There was huge spatial variation in the abundance of zooplankton: densities in hypolimnetic waters were 3 or 4 orders of magnitude higher than the epilimnion. Below the thermocline, horizontal distribution patterns suggest an onshore-offshore gradient of both daphnids and cyclopoids. The horizontal distribution of fish biomass was more patchy and did not present an onshore-offshore gradient.

At dusk, fish and zooplankton presented very strong diel changes in their vertical and horizontal spatial distribution. Daphnid and cyclopoid abundances increased at 6 m whereas they decreased at 16 m (Figure 4). This can be interpreted as an upward migration. The onshore-offshore patterns also suggest an onshore aggregation, as already observed during the day. In contrast, fish biomass decreased at 6 m and increased at 16 m (Figure 4). The horizontal distribution pattern was highly patchy at 16m.

At night, zooplankton abundances strongly increased in the epilimnion (2 and 6 m), and also at 16 m in the metalimnion, however in a lesser extent for daphnids (Figure 4). Given that strong diel vertical migration (DVM), daphnids were more abundant than the cyclopoids in the epilimnion (2 and 6 m). Then again, we observed an increasing

Figure 3 : Vertical physico-chemical profiles of the Lake Annecy. Standard deviations are presented with mean at every 5 meters depth.



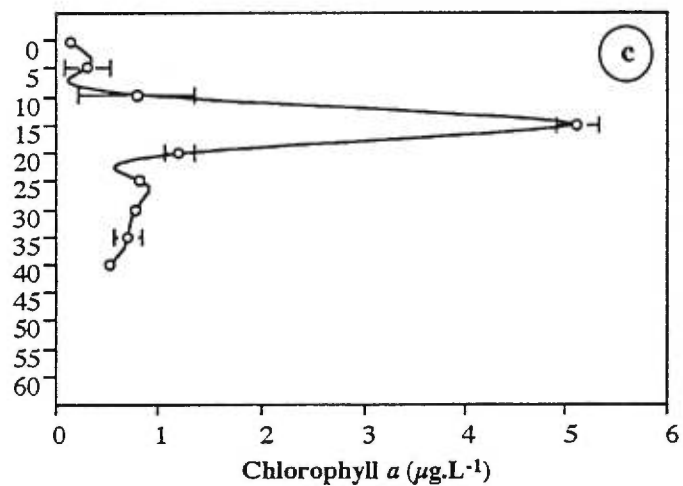
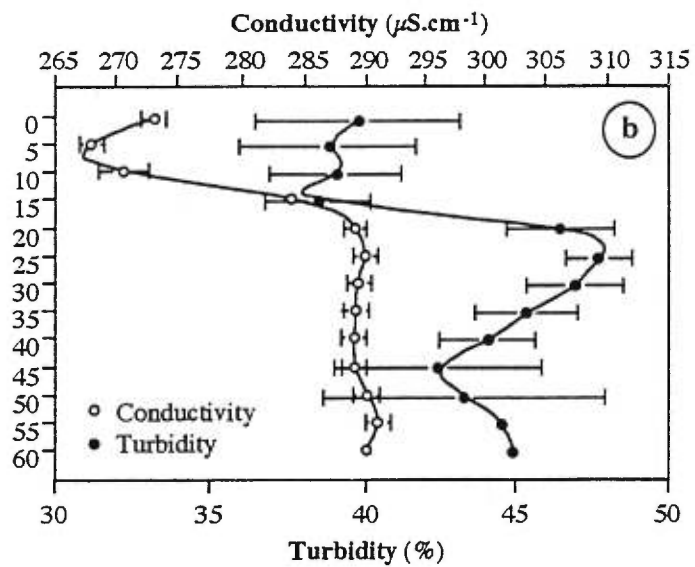
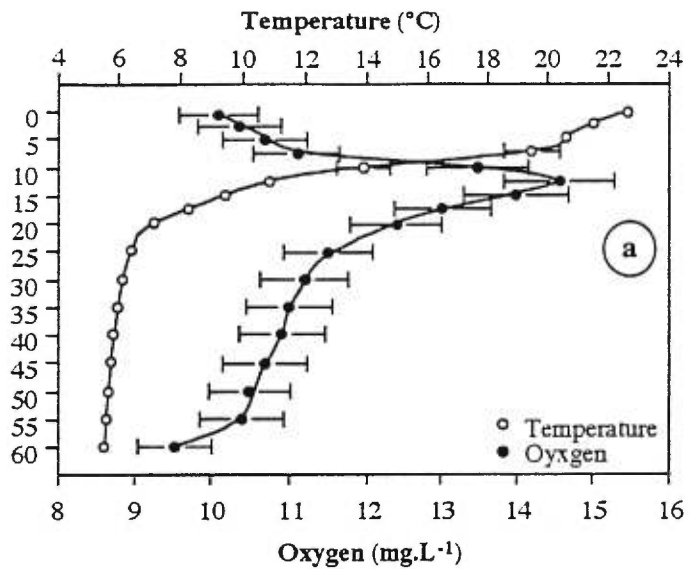
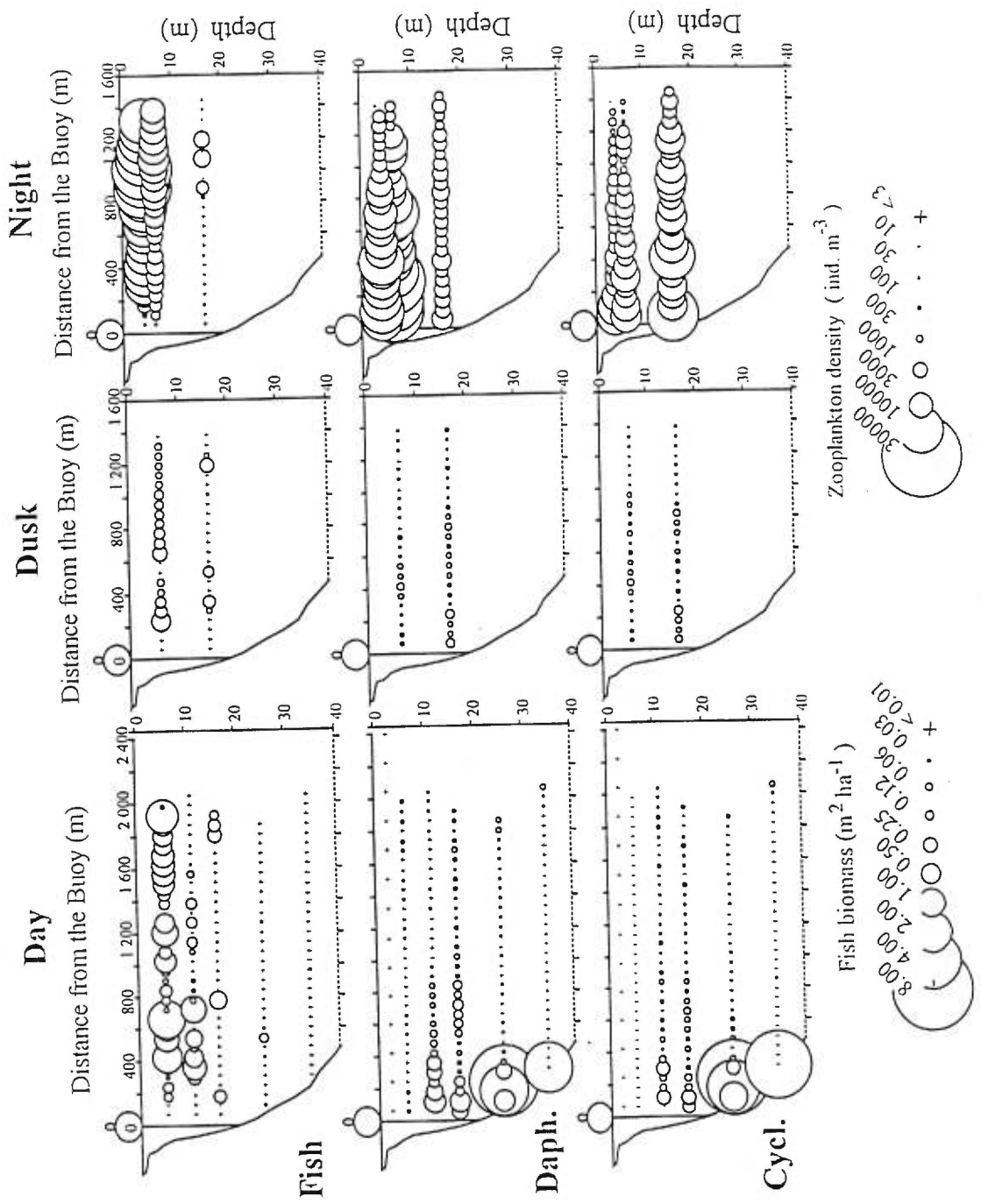


Figure 4 : Horizontal and vertical distribution of fish, daphnids, and cyclopid during the day, dusk and night periods.



offshore-onshore horizontal gradient in the concentration of zooplankton with higher abundances near the shore. In contrast, the fish biomass established a marked decreasing offshore-onshore gradient in the epilimnion. In deeper waters (16 m), fish biomass was lower than that observed at dusk, and more patchy with the highest biomass offshore.

### 2.3.3 *Echograms and size structure of fish*

The onshore-offshore gradient of fish biomass detected at 6 m depth (Figure 4) was probably spread at a larger area of the lake because it was observed in both sides of the lake during consecutive nights (Figures 5b and 5c) and on a wider area the following year at the same season (Vedrines, 1997). At a depth of 7 to 8 m, corresponding to the thermocline and the chemocline (Figures 3a and 3b), a strong discontinuity in fish vertical distribution can be observed on the echogram (Figures 5b and 5c). Indeed, most detected targets were epilimnetic, the remaining ones being distributed erratically in the upper part of the hypolimnion and near the lake bottom. The results of echointegrations suggest : (1) that these abundant epilimnetic fish have a strong contribution to the total ichthyomass present in the open water (Figure 5b); (2) that this epilimnetic biomass avoids the upper part of this stratum during the day; (3) and they occupied the upper 6 m during the night. The major differences between diurnal, twilight, and nocturnal spatial distributions concerned the degree of aggregation of the epilimnetic fish (Figure 5a). During the day, fish were clumped into dense schools. At dusk, these aggregations started breaking, whereas fish maximized the occupation of space at night in this upper layer. These diel variations in fish aggregation patterns were detected on each of the consecutive days of the study.

During the daylight period, only 16 individual target strength were detected in the upper 10 m (Figure 6a). In contrast, individual target strength was much important in the deeper waters (10 m to bottom: exceeding one hundred individuals per transect) allowing the computation of the size spectrum. According to the scattergram (T.S. vs depth) shown on Figure 6a, in this deeper layer the diurnal vertical distribution was characterized by two large patches, one spreading below 40 m, the other one over the lower part of the metalimnion and upper part of the hypolimnion. The size spectrum of these echoes ranged from -48 dB to -30 dB (Figure 6b) and presented a weak mode between -38 and -34 dB. During the night, individual targets were more widely spread in the water column (Figure 6c). They also presented a more variable size and a wider spectrum (Figure 6d). These two characteristics seem related with a nocturnal upward migration of

Figure 5 : Echograms and fish biomass distribution along a transect shore to shore and general repartition of the fish in the upper 20 m (epi- and metalimnion) during the day, dusk, and night periods.

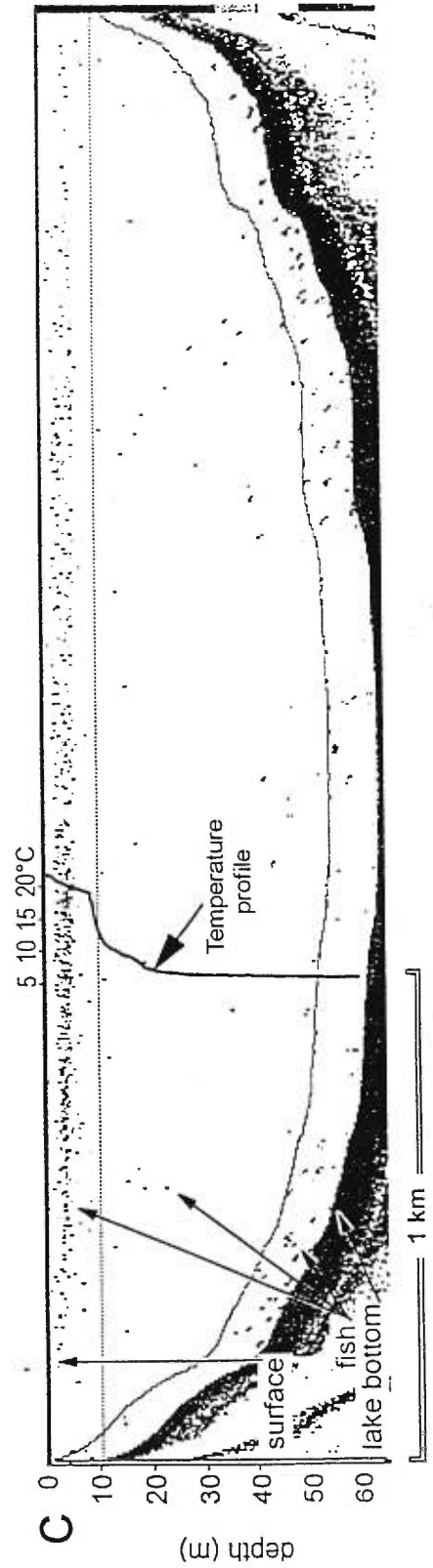
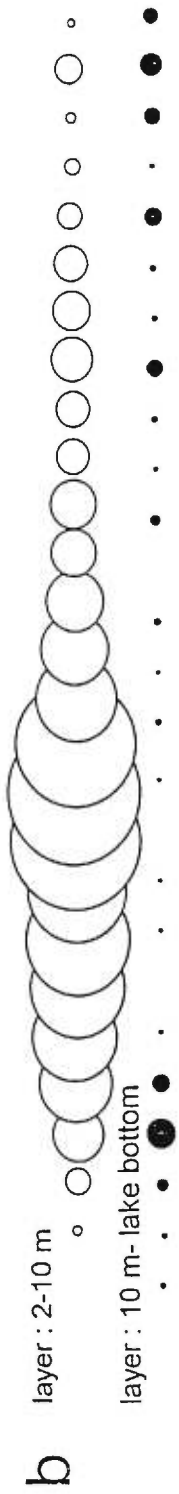
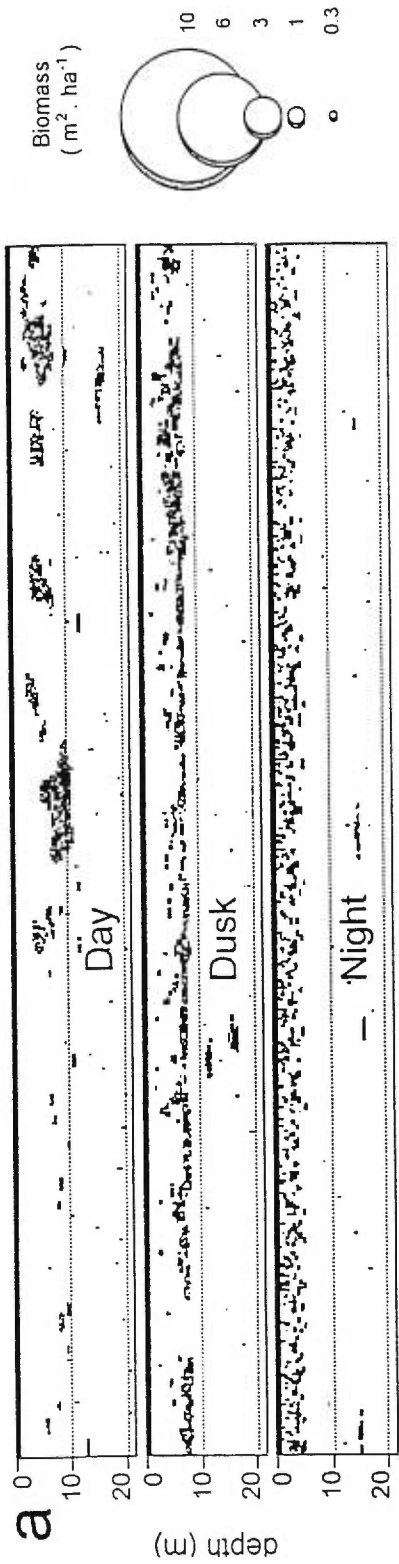
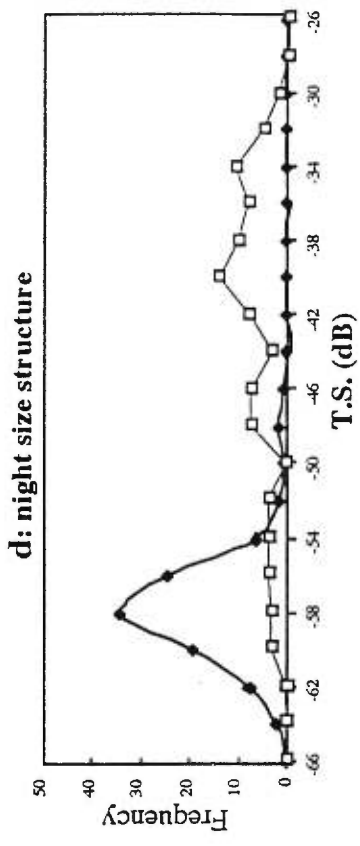
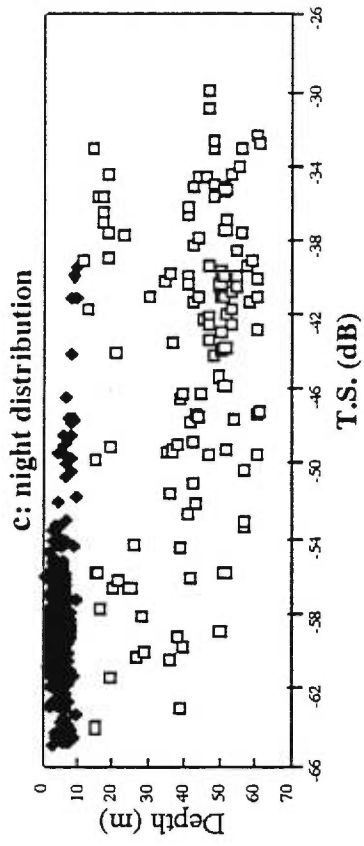
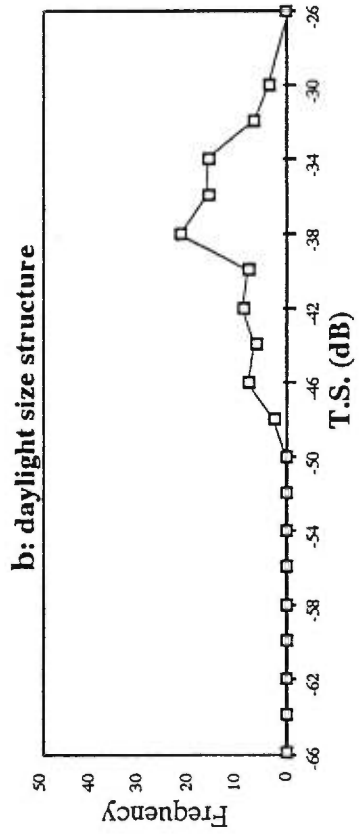
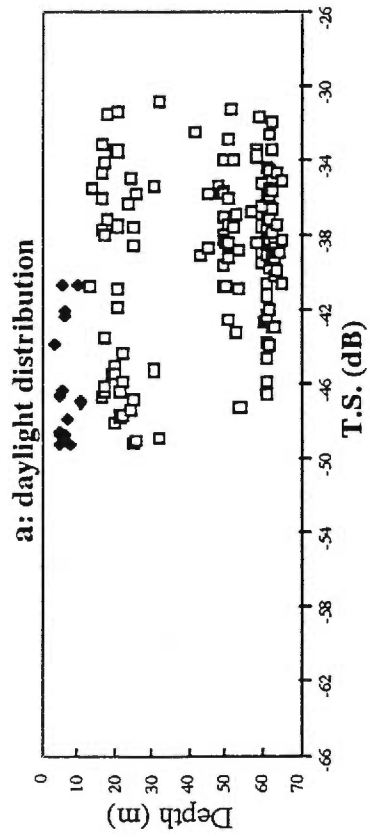


Figure 6 : Day to night vertical distribution and size structure of the acoustic targets detected during the PSM survey. Bold signs are echoes from 0-10m depth and open signs are 10m-bottom of the lake.





the community, leaving the benthos after dark, becoming more easily detectable at night. Below 10 m, the nocturnal size spectrum was somewhat flatter than during the day time. In contrast, epilimnetic targets (0 - 10 m) presented a very distinct nocturnal mode at - 58 dB (Figure 6d). All those distributions are representative of echoes observed few consecutive days and night following the sampling day.

#### 2.3.4 Fish community composition and diet

Nocturnal trawls carried out during the night of June 19th at 1.5 and 4 m depths, enabled us to identify echoes of -58 dB (main mode) as 0+ of *Perca fluviatilis* ( $29 \pm 5$  mm). In fact, perch juveniles were the only specimens caught. Their size distribution in the two samples ranged from 21 to 42 mm (Table I). Given this and the strong contribution of small echoes to total target biomass (Figures 5b, 6c-d), 0+ perch seem to dominate the open water fish biomass. The analysis of the digestive content of a sub-sample of 35 animals revealed that daphnids and cyclopoids were the main food items. Cyclopoids represented more than 75% of the diet content of these juveniles at the two sampled depths (Table I). No trend could be detected in the diet composition in relation to the size structure of the juveniles.

Table I. Size distribution and diet content of some fish (*Perca fluviatilis*) captured during trawlings.

Fish length (mm)	Fish captured at 1.5 m		Fish length (mm)	Fish captured at 4 m	
	Number of daphnids	Number of cyclopoids		Number of daphnids	Number of cyclopoids
21	4	7	27	3	41
21	3	19	29	5	51
23	6	41	29	2	61
23	4	50	30	27	38
24	2	11	30	5	100
26	14	31	32	5	62
26	5	48	32	10	59
28	3	48	32	18	77
29	6	90	33	9	83
30	7	24	33	4	60
30	0	29	34	22	121
31	7	49	34	8	53
31	14	65	36	5	48
32	2	24	36	9	84
33	7	34	42	3	69
34	9	49			
35	3	24			
36	9	100			
36	1	43			
37	6	76			

### 2.3.5 *Spatial autocorrelograms*

In order to test the significance of spatial patterns in the onshore-offshore distribution of fish and zooplankton, we computed the spatial autocorrelograms for the day, dusk, and night periods (Figure 7). During the diurnal period, no significant spatial structure could be detected in the epilimnion (6 m depth series), for the daphnids, cyclopoids, or for the fish biomass. In the metalimnion (11 and 16 m depth series), daphnids and cyclopoids showed significant negative spatial autocorrelation at large scale (> 960 m) and positive autocorrelation at small distance classes (60 and 120 m). This decreasing onshore-offshore gradient detected by mapping was still significant down to 25 m depth for cyclopoids but was no longer significant in the hypolimnion for daphnids (Figure 7). Significant spatial autocorrelation was however detected at small scales (60 and/or 120 m) in this layer (25 and 34 m depth series). At the depth sampled with the PSM, fish biomass did not present significant spatial structure in the meta- and hypolimnion with the exception of 34 m depth where biomass were similar at distance classes of 1080 m.

During the dusk period, cyclopoid copepods at 6 and 16 m depths showed a weak, but significant, decreasing nearshore-offshore gradient, with negative values in high distance classes (Figure 7). However, these spatial structures only occurred in the epilimnion (6 m) for the daphnids. Fish biomass did not show significant horizontal spatial structure at this period.

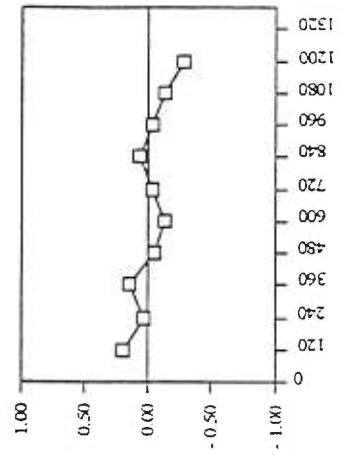
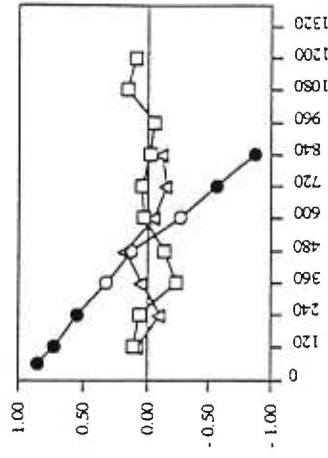
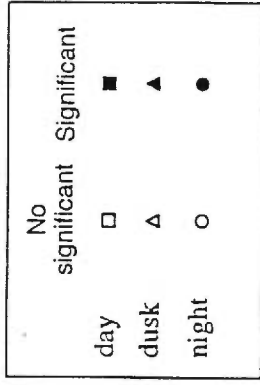
At night, the horizontal spatial structures observed in the metalimnion (11 and 16 m) during the day were detected in the epilimnion (2 and 6 m depth series) for both daphnids and cyclopoids (Figure 7). During this period, significant spatial structures were observed for fish in the epilimnion (6m depth series), with positive autocorrelation at small distances (60 m) and negative at large distances (> 720 m).

### 2.3.6 *Spatio-temporal coupling between daphnids and cyclopoids distributions*

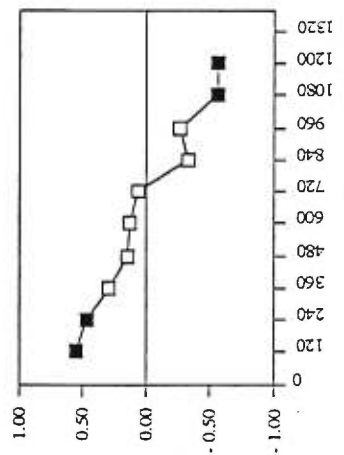
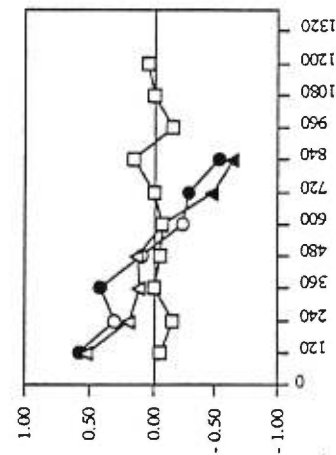
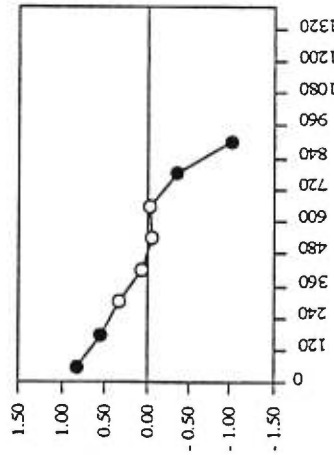
The spatial relationships between daphnids and cyclopoids depended on the depth and the period of period of the day (Tables II and III). During the day, the correlation between daphnids and cyclopoids in the epilimnion (6 m) was weak but significant ( $r = 0.313$ ;  $P < 0.001$ ) (Table IIa). At dusk, this relationship increased ( $r = 0.549$ ) (Table IIb)

Figure 7 : Spatial correlogramms obtained for the daphnids, cyclopoid copepods and fish repartition during the day, dusk, and night periods. Bold signs represent significant autocorrelation, wherease open signs indicate no significant autocorrelation.

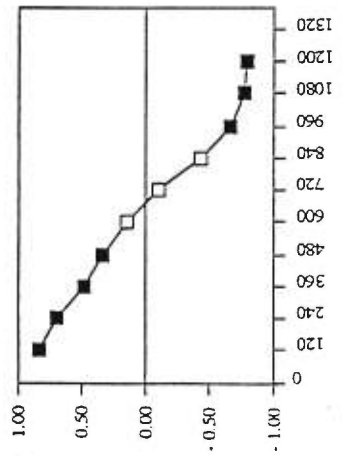
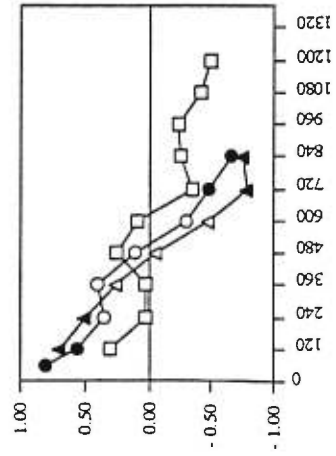
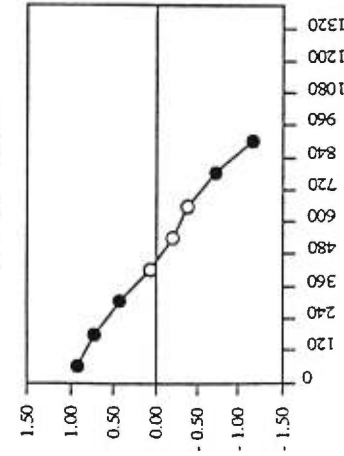
# FISH



# CYCLOPOIDS



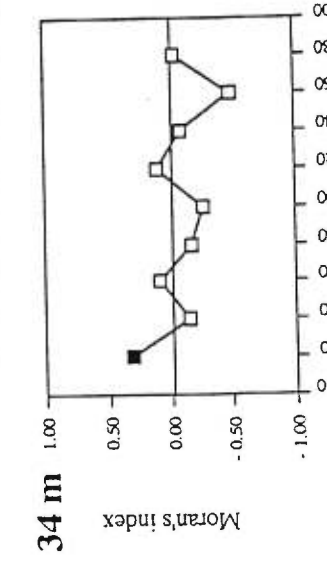
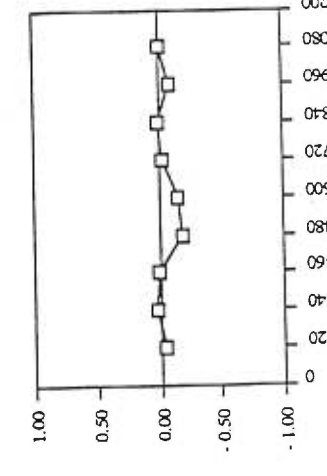
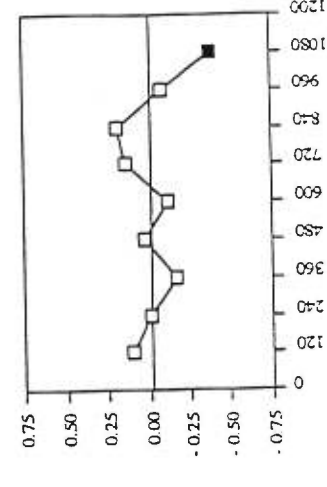
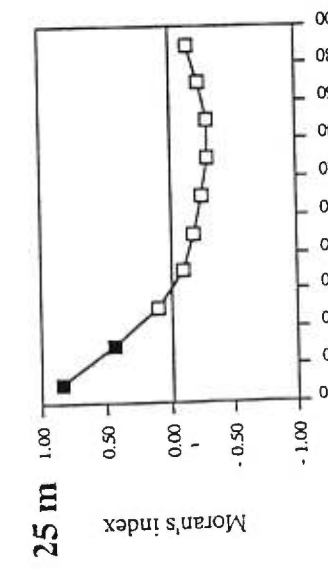
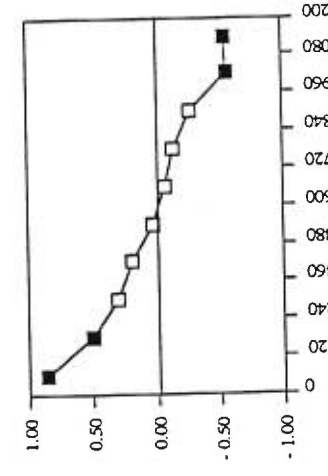
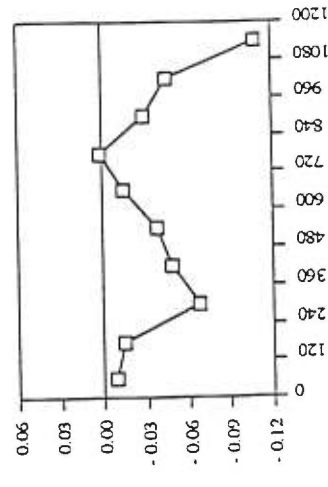
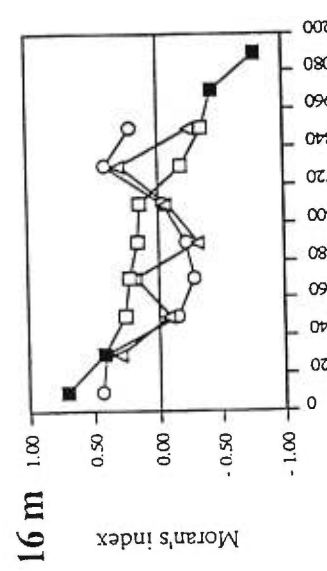
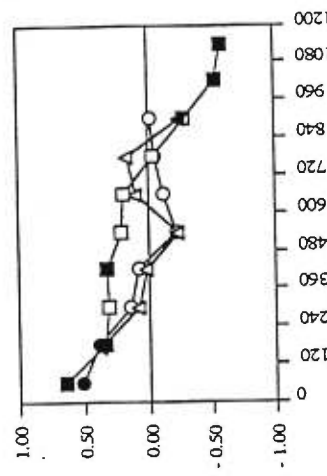
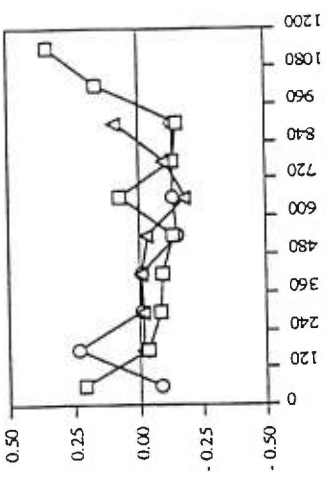
# DAPHNIDS



2 m

6 m

11 m



Distance (m)

Distance (m)

Distance (m)

16 m

25 m

34 m

Moran's index

Moran's index

Moran's index

while it became stronger at night ( $r = 0.932$ ) (Table IIc). By removing the effect of space, the correlations level between daphnids and cyclopoids diminished during the three period of the day ( $P < 0.001$ ). These results could imply a common structural factor.

In the metalimnion (16 m depth series), relationships between daphnids and cyclopoids were almost constant ( $r = 0.664$  to  $0.699$ ) during the three periods of the day (Tables IIIa to IIIc). As we observed for the epilimnion, when removing the effect of space, the level of correlation between zooplankton decreased at the three period of the day.

### ***2.3.7 Spatio-temporal coupling between fish and zooplankton distribution***

In the epilimnion (6 m depth series), no relationship was observed between fish either both daphnids or cyclopoids during the day and dusk periods (Tables IIa, IIb). However at night, a positive correlation was detected between fish and zooplankton ( $r \leq 0.289$ ;  $P < 0.001$ ) (Table IIc). During the day, the daphnids and cyclopoids presented either a significant ( $0.224$ ;  $P < 0.001$ ) or a non significant spatial autocorrelation with space ( $0.072$ ;  $P = 0.145$ ). This autocorrelation with space increased progressively through the night period (Tables IIa to IIc). In the goal to determine if the spatial structure of the zooplankton is related to the fish, we referred to the three possibilities described in the section 2.2.1. During the day and evening, the spatial structure of the daphnids and cyclopoids (Table IIa, IIb) is independent from the spatial structure of the fish. The majority of the zooplankton was in meta- and hypolimnetic waters and thus limited interactions with perch juveniles. On the other hand, the spatial structure of zooplankton at night was partly explained by the fish and by other factor(s) not retained in this study because the partial correlation between zooplankton and fish became negative when removing the effect of space (Table IIc). This could imply that positive relationship between zooplankton and fish established with simple correlation was spurious, while partial correlation could indicate that zooplankton at night avoided zone of high biomass of fish.

No significant relationship was observed between zooplankton and fish in the metalimnion during the three periods of the day (Tables IIIa,b,c). Both zooplankton categories also presented variable autocorrelation during the three periods of the day. As realized for the epilimnion, we verified if the spatial structure of the zooplankton was

TABLE II : Simple (above the diagonal) and partial (below the diagonal) Mantel statistics and associated probabilities for (a) day, (b) dusk, and (c) night sampling at 6 m depth.

a) DAY				
	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.313</b> ( $< 0.001$ )	0.010 (0.443)	<b>0.224</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = 0.313$ ( $< 0.001$ ) $\Delta S = 0.305$ ( $< 0.001$ )	-----	0.011 (0.438)	0.072 (0.145)
FISH	$\Delta C = 0.007$ (0.458) $\Delta S = -0.014$ (0.421)	$\Delta D = 0.009$ (0.449) $\Delta S = 0.004$ (0.478)	-----	0.103 (0.031)
SPACE	$\Delta C = 0.213$ ( $< 0.001$ ) $\Delta F = 0.224$ ( $< 0.001$ )	$\Delta D = 0.002$ (0.487) $\Delta F = 0.071$ (0.147)	$\Delta D = 0.104$ (0.024) $\Delta C = 0.103$ (0.030)	-----
b) DUSK				
	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.549</b> ( $< 0.001$ )	- 0.160 (0.099)	<b>0.420</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = 0.539$ ( $< 0.001$ ) $\Delta S = 0.486$ ( $< 0.001$ )	-----	- 0.137 (0.146)	<b>0.308</b> ( $< 0.001$ )
FISH	$\Delta C = -0.103$ (0.195) $\Delta S = -0.270$ (0.033)	$\Delta D = -0.059$ (0.318) $\Delta S = -0.210$ (0.065)	-----	0.191 (0.026)
SPACE	$\Delta C = 0.317$ ( $< 0.001$ ) $\Delta F = 0.466$ ( $< 0.001$ )	$\Delta D = 0.101$ (0.142) $\Delta F = 0.343$ ( $< 0.001$ )	$\Delta D = 0.289$ (0.010) $\Delta C = 0.249$ (0.012)	-----
c) NIGHT				
	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.932</b> ( $< 0.001$ )	<b>0.252</b> (0.005)	<b>0.626</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = 0.928$ ( $< 0.001$ ) $\Delta S = 0.891$ ( $< 0.001$ )	-----	<b>0.289</b> (0.002)	<b>0.616</b> ( $< 0.001$ )
FISH	$\Delta C = -0.052$ (0.317) $\Delta S = -0.403$ (0.001)	$\Delta D = 0.155$ (0.087) $\Delta S = -0.315$ (0.007)	-----	<b>0.741</b> ( $< 0.001$ )
SPACE	$\Delta C = 0.182$ ( $< 0.001$ ) $\Delta F = 0.675$ ( $< 0.001$ )	$\Delta D = 0.113$ (0.136) $\Delta F = 0.624$ ( $< 0.001$ )	$\Delta D = 0.772$ ( $< 0.001$ ) $\Delta C = 0.745$ ( $< 0.001$ )	-----

Mantel test is significant at the Bonferroni-corrected probability level of  $(0.05/6 = 0.008)$ . Partial Mantel test is significant at the Bonferroni-corrected probability level of  $(0.05/12 = 0.004)$ .  $\Delta C$ ,  $\Delta D$ ,  $\Delta F$ ,  $\Delta S$  = removing the effect of copepods, daphnids, fish and space.

TABLE III : Simple (above the diagonal) and partial (below the diagonal) Mantel statistics and associated probabilities for (a) day, (b) dusk, and (c) night sampling at 16 m depth.

a) DAY	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.664</b> ( $< 0.001$ )	- 0.070 (0.260)	<b>0.384</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = \mathbf{0.690}$ ( $< 0.001$ ) $\Delta S = \mathbf{0.591}$ ( $< 0.001$ )	-----	0.188 (0.052)	<b>0.492</b> ( $< 0.001$ )
FISH	$\Delta C = - 0.265$ (0.016) $\Delta S = - 0.132$ (0.121)	$\Delta D = \mathbf{0.314}$ (0.003) $\Delta S = 0.141$ (0.108)	-----	0.134 (0.044)
SPACE	$\Delta C = 0.088$ (0.109) $\Delta F = \mathbf{0.398}$ ( $< 0.001$ )	$\Delta D = \mathbf{0.343}$ ( $< 0.001$ ) $\Delta F = \mathbf{0.479}$ ( $< 0.001$ )	$\Delta D = 0.175$ (0.021) $\Delta C = 0.049$ (0.265)	-----
b) DUSK	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.662</b> ( $< 0.001$ )	- 0.062 (0.242)	<b>0.254</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = \mathbf{0.668}$ ( $< 0.001$ ) $\Delta S = \mathbf{0.640}$ ( $< 0.001$ )	-----	0.052 (0.320)	<b>0.253</b> ( $< 0.001$ )
FISH	$\Delta C = - 0.130$ (0.134) $\Delta S = - 0.091$ (0.156)	$\Delta D = 0.125$ (0.176) $\Delta S = 0.028$ (0.402)	-----	0.100 (0.121)
SPACE	$\Delta C = 0.119$ (0.087) $\Delta F = \mathbf{0.262}$ ( $< 0.001$ )	$\Delta D = 0.117$ (0.111) $\Delta F = \mathbf{0.250}$ (0.001)	$\Delta D = 0.120$ (0.083) $\Delta C = 0.090$ (0.151)	-----
c) NIGHT	DAPHNIDS	CYCLOPOIDS	FISH	SPACE
DAPHNIDS	-----	<b>0.699</b> ( $< 0.001$ )	- 0.060 (0.344)	<b>0.332</b> ( $< 0.001$ )
CYCLOPOIDS	$\Delta F = \mathbf{0.698}$ ( $< 0.001$ ) $\Delta S = \mathbf{0.653}$ ( $< 0.001$ )	-----	- 0.117 (0.235)	<b>0.510</b> ( $< 0.001$ )
FISH	$\Delta C = 0.032$ (0.396) $\Delta S = - 0.037$ (0.397)	$\Delta D = - 0.105$ (0.220) $\Delta S = - 0.093$ (0.276)	-----	0.074 (0.219)
SPACE	$\Delta C = - 0.039$ (0.292) $\Delta F = \mathbf{0.329}$ ( $< 0.001$ )	$\Delta D = \mathbf{0.411}$ ( $< 0.001$ ) $\Delta F = \mathbf{0.506}$ ( $< 0.001$ )	$\Delta D = - 0.058$ (0.255) $\Delta C = - 0.017$ (0.423)	-----

Mantel test is significant at the Bonferroni-corrected probability level of  $(0.05/6 = 0.008)$ . Partial Mantel test is significant at the Bonferroni-corrected probability level of  $(0.05/12 = 0.004)$ .  $\Delta C$ ,  $\Delta D$ ,  $\Delta F$ ,  $\Delta S$  = removing the effect of copepods, daphnids, fish and space.



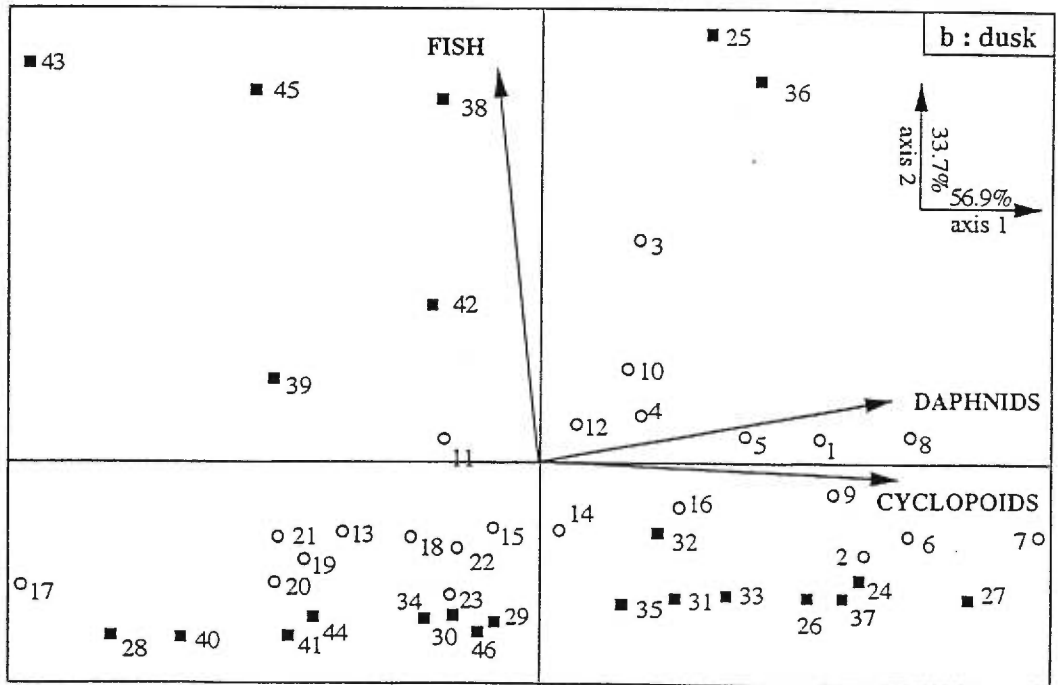
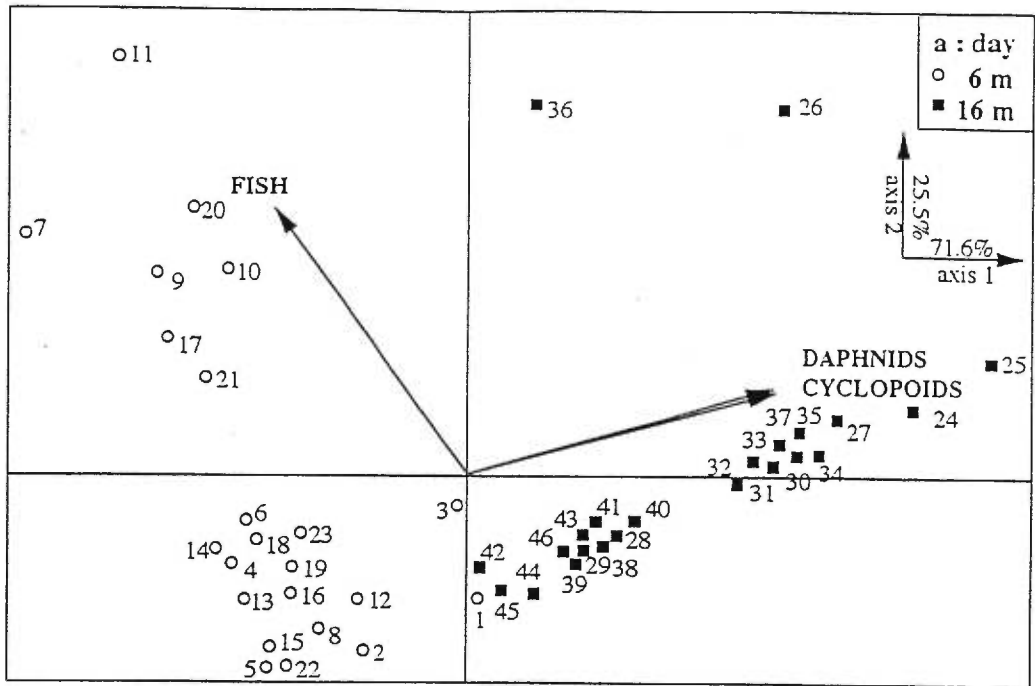
linked to the fish repartition according to the procedure described in the section 2.2.1. The spatial structure of the zooplankton was independent of the spatial repartition of the fish, since the relationship between zooplankton and fish was non significant once the spatial effect removed (Tables IIIa,b,c). Simple and partial Mantel tests did not allow to clearly establish link between spatial distribution of fish and zooplankton during the three period of the day. The effect of fish seems difficult to perceive when only regarding the horizontal plan, i.e. when considering both strata (epi- and metalimnion) separately. The PCA help us to understand the dynamic of the spatial relationships between zooplankton and fish by jointly considering both horizontal and vertical plans (Figures 8a,b, c).

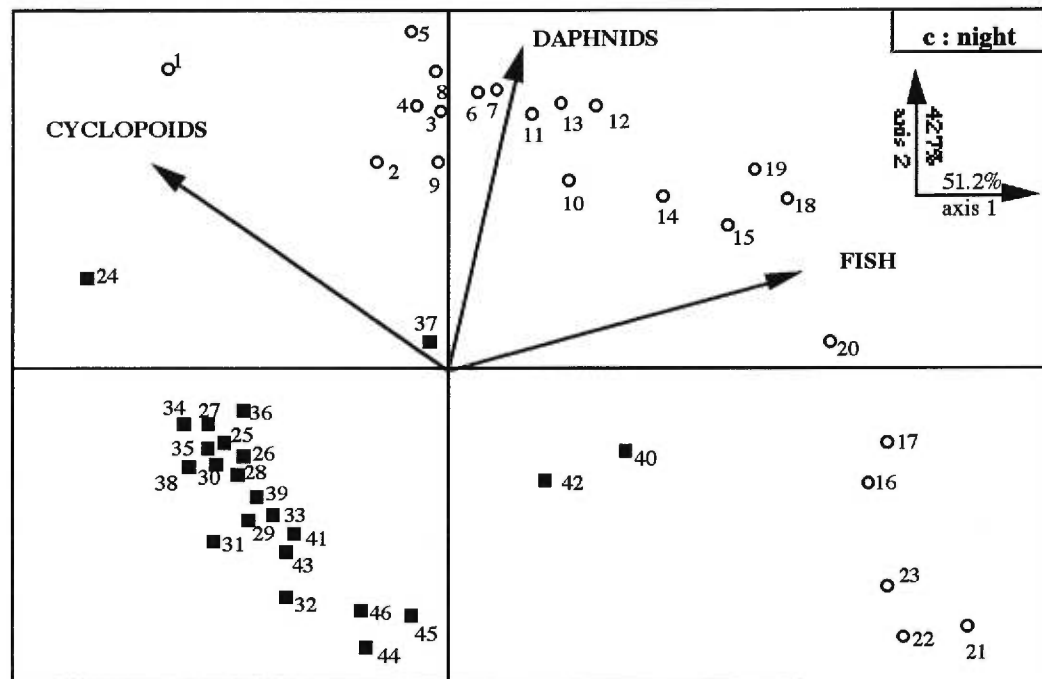
During the diurnal period, both daphnids and cyclopoids were distributed in a weak (angle  $\approx 110^\circ$ ) but negative fashion to the fish (Figure 8a). According to the distribution of the stations along the two first axis, 71.6% of the total diurnal variance appeared to be explained by depth, and only 25.5% by the horizontal axis (horizontal gradient along which highest densities of zooplankton occurred in the onshore region). Daphnids and cyclopoids were more abundant in the deepest waters, while most of the fish biomass was rather concentrated in surface waters (opposition of epilimnetic and metalimnetic stations).

For the dusk period (Figure 8b), the largest part of the total variability (56.9%) was related to the horizontal axis (zooplankton occupied a wider onshore zone than during daytime). Then, the second axis of the PCA indicated a vertical separation between zooplankton and fish by explaining 33.7% of the variability (the ascent was then not completed). The angles between fish and both daphnids and cyclopoids were almost at  $90^\circ$ , suggesting a non significant link between fish and zooplankton.

At night, in contrast to the periods of full or even weak light intensities, half (51.2%) of the variance was related to the vertical segregation between fish and zooplankton (Figure 8c). As observed during the day, the second axis explaining 42.7% of the nocturnal variance characterized a horizontal gradient of zooplankton density. The cyclopoids density was clearly in opposition with the fish biomass. Thus, both horizontal and vertical spatial dimensions were involved in the spatio-temporal relationships between zooplankton and fish.

Figure 8: Principal component analysis of the distribution of the daphnids, cyclopoid copepods and fish collected at 6 and 16 m during the (a) day, (b) dusk, and (c) night periods. Stations are identified according to their spatial repartition. Stations 1 to 23 were sampled at 6 m depth, stations 24 to 46 at 16 m depth, both series are ordered from onshore towards offshore area.





## 2.4 DISCUSSION

### 2.4.1 Spatio-temporal distribution of fish biomass

Juvenile perch in Lake Annecy, accounted for most of epilimnetic fish biomass in the spring of 1996. The highest density of perch juveniles in the pelagic zone during the night is consistent with that have been reported for perch species (*Perca fluviatilis* and *P. flavescens*) (Whiteside et al., 1985; Post and McQueen, 1988; Post et al., 1995; Imbrock et al., 1996; Scheuerell, 1996). However, all previous works mention a contagious distribution of the juveniles in the offshore zone rather than an onshore-offshore gradient. Hartmann (1984) also reported increasing yields of percids from West to Eastern side of the Lake Constance, but this gradient was only developed throughout the littoral zone. The spatial structure observed in Lake Annecy could be related to the size of the lake because greater horizontal distances are involved in larger lakes (Post and McQueen, 1988). During the day, such a gradient did not occur because juveniles were dispersed in schools in the pelagic habitat indicating a possible anti-predator response or searching behaviours (Treasurer, 1988; Bone et al., 1995; Flik et al., 1997). However, this schooling is also characteristic of older perch (e.g. Imbrock et al., 1996).

Most of the perch juveniles stay in the upper ten meters of the water column where the temperature exceeded 14 °C, a behaviour consistent with that reported in other studies (Whiteside et al., 1985; Post and McQueen, 1988; Flik et al., 1997). Indeed, perch juveniles have relatively high temperature requirements for growth (Houde, 1989; Imbrock et al., 1996). High temperatures provide an enhancement to foraging ability in terms of distance attack reactions, swimming speed, and capture rate (Bergman, 1987). Light is also related with higher requirements of this percid for the detection of its prey (Bergman, 1988), and with avoidance of either large piscivores (Werner, 1986) or cannibalism by adults (Wang and Eckmann, 1994). The daytime echograms allowed us to distinguish two spatially segregated other fish populations: the metalimnetic and the hypolimnetic aggregations of echoes could correspond to whitefish and Arctic Charr populations respectively. This distribution is typical of large whitefish in alpine lakes (Juget et al., 1995), where the species distribution in the water column is controlled by the thermal structure (Brandt et al., 1981). The good oxygenation in the hypolimnetic waters of Lake Annecy allows for such vertical segregation. This vertical structure did not occur at night when salmonids were probably searching for prey (Ponton, 1986; Ventlingschwank and Meng, 1995).

#### **2.4.2 *Spatio-temporal distribution of zooplankton***

Both daphnids and cyclopoids densities presented a decreasing gradient from the onshore to the offshore area. This horizontal pattern was first detected in deep waters during the day and progressively shifted towards the surface during the dusk to the night period. This ascent is characteristic of a diel vertical migration of zooplankton as observed in other sub-alpine lakes (e.g.: Geller, 1986; Gliwicz, 1986; Taleb et al., 1993; Angeli et al., 1995b). Our study provides the first record on large scale (1 to 2.5 km) of such vertical movement. Bast and Seitz (1993) and Taleb et al., (1993) have studied the DVM of several species in relation to their horizontal distribution. They detected DVM for most species, with some differences of migration amplitudes relative to the sampling stations, but no apparent horizontal gradient. Although these works were carried out at small scale (*vs* lake size: 0.1 and 0.6 km<sup>2</sup>) and with low spatial resolution (less than 5 stations), they clearly showed that differences in abundances at different sampling locations can be considerably large, especially if several species are considered. Our results also revealed very strong horizontal and vertical variations of the abundances of daphnids and cyclopoids during the night. These results combined with those of others

studies (Bast and Seitz, 1993; Taleb et al., 1993) underline the need to consider both horizontal and vertical axes in the study of ecological processes.

#### 2.4.3 *Spatio-temporal interactions between fish and zooplankton*

As we hypothesized, zooplankton presented an inverse horizontal and vertical distribution to the fish biomass distribution during the diel cycle. This segregation between zooplankton and fish suggests an avoidance behaviour of the prey to their predators. The strong day to night differences in the zooplankton densities at the surface ( $\sim 10$  vs  $5000$  ind.m<sup>-3</sup>) reinforces the hypothesis that zooplankton change their vertical distribution to minimize the predators' effects. Predation is now considered as the major process causing DVM (Zaret and Suffern, 1976; Lampert, 1992, 1993). In spite of this spatial opposition at the whole transect scale, we did not observe strong correlations between zooplankton and fish during the three periods of the day (Mantel tests and PCA). Rose and Leggett (1990) suggested that the pattern of spatial correlation between predator and prey is strongly influenced by either the presence or absence of refuge areas for the prey or by the activity level of the predator. Thus, during the daytime, zooplankton are expected to be spatially displaced from fish because of the shoaling behaviour of fish and the strong vertical migration of zooplankton. In Lake Annecy, maximal daytime abundance of zooplankton occurred in very deep waters (25 m depth series) until the night. Thus, zooplankton escaped from light-dependent mortality imposed by visually orienting planktivorous populations such as either the young age-classes of perch, which exhibit more efficient foraging activity and performances at higher temperature (Zaret and Suffern, 1976; Zaret, 1980; Bergman, 1987), or the older ones in onshore regions and slightly deeper layers. Such diurnal sub-littoral, meta- or hypolimnetic zooplanktonic aggregations could also involve advantages in term of optimal foraging for other planktivorous species with a lower temperature preference than the perch (e.g. Whitefish).

The strongest correlation observed between zooplankton and fish occurred at night when visually orienting planktivorous predators are less efficient. This result supports the hypothesis of Sih (1984) that positive correlations between predator and prey densities are to be expected only when prey do not move to avoid being eaten, i.e. share the same space that their predators. In Lake Annecy, both zooplankton and metalimnetic fish moved towards the surface at night when sight-predation risk is reduced (Gliwicz, 1986; Lampert, 1992). However, this later hypothesis cannot be generalized, because Rose and

Leggett (1990) showed that a correlation between predator and prey can be positive or negative depending on the scale of observation, especially when the scale of the prey refuge areas is considered.

Two potential explanations for the opposite horizontal onshore-offshore distribution of fish and zooplankton can be suggested. The first is with the highest density of perch juveniles in the offshore area, the zooplankton would be more susceptible to predation, and therefore, onshore migration would provide a refuge. Recent findings indicate that DVM in many zooplankton species can be induced by kairomones exuded by predators (Loose, 1993; Pijanowska, 1993). If more fish biomass or higher concentrations of fish exudates are present, the strength of zooplankton migration must increase (Ringelberg, 1991; Loose, 1993; Loose and Dawidowicz, 1994; Ringelberg et al., 1997). Thus, the occurrence of an opposite pattern in the horizontal distribution of predators and prey suggests that highest fish biomass in offshore region could have induced horizontal movement of the prey. Moreover, the fact that in early summer fish biomass is strongly represented by 0+ perch allows to consider such a spatial structure is maintained during the pelagic phase of larval and post larval fish stages. The high biomass also means very likely higher fish exudates concentrations in this zone, since juvenile metabolism, for instance excretion, is 4-fold higher than that of adults per weight unit (Post, 1990). In habitats where predation exerted, a non-responding behaviour would be disadvantageous due to the high risk of mortality (Loose and Dawidowicz, 1994). Post and McQueen (1988) also observed opposite distributions between zooplankton and perch juveniles in Lake St. George (Ontario). They also found that when perch juveniles were standing offshore during both day and night, the highest densities of their preferred prey (cyclopoids) occurred onshore. This relationship evolved in time and once juveniles moved into the littoral zone during the day, the densities of cyclopoids increased offshore. Such zooplankton diel horizontal movements (DHM) as behavioural antipredator defence have already been suggested (Kairesalo, 1980; Davis, 1985; Bast and Seitz, 1993; Taleb et al., 1993), but the attenuation of the predator effect throughout an horizontal gradient was not yet demonstrated. Thus, the strong inverse horizontal distribution of fish and zooplankton observed in Lake Annecy could support the suggestion of Holomuzki (1989) that when the vulnerability of the prey is high, the amplitude of their movements is larger.

Another explanation is that the impact of fish on zooplankton effectively increases with increasing distance from the shore (with the increase of their biomass), and that

planktivory reduces progressively the zooplankton density towards the offshore zone. In June the density of the major zooplankton in Lake Annecy was ten fold lower offshore than onshore. During this period, given the high contribution of 0+ perch to fish biomass and their higher energetic needs than adults per biomass unit, juveniles should have a strong impact on the zooplankton communities in the offshore area on which they feed (Post and McQueen, 1987; Whiteside, 1988). A few works have suggested that the juvenile's voraciousness, related to their energetic needs (Post, 1990), would have a strong contribution to the mid-summer decline and that it could lead to a consumption of up to 80 - 100 % of the zooplankton production (Rand et al., 1995; Post et al., 1997). Post (1990) and Houde (1989) showed that fish larvae can have daily consumption rates exceeding their own biomass. The interactions between larval fish and their zooplankton prey can be pivotal in determining larval growth, survival, recruitment, food web structure, and seasonal successions (Houde, 1987; Post and Prankevicus, 1987; Post and Rusdtam, 1992). Thus, the inverse diel distribution patterns between zooplankton and fish could be shaped by both predation losses and antipredator behaviour (DVM and DHM).

#### *2.4.4 Behavioural response of zooplankton to fish spatio-temporal distribution*

There was a strong spatial overlap in the horizontal and vertical distribution of cyclopoids and daphnids during the day. However, although both zooplankton categories demonstrated diel vertical migration apparently to avoid predators, nocturnal abundances of cyclopoid were less important near the surface (2 and 6 m depth series) and greater at the thermocline (16 m) than the daphnids. According to the stomach contents of the 0+ perch, cyclopoids were then the dominant item in their diet. This dominance could be due to the fact that juveniles (under 30 - 35 mm in length) feed mainly on copepods (Leslie and Moore, 1985; Schael et al., 1991). The cyclopoids' spatial distribution was clearly in opposition to that of the fish during the night. Thus, this difference in the spatial distribution of daphnids and cyclopoids could be shaped by the highest predation pressure on cyclopoid copepods. Several studies have concluded that DVM amplitudes increased when species were subject to intensive predation by fish while less-predated species moved less intensively (Geller, 1986; Gliwicz, 1986; Angeli et al., 1995b). Both zooplankton categories in Lake Annecy were subject to predation by perch juveniles and both made DVM, but cyclopoids copepods being the more heavily predated prey, could reduce their ascension towards the surface at night to avoid predators. This distinct behaviour by cyclopoids can be viewed as a defensive strategy to avoid predators at night.



## 2.5 IMPLICATION OF THESE RESULT AND CONCLUSION

This study shows that high horizontal and vertical variabilities could be detected in the zooplankton distribution, especially in large lakes (Bast and Seitz, 1993; Taleb et al., 1993; this study). Large aggregations of zooplankton detected in deep waters, combined with the aggregated distributions of fish juveniles could be the result of the predator-prey interactions, and suggest that standard sampling designs are likely to miss the detection of spatio-temporal relationships observed in this study. As mentioned by Megard et al., (1995), the densest zooplankton aggregations are likely to be of major importance for foraging fishes but are so infrequent that they are unlikely to be detected with conventional sampling methods. Coupling high frequency sampling of fish biomass and size by echosounding and continuous zooplankton sampling with the PSM allows us to detect phenomena that can happen at large spatial and short temporal scales, i.e. at the most critical one for obtaining good description of the patterns. The patterns at these two scales are difficult to resolve with conventional sampling methodology. Thus, to apprehend such phenomena in large lakes and adequately study predator-prey relationships, we need to use appropriate sampling strategies.

Although multiple driving forces can explain the DVM and DHM, the observed spatial distribution of zooplankton in Lake Annecy during the day to night study period could be shaped both by predation losses by percid juveniles and by antipredator behaviour by zooplankton. Thus, in this alpine lake, predation could strongly affects the spatio-temporal distribution of zooplankton. However, although the pre-sampling indicated the regularity of the observed spatio-temporal distributions of both zooplankton and fish, this study was only carried out on a diel cycle. Future works should be addressed to better define the temporal evolution of the dynamic of the predator-prey relationships in such aquatic system. Since juvenile perch are visually orienting planktivorous predators, it would be also valuable to accurately determine the critical temporal window of their impact on zooplankton. The twilight period could be particularly important in the spatial restructuring for food searching for both fish and zooplankton. Light attenuation plays a key role as a biological clock in the spatio-temporal dispersion and migration of both zooplankton and fish, as well as on biotic interactions.

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## CHAPITRE 3

### TOTAL PHOSPHORUS - CHLOROPHYLL *a* RELATIONSHIPS IN SOUTHERN QUÉBEC LAKES, WITH EMPHASIS ON REGIONAL VARIATIONS AND CHLOROPHYLL *a* SIZE FRACTIONS

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## RÉSUMÉ

Cette étude est une première tentative à estimer les réponses de la biomasse algale et les différentes classes de taille du phytoplancton aux variations de la concentration en phosphore total (TP) et de la géologie du bassin versant dans les lacs du sud du Québec. La biomasse algale totale a été estimée par les concentrations en chlorophylle *a* (Chl *a*), et celles-ci furent divisées en 4 classes de taille opérationnelles : le picophytoplancton, < 3  $\mu\text{m}$ ; le nanophytoplancton, 3 - 20  $\mu\text{m}$ ; le nano- plus picophytoplancton, < 20  $\mu\text{m}$ ; et le microphytoplancton, > 20  $\mu\text{m}$ .

Nous testions dans un premier temps si la relation TP-Chl *a* pour la biomasse algale totale et pour ses quatre classes de taille était différente entre des groupes de lacs situés dans deux régions géologiques; dans cette comparaison nous opposons des lacs reposant sur un socle de type sédimentaire (Canton de l'Est) à des lacs situés sur un socle de type igneux (Laurentides). Dans le gradient trophique très limité de cette étude (TP: 3 - 34  $\mu\text{g.L}^{-1}$ ; Chl *a*: 0.3 - 7.5  $\mu\text{g.L}^{-1}$ ), la réponse de la biomasse algale au TP ne variait pas à l'échelle régionale, ni pour la Chl *a* totale, ni pour les 4 classes de taille. Les lacs des Cantons de l'Est ne montraient pas une production de Chl *a* plus élevée par unité de TP par rapport aux lacs des Laurentides, bien que la biomasse algale du microphytoplancton tendait à être plus élevée dans les lacs plus eutrophes des Cantons de l'Est.

Notre étude est également une des premières tentatives à générer une nouvelle série de modèles prédictifs TP-Chl *a* déterminant la réponse quantitative de la biomasse algale totale et de ses 4 classes de taille face aux gradients de TP dans les lacs du sud du Québec. Le modèle pour la biomasse algale totale a été comparé aux modèles construits pour différentes régions géologiques à travers le Canada. La chlorophylle *a* totale semblait varier de la même façon selon les concentrations de TP pour des lacs de géologie similaire. L'étendue des pentes de la relations TP-Chl *a* pour les lacs du sud du Québec (0.93 - 1.22) est semblable à celle enregistrée pour d'autres modèles construits à travers le monde (0.7 - 1.6), ainsi que pour un large gradient de TP (0.5 - 1000  $\mu\text{g.L}^{-1}$ ).

Nous avons aussi testé l'hypothèse que les pentes des nouveaux modèles de régression TP-Chl *a* développés pour les classes de taille algale augmenteraient de façon consistante de la plus petite à la plus grosse classes de taille, tel que suggéré par les modèles sigmoïdaux TP-Chl *a*. Nous avons observé que les concentrations de Chl *a* pour la plus grosse classe de taille (microphytoplancton) augmentaient plus rapidement



avec l'enrichissement en phosphore que les plus petites classes de taille (pico-, nano-, et nano- plus picophytoplancton). Cependant, il n'y avait pas d'augmentation progressive des pentes de la relation TP-Chl *a* pour le pico- (pente = 1.08), le nano- (0.82), et le microphytoplancton (1.23). Lorsqu'inclut comme variable additionnelle, l'alcalinité de l'eau augmentait le pouvoir de prédiction de la biomasse algale et présentait des effets différentiels sur deux des petites classes de taille de la Chl *a*, ce qui pourrait refléter des changements contrastant dans le broutage des herbivores zooplanctoniques.

## ABSTRACT

The study is a first attempt to estimate the responses of algal biomass and size structure in southern Québec lakes to variations in total phosphorus (TP) concentrations and watershed geology. Total algal biomass was estimated using measurements of chlorophyll *a* (Chl *a*), and the total chlorophyll was divided into four operational size fractions: picophytoplankton, < 3  $\mu\text{m}$ ; nanophytoplankton, 3 - 20  $\mu\text{m}$ ; nano- plus picophytoplankton, < 20  $\mu\text{m}$ ; and microphytoplankton, > 20  $\mu\text{m}$ .

We first tested the hypothesis that TP-Chl *a* relationships for total algal biomass and its size fractions would differ among lakes of different regional geology; in this comparison we contrasted lakes in sedimentary watersheds (Eastern Townships region) with lakes in igneous watersheds (Laurentian region). Along the limited lake trophic gradient in our data set of southern Québec lakes (TP: 3 - 34  $\mu\text{g.L}^{-1}$ ; Chl *a*: 0.3 - 7.5  $\mu\text{g.L}^{-1}$ ), the responses of algal biomass to TP did not vary at the regional scale, for both total Chl *a* and the four Chl *a* size fractions. Eastern Townships lakes did not exhibit a significantly higher yield of Chl *a* per unit of TP than did Laurentian lakes, although algal biomass in the microphytoplankton tended to be higher in the most eutrophic lakes of the Eastern Townships region.

Our study is a first attempt to generate a series of new TP-Chl *a* predictive models relating the quantitative responses of total algal biomass and four empirical size fractions to TP gradients in southern Québec lakes. The model for total algal biomass was compared to models from different geological regions across Canada. Total chlorophyll *a* in lakes from similar regional geology appeared to respond in a similar manner to TP.

The range of slopes of the TP-Chl *a* relationships in southern Québec lakes (0.93 - 1.22) is similar to the range of slopes (0.7 - 1.6) of other models developed in lakes worldwide, and across large TP range (0.5 - 1000  $\mu\text{g}\cdot\text{L}^{-1}$ ).

We also tested the hypothesis that the slopes of the new TP-Chl *a* regression models developed for algal size fractions would increase consistently from the smallest to the largest algal size fractions, as suggested by sigmoidal TP-Chl *a* models. We found that Chl *a* concentrations in the largest size fraction (microphytoplankton) increased more rapidly with phosphorus enrichment than in either of the smallest fractions (pico-, nano-, and nano- plus picophytoplankton). However, there was no consistent trend in the magnitudes of the slopes of TP-Chl *a* relationships for pico- (slope = 1.08), nano- (0.82), and microphytoplankton (1.23). When included as additional variable, water alkalinity improved the prediction of algal biomass and presented differential effects on two small Chl *a* size fractions which might reflect contrasting changes in zooplankton herbivore grazing.

### 3.1 INTRODUCTION

Eutrophication is a major global environmental problem influencing the water quality of lakes and reservoirs worldwide, and nuisance summer growths of phytoplankton in these waterbodies is one of the most visible expressions of this excess nutrient loading (OECD 1982; Smith 1998). During the past three decades, numerous studies have examined relationships between nutrient loading, water column nutrient concentrations, and algal biomass (Vollenweider 1968; Dillon and Rigler 1974; Smith 1982; Pridmore et al. 1985; Dillon et al. 1988; McCauley et al. 1989; Prairie et al. 1989; Seip 1990; Seip et al. 1992; Vyhnalek et al. 1994; Chow-Fraser et al. 1994; Meuwig and Peters 1996). However, the quantitative response of algae to nutrient is highly variable among waterbodies and regions, and can be influenced by a number of physical, chemical, and biological factors (Nicholls and Dillon 1978; Hoyer and Jones 1983; Pace 1984; Ahlgren et al. 1988; Smith 1990; Seip and Goldstein 1994; Mazumder 1994a, 1994b) as well as by data aggregation into seasonal or long term means (France et al. 1994; Jones et al. 1998). Variability among lakes in the response of algal biomass to nutrients is the focus of the work reported here.

Although direct microscopic methods can be used to estimate phytoplankton biomass (Crumpton 1987; Watson and McCauley 1988), the laboratory procedures involved in these measurements are time consuming, expensive, and require personnel very experienced in algal taxonomy. Chlorophyll *a* is commonly used as an alternative measurement of algal biomass because it is much more rapid and convenient to perform, and reliable. Several workers have reported significant correlations between chlorophyll *a* and direct microscopic measurements of algal biomass (Desortova 1981; Canfield et al. 1985). Similarly, Labauch (1995) observed a linear relationship ( $r^2=0.72$ ) between algal biovolume and chlorophyll *a*, but only for low- to moderate productivity lakes, in which median concentrations of chlorophyll *a* during open-water periods were  $< 20 \mu\text{g.L}^{-1}$ . Concentrations of chlorophyll *a* are thus a much more commonly used index of lake trophic state, and empirical Total Phosphorus - Chlorophyll *a* (TP-Chl *a*) models have been developed and used successfully worldwide in the practical management of eutrophication (Schindler 1978; OECD 1982; Reckhow and Chapra 1983; Seip et al. 1992; Cooke et al. 1993; Meeuwig and Peters 1996; Correll 1998).

The primary production of phytoplankton communities is typically channeled into a wide diversity of different taxa, and significant shifts in algal species composition and

functional attributes typically occur across a lake trophic state gradient (Smith 1990; McCauley et al. 1989; Duarte et al. 1992; Watson et al. 1992; Seip and Reynolds 1995). As a result of these shifts in taxonomic composition, pronounced changes in algal size structure also occur with nutrient enrichment. For example, Kalff and Knoechel (1978) concluded that the summer net plankton biomass increased disproportionately faster than nanoplankton biomass with increasing nutrient loading. This trend was confirmed by Watson and co-workers, who found that the biomass of algae  $< 35 \mu\text{m}$  did not respond to increasing nutrient availability at the same rate as the biomass of algae  $> 35 \mu\text{m}$  (Watson and Kalff 1981; Watson and McCauley 1988; Watson et al. 1992). Moreover, Seip and Reynolds (1995) developed response surface models relating phytoplankton functional attributes such as phytoplankton cell volume and growth rate to trophic state gradients and season. Size-specific responses to nutrient enrichment can result in significant variation in epilimnetic chlorophyll concentrations and lake responses to TP gradient because the chlorophyll content of algal cells is influenced in part by cell size (Vörös and Padisák 1991; Labauch 1995). However, sufficiently high variance has been observed in the chlorophyll *a* content per unit phytoplankton biovolume that some authors consider this relationship to be noisy and difficult to predict (Dillon et al. 1988; Aleya and Amblard 1989).

In this study we have explored the relationship of both algal biomass (reported here as concentrations of Chl *a*) and algal size structure to variations in total phosphorus (TP) concentrations, and lake and watershed characteristics for 27 lakes located in southern Québec, Canada. In our studies of algal size structure, we have used the size classification system defined by Sieburth et al. (1978): picophytoplankton (Pico:  $< 3 \mu\text{m}$ ), nanophytoplankton (Nano:  $3 - 20 \mu\text{m}$ ), and microphytoplankton (Micro:  $> 20 \mu\text{m}$ ). In addition, we divided the phytoplankton into two categories according to their presumed susceptibility to grazing by zooplankton herbivores: edible algae (nano- plus picophytoplankton: NaPi  $< 20 \mu\text{m}$ ) and inedible algae (microphytoplankton: Micro  $> 20 \mu\text{m}$ ). Although we recognized that there are inherent limitations to size fractionation methodologies involving screens (Munawar et al. 1982; Stockner and Antia 1986), successful size fractionation of the phytoplankton can be accomplished using Nitex meshes and filters of known pore size. We believe that the mechanical separation of the total chlorophyll *a* content of a whole water sample into empirically-defined chlorophyll size fractions, such as those we reported here, is a reasonable alternative to direct microscopic examination. This mechanical algae separation has been successfully used in several recent studies (Lafond et al. 1990; Angeli et al. 1995; Pinel-Alloul et al. 1996).

In our analyses of the data from southern Québec lakes, we first tested the hypothesis that TP-Chl *a* relationships for total chlorophyll *a* and for chlorophyll *a* size fractions derived from lakes located in watersheds having sedimentary geology would differ significantly from TP-Chl *a* relationships obtained for lakes located in igneous watersheds. Regional variations in watershed geology and physiography, climate, lake morphometry and trophic, and phytoplankton community structure may account for differences in nutrient inputs to lakes, responses of algal biomass to nutrient inputs, and variation in TP-Chl *a* relationships (Glober and Silberbauer 1985; Seip et al. 1992; Seip and Goldstein 1994; D'arcy and Carignan 1997). Regionally-developed TP-Chl *a* models potentially have greater practical utility than global eutrophication models when attempting to resolve lake management problems, which are typically of a regional nature (Kalff 1991). We thus developed a series of TP-Chl *a* relationships for the 27 southern Québec lakes, and compared these models to published models derived from lakes located in other geological regions of Canada.

Because shifts in algal community structure along lake trophic gradient may influence the structure of empirical TP-Chl *a* models (Reynolds 1984; McCauley et al. 1989; Prairie et al. 1989; Watson et al. 1992), we also tested the hypothesis that the regression parameters (i.e., the slope and intercept) of the new TP-Chl *a* relationships would differ significantly among the size fractions examined (< 3  $\mu\text{m}$ , 3-20  $\mu\text{m}$ , < 20  $\mu\text{m}$  and > 20  $\mu\text{m}$ ). We initially hypothesized that the slope of these regressions models would increase consistently from the smallest algal size fractions to the largest ones, as suggested by the sigmoid TP-Chl *a* models (McCauley et al. 1989; Watson et al. 1992; Chow-Fraser et al. 1994). Finally, multiple regression models including additional lake characteristics were evaluated in an attempt to improve the predictability of the Chl *a* size fractions.

## 3.2 MATERIALS AND METHODS

### 3.2.1 *Study Lakes*

In an attempt to reflect the geographical variability of lake environments in southern Québec, and to sample waterbodies having a large range of trophic states and other chemical conditions, we chose a total of 27 glacial lakes from two contrasting regions: the Laurentians and the Eastern Townships (Figure 1, Table I). The 21 Laurentian lakes are located in the southeastern part of the Precambrian Shield, 80 km north of Montréal (46°N; 74°W). The bedrock in this region is mainly gneiss and granite,

Figure 1 : Map of the study area and lakes.

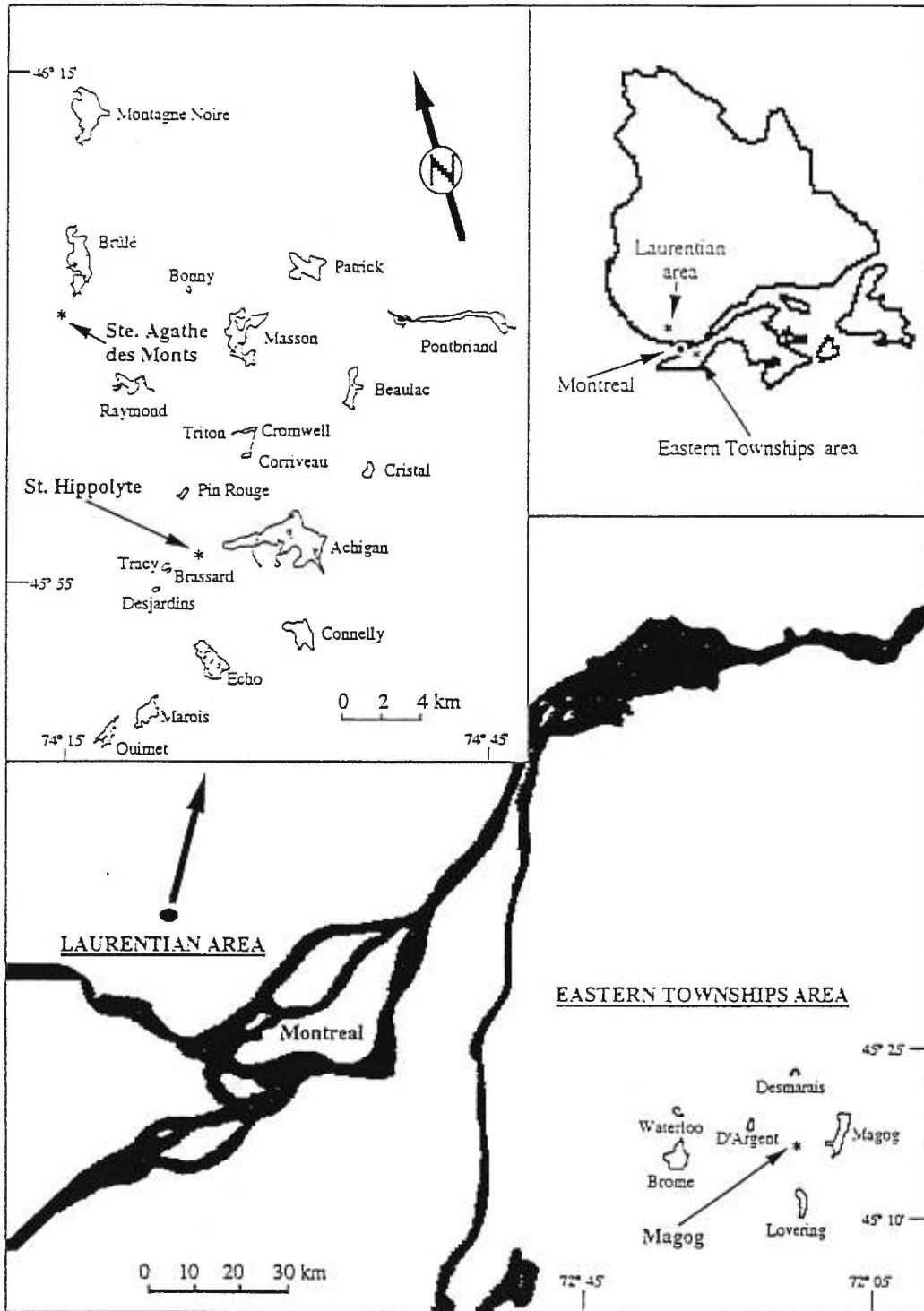


TABLE I : Morphometric features of the southern Québec lakes.

Lake (year of sampling)	Elevation (m)	Latitude (N)	Longitude (W)	Lake area (km <sup>2</sup> )	Drainage area (km <sup>2</sup> )	Max depth (m)	Mean depth (m)	Lake volume x 10 <sup>4</sup> m <sup>3</sup>
<u>Laurentians</u>								
Achigan (93)	207	455633	735839	5.37	88.70	26.8	12.9	6948.08
Beaulac (94)	332	460124	735400	0.87	4.23	9.3	5.35	463.52
Bonny (93)	360	460515	740531	0.07	0.19	10.7	4.74	32.36
Brassard (94)	365	455528	740352	0.04	0.11	6.1	1.81	6.70
Brûlé (94)	378	460547	741652	2.68	141.2	24.4	8.42	2259.58
Connolly (93)	195	455354	735751	1.21	22.1	20	7.85	950.25
Corriveau (93-95)	325	455847	740000	0.06	13.9	13.7	7.11	43.54
Cristal (93)	264	455829	735328	0.29	1.88	18.5	9.51	274.56
Cromwell (93)	340	455920	735958	0.11	10.11	10	3.07	32.38
Desjardins (93)	351	455457	740424	0.06	0.24	4.6	2.13	11.99
Echo (94)	241	455308	740123	1.76	10.23	9.1	2.46	432.80
Marois (93)	299	455100	740829	0.99	6.03	22.7	10.53	660.85
Masson (93)	302	460241	740203	2.71	31.69	45.7	10.2	2763.71
Montagne Noire (94)	456	461149	741618	2.81	9.96	33.5	13.29	3729.85
Ouimet (93-95)	302	455025	740938	0.59	5.84	18.3	5.24	309.16
Patrick (93)	347	460621	735848	1.51	61.73	30.5	10.79	1625.68
Pin Rouge (93-95)	332	455737	740228	0.15	6.64	15.2	5.07	76.71
Pontbriand (93)	149	460311	734623	1.96	1258	9.3	2.94	574.62
Raymond (94)	309	460010	740931	0.62	245.78	21.2	5.66	352.00
Tracy (93)	349	455535	740400	0.08	0.13	24.4	8.92	69.44
Triton (93)	340	455915	740028	0.02	0.14	3.2	1.93	3.61
<u>Eastern Townships</u>								
Brome (94)	196	451448	723016	14.39	172.9	12.2	5.88	8465.43
D'Argent (94)	248	451836	721850	1.00	64.03	15.6	4.47	446.91
Desmarais (94)	200	452736	720656	0.24	1.57	7	2.52	60.90
Lovering (94)	241	450956	720909	4.94	41.30	22.9	8.80	4351.12
Magog (94)	193	451808	720229	10.95	1950.16	19.2	7.98	8743.04
Waterloo (94)	207	452000	723108	1.47	32.46	4.9	3.35	493.37

and is covered by morainic soils and boreal forests. The 6 Eastern Townships lakes are located 100 km south of Montréal (45°N; 72°W) in a well-buffered calcareous region containing mixed crystalline and sedimentary rocks, and covered primarily by deciduous forests. The climate in both regions is temperate, and summer total precipitation during this study was 280 mm, 511.4 mm and 247.8 mm in 1993, 1994 and 1995, respectively. The surface area of the lakes ranged from 0.02 km<sup>2</sup> to 14.39 km<sup>2</sup>, and their drainage area varied between 0.11 km<sup>2</sup> and 1950.16 km<sup>2</sup> (Table I). Maximum lake depth ranged from 3.2 m to 45.7 m, and mean lake depth varied from 1.81 m to 13.29 m. Lake volume ranged from a minimum of 3.61 x 10<sup>4</sup> m<sup>3</sup> to 8743 x 10<sup>4</sup> m<sup>3</sup>. Most of the lakes were dimictic, but 4 shallow lakes (Desjardins, Pontbriand, Triton and Waterloo) did not stratified completely during summer.



### 3.2.2 *Field sampling*

Sampling was carried out once a month from June to August in 12 lakes in 1993 and in 12 lakes in 1994 (see Table I). In addition, 3 lakes (Corriveau, Pin Rouge and Ouimet) were monitored each summer from 1993 to 1995. At each sampling date, water transparency was measured using a black and white Secchi disk at the deepest site of each lake. In order to determine the depth of the epilimnion, profiles of temperature and dissolved oxygen were established at 0.5 m intervals with a YSI model 51B electronic temperature/oxygen meter. Thereafter, at three stations two or three replicate water samples were collected from the epilimnion using a 6 L Van Dorn bottle and were mixed for later analyses. Water samples for chlorophyll *a* and water chemistry (conductivity, pH, alkalinity, apparent water color, and DOC) were mixed and stored in amber and clear polyethylene bottles in a cooler. Water for nutrients analyses (TN and TP) was separately kept in sterilized bottles.

### 3.2.3 *Laboratory analyses*

Measurements of pH and conductivity were made using a Fisher Acumet model 620 pH meter and a Cole Parmer model 1484 conductivity meter, and standardized to 25 °C. Alkalinity was determined by titrating a 200 mL water sample to pH 4.5 with 0.06 N HCl (APHA 1992). Apparent water color was determined spectrophotometrically at 440 nm (Cuthbert and Del Giorgio 1992) and the absorbance values were converted to standard platinum units (Environment Canada 1979). Water samples collected for TP and TN were placed in sterilized 30-ml tubes previously soaked in a HCl acid bath (10% v/v) and rinsed with deionized distilled water; they were finally stored at 4°C in a refrigerator until analysis. All nutrients were analysed on an Alpkem autoanalyzer (model RFA 300). Total phosphorus (TP:  $\mu\text{g P.L}^{-1}$ ) was measured using the molybdenum blue colorimetric assay with 10 cm cuvettes after acidic persulfate digestion (Murphy and Riley 1962). Total nitrogen (TN:  $\mu\text{g N.L}^{-1}$ ) was analysed colorimetrically using 2 or 5 cm flow cells following the indophenol blue method (Armstrong et al. 1967) after digestion by alkaline persulfate oxydation. Water samples for DOC (Dissolved Organic Carbon) were filtered through Whatmann GF/F glass-fiber filters that had been precombusted at 500°C. The DOC samples were stored in 60 ml polyethylene bottles at 4°C, and analyzed within 72 hours. The DOC concentration was determined by conductimetry after persulfate-UV oxidation (Kaplan 1992).

Both total chlorophyll *a* concentrations and the chlorophyll *a* concentrations in each of the four operationally-defined size fractions (Pico:  $< 3 \mu\text{m}$ , Nano: 3 to  $20 \mu\text{m}$ , NaPi:  $< 20 \mu\text{m}$ , and Micro:  $> 20 \mu\text{m}$ ) were determined by fluorometry. For measurements of total chlorophyll *a*, 300 mL of epilimnetic water were filtered through  $0.45 \mu\text{m}$  cellulose Millipore™ membranes in subdued light; these filters were chosen because cellulose membranes retain more chlorophyll than glass-fiber filters (Munuwar et al. 1982). For the NaPi size fraction ( $< 20 \mu\text{m}$ ), 300 mL of epilimnetic water was sieved through  $20 \mu\text{m}$  Nitex mesh nets before filtration onto  $0.45 \mu\text{m}$  cellulose membranes. Similarly, for the Pico size fraction ( $< 3 \mu\text{m}$ ), 300 mL of epilimnetic water was filtered through  $3 \mu\text{m}$  porosity polycarbonate Nucleopore™ filters at a low vacuum of 10 to 15 cm Hg (Hobbie et al. 1977), and the particles present in this filtrate were then captured by filtration onto  $0.45 \mu\text{m}$  cellulose membranes. Polycarbonate filters provided a uniform nominal pore diameter, allowing a more consistent size-fractionation of the picophytoplankton (Stockner and Antia 1986). The chlorophyll concentrations in the two other size fractions were estimated by difference: Chl *a* in the inedible Micro size fraction ( $> 20 \mu\text{m}$ ) was calculated as the difference between the total Chl *a* concentration and that in the NaPi size fraction ( $< 20 \mu\text{m}$ ). Similarly, Chl *a* in the Nano size fraction (3 -  $20 \mu\text{m}$ ) was calculated as the difference between the Chl *a* concentration in the NaPi size fraction ( $< 20 \mu\text{m}$ ) and that in the Pico size fraction ( $< 3 \mu\text{m}$ ).

All systems were rinsed with distilled water between successive filtrations in order to avoid the retention of residual particles smaller than the effective pore size of Nitex nets or polycarbonate filters.  $\text{MgCO}_3$  was added to the samples at the end of filtration to prevent chlorophyll degradation in acidic waters. The membrane filters were then folded and wrapped in aluminium foil, and stored at  $-20^\circ\text{C}$ . Chlorophyll *a* was extracted in 90% acetone for 24 hrs at  $4^\circ\text{C}$ , and measured using a Turner fluorometer model 10-AU (precision:  $\pm 0.11 \mu\text{g.Chl } a\text{L}^{-1}$ ) after spectrophotometric calibration (Strickland & Parsons 1968). Calibration of the fluorometer was performed using total chlorophyll *a* concentrations in five 300 mL water samples collected in Lake Cromwell (Table I). Chlorophyll *a* concentrations were not corrected for pheopigments, because acidification produced a white precipitate in the samples filtered on cellulose membranes (Munuwar et al. 1982). The precision of the fluorometric technique for pigment determination is considered excellent for the recovery of both chlorophyll and pheopigment, and the interference from the presence of chlorophyll *b* is not a serious problem in taxonomically diverse phytoplankton populations (Lorenzen 1967).

### 3.2.4 Statistical methods

Individual lakes were the basic sampling unit for statistical tests in this study, and all replicate data from each sampling station (3) and sampling date (June, July, August) were averaged to obtain summer means for all variables in each lake. Data integration into seasonal means greatly strengthens Chl *a* - TP relationships without any difference in linear regression models (Jones et al. 1998). All data except pH were log<sub>10</sub>(x) transformed to stabilize the variance and normalize the residuals to meet normality assumptions of regression analyses. A Pearson correlation matrix helped to identify significant relationships between the variables (Table II). Because the probability of a type I error becomes larger than the nominal value when several tests of significance (n) are carried out simultaneously, a Bonferroni correction was applied by adjusting the level significance  $\alpha' = \alpha/n$  and by comparing probabilities  $p_i$  to  $\alpha'$  (Hochberg 1988).

Lake Brassard was removed from all following statistics because it strongly increased the variability of the models (Figs. 3c,d,e). The analysis of the residuals (Cook's distance, DFFITS, and DFBETAS) indicated that this lake after exclusion causes major changes in the fitted regression function. This lake was small (0.04 km<sup>2</sup>), shallow (6m) and was only colonized by one planktivorous fish species (Lake Chub), which allowed an important development of small algae (Figs. 3c,d,e). Analyses of covariance (ANCOVA) were used to test the hypothesis that TP-Chl *a* relationships for the total chlorophyll *a* and the size fractions would differ among the two geological regions (Laurentians and Eastern Townships). The model used for ANCOVA analyses (Montgomery and Peck 1982) is:

$$Y = \beta_0 + \beta_1 X_1 + a_i C_i + d_i X_1 C_i + \epsilon \quad (1)$$

where  $Y$  is the dependent variable (here both total chlorophyll *a*, and chlorophyll *a* in each of the four size fractions) and  $\epsilon$  is an error term.  $X_1$  is the dummy variable coding for lake regions as following: 0 = Eastern Townships region and 1 = Laurentian region. The  $C_i$  is the abiotic covariable in the model (TP) and  $X_1 C_i$  is the interaction term. Significant probabilities either for the main factor ( $X_1$ : region in our case) or for the interaction term ( $X_1 C_i$ ) indicated a difference in the intercept and in the slope between regressions. Before each ANCOVA test, we verified the homogeneity of variance of dependent variables using a Bartlett's test. Simple ordinary least squares (OLS) regression analyses were used to quantify the relationships between total chlorophyll *a*, or

chlorophyll *a* in each size fraction, and TP concentration (Neter et al. 1990). We also used ANCOVA to test the hypothesis that the regression parameters (slope and intercept) of the TP-Chl *a* relationships would differ significantly among the chlorophyll *a* size fractions (Pico: < 3  $\mu\text{m}$ , Nano: 3 - 20  $\mu\text{m}$ , NaPi: < 20  $\mu\text{m}$  and Micro: > 20  $\mu\text{m}$ ), and that the regression slopes would increase consistently from the small to the large size fractions. To establish the best models to predict total Chl *a* and Chl *a* in each size fraction, stepwise multiple regressions were performed on the log-transformed data, with the level for entry of individual variables set at  $\alpha = 0.05$  (Neter et al. 1990). Among the transformed abiotic variables, pairwise (bivariate) correlations greater than 0.60 occurred for some variables (see Table II). Instead of arbitrarily excluding one or several of those variables on the basis of pairwise correlations, with potential loss of information (James and McCulloch 1990), all abiotic variables were included in the regressions. After a variable selection was completed, models were screened for multicollinearity by examination of the tolerance of individual variables (Tabachnick and Fidell 1989). Variables with tolerances less than 0.20 appearing in some models were dropped and parameters were recalculated to yield alternative reduce models. Tolerances of individual variables were greater than 0.89 in all final equations. Because the sampling periods or the temporal scale chosen for estimating total phosphorus and chlorophyll *a* can be a potential source of variability in TP-Chl *a* models (Nicholls and Dillon 1978; France et al. 1994; Jones et al. 1998), we performed statistical comparisons of Québec TP-Chl *a* models to other published models in Canadian lakes only if these models originally had been developed using summer aggregated data, as in our study. All statistical analyses were performed on a Macintosh computer using SPSS 4.0 (Nie et al. 1984).

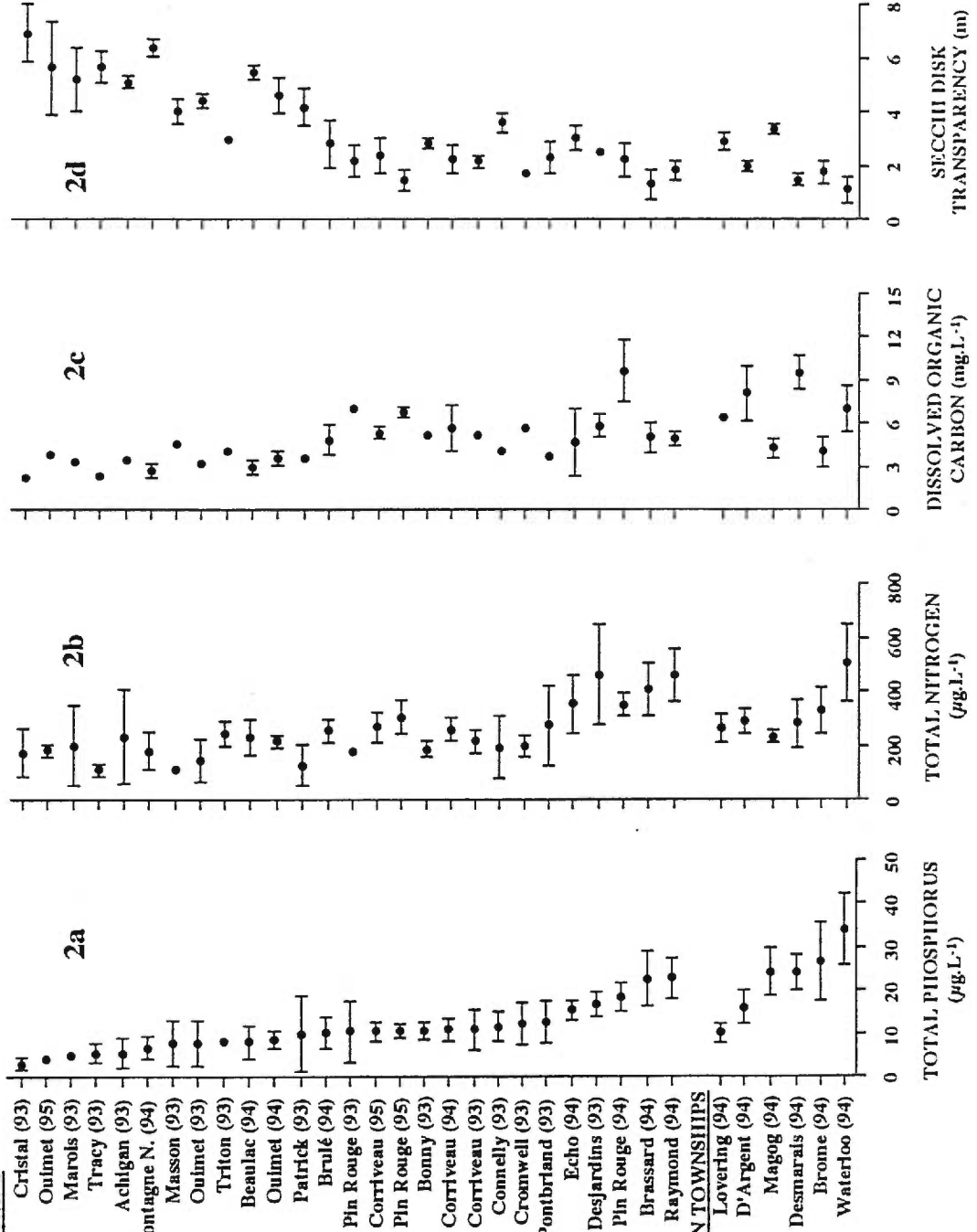
### 3.3 RESULTS AND DISCUSSION

#### 3.3.1 *Lake characteristics*

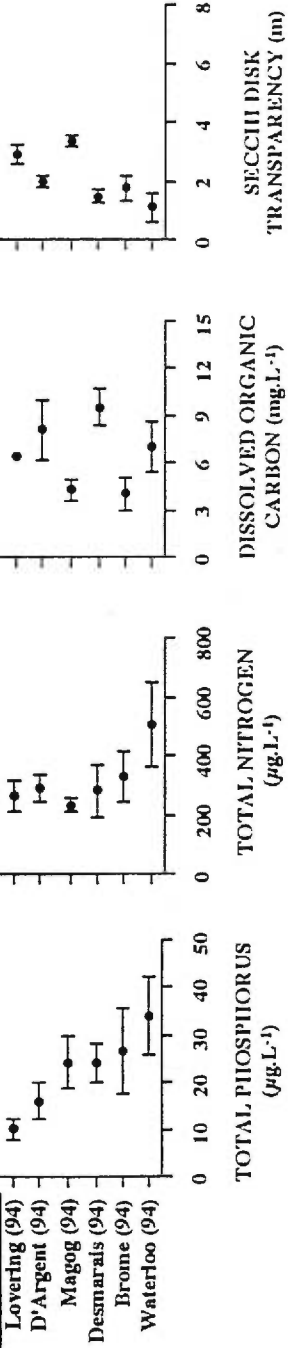
The characteristics of the 27 southern Québec lakes are presented in Figure 2a -h. Within each region, the lakes were ranked in ascending order by their summer mean TP concentrations. Our lake data set showed relatively modest ranges of trophic conditions (TP: 3 - 34  $\mu\text{g.L}^{-1}$ ; TN: 111 - 504  $\mu\text{g.L}^{-1}$ ; Chl *a*: 0.34 - 7.55  $\mu\text{g.L}^{-1}$ ), but more variable water characteristics (DOC: 2.2 - 9.6  $\text{mg.L}^{-1}$ ; Secchi: 1.13 - 6.90 m; water color: 11.67 - 170.17  $\text{mg Pt.L}^{-1}$ ; pH: 5.9 - 8.4; alkalinity: 4.98 - 49.61  $\text{mg CaCO}_3.\text{L}^{-1}$ ; conductivity: 24.7- 193.9  $\mu\text{Siemens.cm}^{-1}$ ). Epilimnetic TN:TP ratios in the southern Québec lakes were typically > 10:1 by weight.

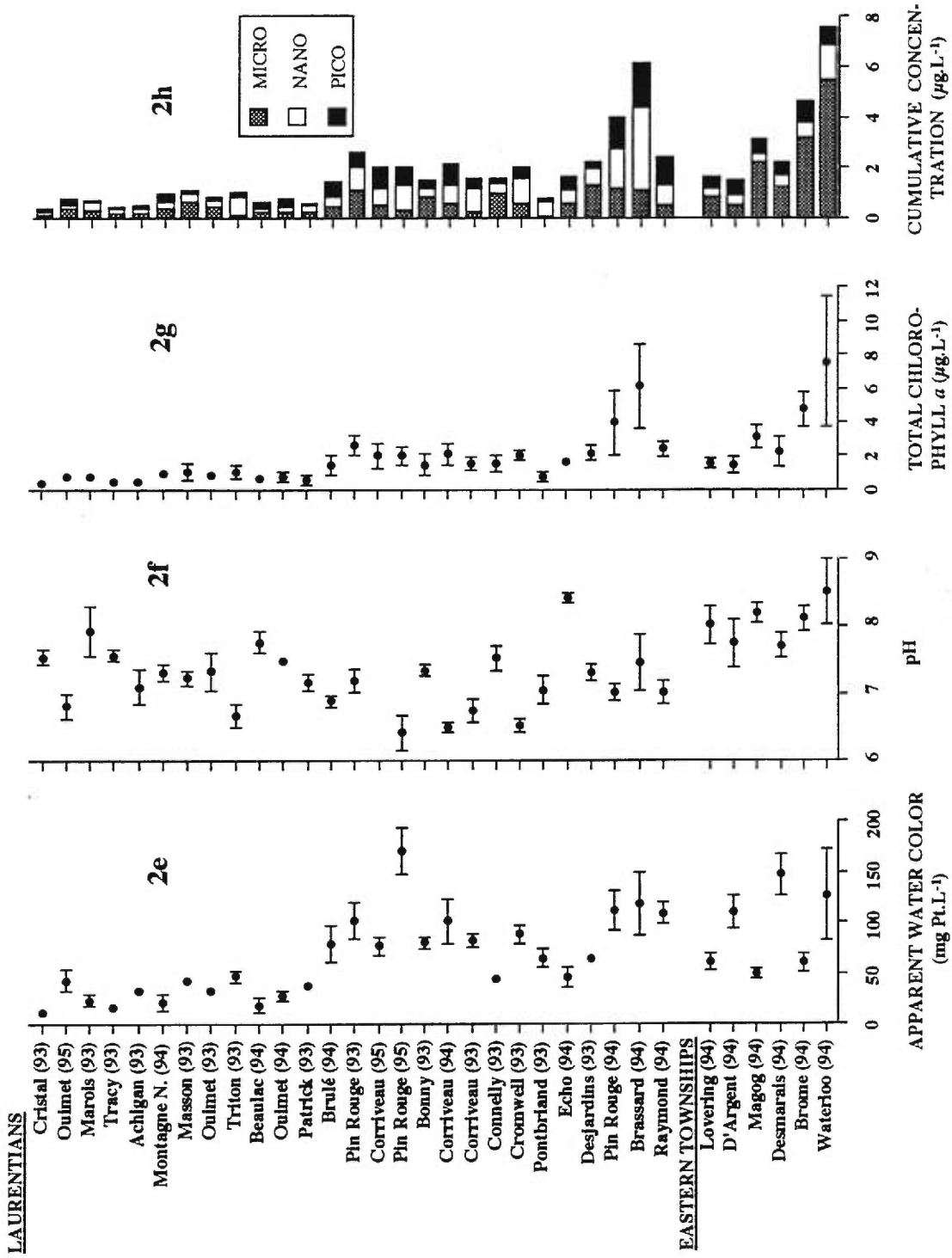
Figure 2 : Summer mean values and standard deviations of water quality variables. a) : total phosphorus; b) : total nitrogen; c) : dissolved organic carbon; d) : Secchi disk transparency; e) : apparent water color; f) : pH; g) : total chlorophyll *a* ; and h) : cumulative relative concentration of chlorophyll *a* of each algae size fraction.

LAURENTIANS



EASTERN TOWNSHIPS





The Laurentian lakes have variable Secchi water transparencies (1.3 - 6.9 m); generally low to medium total phosphorus (3 - 23  $\mu\text{g P.L}^{-1}$ ) and nitrogen (110 - 463  $\mu\text{g N.L}^{-1}$ ) concentrations; circumneutral to slightly acidic softwaters (pH: 5.9 - 7.8, except Lake Desjardins with a pH of 8.4); and low chlorophyll *a* concentrations (0.3 - 6.4  $\mu\text{g.L}^{-1}$ ), indicating an oligo-mesotrophic status.

There is also a slight gradient of alkalinity (5 - 40.9  $\text{mg.CaCO}_3\text{.L}^{-1}$ ), DOC concentrations (2.2 - 9.6  $\mu\text{g.L}^{-1}$ ) and apparent water color (11.7 - 111.6  $\text{mg Pt.L}^{-1}$ ) in the Laurentian lakes. The Eastern Townships lakes were characterized by higher concentrations of total phosphorus (TP: 10 - 34  $\mu\text{g P.L}^{-1}$ ) and total nitrogen (TN: 232 - 504  $\mu\text{g N.L}^{-1}$ ), and by higher pH (7.7 - 8.5) and alkalinity (29 - 46  $\text{mg CaCO}_3\text{.L}^{-1}$ ) levels than the Laurentian lakes. The ranges in apparent water color (50.1 - 146.9  $\text{mg Pt.L}^{-1}$ ) and DOC (4.0 - 9.5  $\mu\text{g.L}^{-1}$ ) concentrations are relatively similar to those observed in the Laurentian lakes, but with a slight shift to higher values. The Eastern Townships lakes also have lower Secchi water transparencies (1.1 - 3.4 m) and slightly higher chlorophyll *a* concentrations (1.4 - 7.6  $\mu\text{g.L}^{-1}$ ) than the Laurentian lakes, indicative of meso-eutrophic states.

Lake trophic state variables (nutrients, DOC, water color, chlorophyll) in southern Québec lakes were highly correlated; out of 91 pairs of trophic and chemical variables, 59.3 % were significantly correlated ( $P < 0.05$ ) after Bonferroni correction (Table II). Nutrients, water color and transparency are strongly correlated with chlorophyll *a*, but no significant relationships were observed with water pH, alkalinity and conductivity. Total Chl *a* and Chl *a* in each size fraction were positively related to TP, TN, apparent water color and DOC ( $r = 0.45-0.87$ ), whereas Secchi water transparency and TN:TP ratio were negatively correlated with chlorophyll ( $r = - 0.56$  to  $- 0.90$ , Table II; total Chl *a* and Micro only).

Among the different water chemical variables, highly significant positive relationships were observed between TP and TN, water color, and DOC ( $r = 0.54$  to  $0.92$ ), and negative relationships were found between TP, TN, water color, DOC, and Secchi transparency and TN:TP ratio ( $r = - 0.50$  to  $- 0.93$ ). Water alkalinity, conductivity and pH were well correlated ( $r = 0.80$  to  $0.90$ ). Positive relationships were also observed between total Chl *a* and Chl *a* in each size fraction ( $r = 0.46$  to  $0.92$ ). No significant relationships were observed between total Chl *a* or Chl *a* size fractions, and lake morphometric variables (Table I), except for maximum depth and mean depth, which



were negatively correlated with total chlorophyll *a*, and with the Nano and NaPi size fractions (results not shown).

Table II. Pearson correlation matrix for the log (base 10) transformed dependent and independent variables; Tchl = Total Chlorophyll *a* ( $\mu\text{g.L}^{-1}$ ), Micro = microphytoplankton, NaPi = nano- plus picophytoplankton, Nano = nanophytoplankton, and Pico = picophytoplankton). TP = Total Phosphorus ( $\mu\text{g.L}^{-1}$ ); TN = Total Nitrogen ( $\mu\text{g.L}^{-1}$ ); Color = apparent water color (mg Pt.L $^{-1}$ ); DOC = Dissolved Organic Carbon (mg.L $^{-1}$ ); Secc = Secchi disk transparency (m); N:P = ratio TN/TP; Alkal = Alkalinity (mg CaCO $_3$ .L $^{-1}$ ); Cond = Conductivity ( $\mu\text{mhos.cm}^{-1}$ ). Correlations significant at a probability level of  $P < 0.05$  are underlined once, and those where  $P \leq 0.01$  are underlined twice.

	Tchl	Micro	NaPi	Nano	Pico	TP	TN	Color	DOC	Secc	N:P	Alkal	Cond
Tchl													
Micro	<u>0.84</u>												
NaPi	<u>0.91</u>	<u>0.54</u>											
Nano	<u>0.83</u>	<u>0.46</u>	<u>0.94</u>										
Pico	<u>0.83</u>	<u>0.53</u>	<u>0.92</u>	<u>0.77</u>									
TP	<u>0.87</u>	<u>0.72</u>	<u>0.77</u>	<u>0.69</u>	<u>0.69</u>								
TN	<u>0.69</u>	<u>0.45</u>	<u>0.71</u>	<u>0.63</u>	<u>0.67</u>	<u>0.70</u>							
Color	<u>0.81</u>	<u>0.56</u>	<u>0.86</u>	<u>0.82</u>	<u>0.74</u>	<u>0.77</u>	<u>0.61</u>						
DOC	<u>0.72</u>	<u>0.56</u>	<u>0.72</u>	<u>0.67</u>	<u>0.60</u>	<u>0.66</u>	<u>0.54</u>	<u>0.92</u>					
Secc	<u>-0.87</u>	<u>-0.58</u>	<u>-0.90</u>	<u>-0.88</u>	<u>-0.76</u>	<u>-0.83</u>	<u>-0.69</u>	<u>-0.93</u>	<u>-0.83</u>				
N:P	<u>-0.56</u>	<u>-0.58</u>	-0.40	-0.37	-0.32	<u>-0.73</u>	-0.03	<u>-0.50</u>	-0.42	<u>0.51</u>			
Alkal	0.15	<u>0.46</u>	-0.14	-0.22	-0.05	0.32	0.24	-0.11	0.04	0.01	-0.21		
Cond	-0.04	0.31	-0.32	-0.33	-0.25	0.10	0.03	-0.28	-0.12	0.19	-0.11	<u>0.88</u>	
pH	0.13	0.43	-0.15	-0.18	-0.09	0.28	0.15	-0.18	-0.09	0.06	-0.25	<u>0.90</u>	<u>0.80</u>

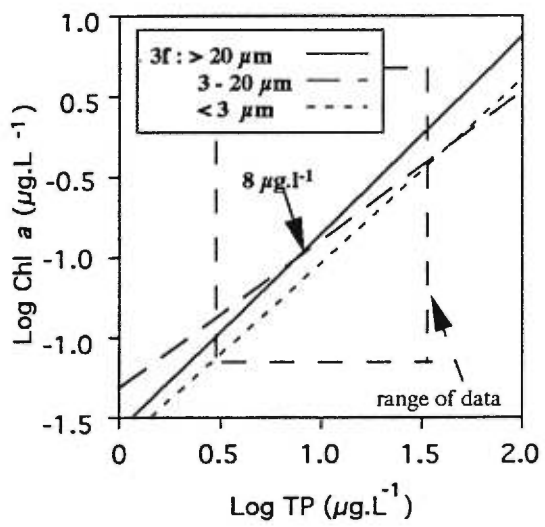
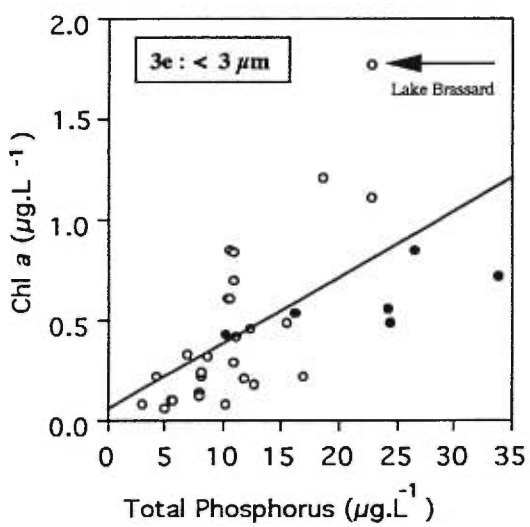
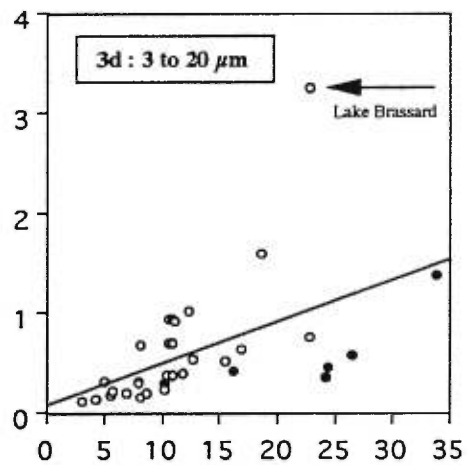
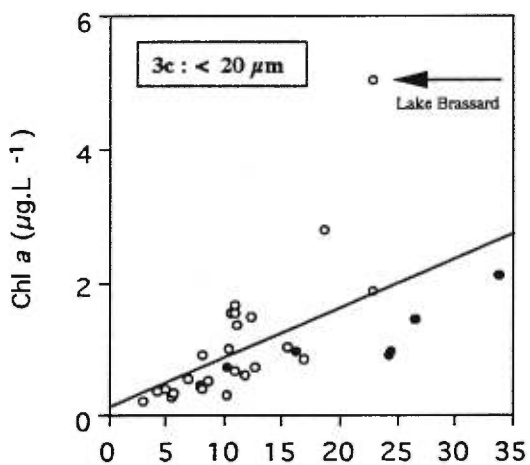
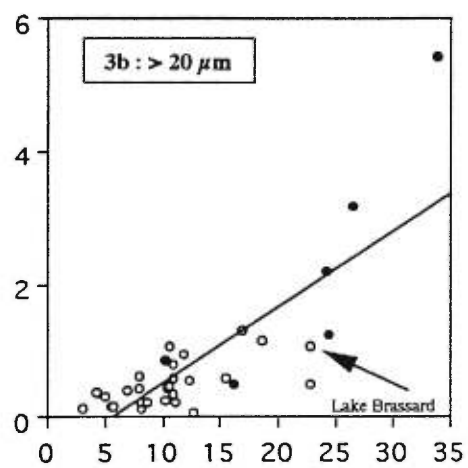
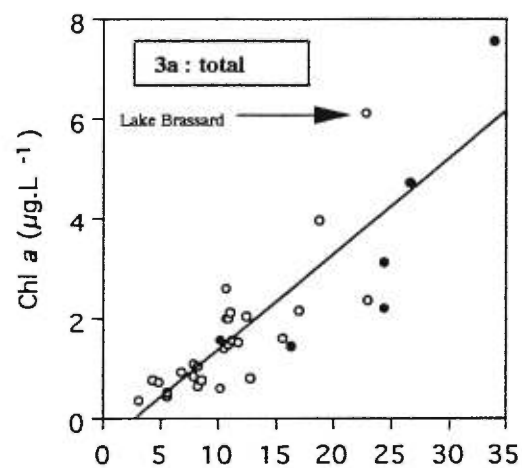
### 3.3.2 Effects of watershed geology on TP-Chl *a* relationships

We rejected the hypothesis that TP-Chl *a* relationships obtained from the Eastern Townships lakes (sedimentary watersheds) differed significantly from TP-Chl *a* relationships obtained from the Laurentian lakes (igneous watersheds). The ANCOVA analyses indicated that there was no statistically significant effect of regions on TP-Chl *a* relationships for both the total chlorophyll *a* and the 4 chlorophyll *a* size fractions ( $P > 0.205$ : Table III, Figs. 3a-e).

Table III. Summary of ANCOVA analyses performed on TP-Chl *a* relationships to test regional effect (0=Eastern Townships; 1=Laurentians) for total chlorophyll *a* and its size fractions. a) Tchl; b) Micro; c) NaPi; d) Nano; e) Pico; covariate = TP. See Table II for variables names.

Source	Sum of Square	d.f.	F-ratio	P
<u>a) Tchl</u>				
Region	< 0.01	1	0.17	0.686
TP	0.83	1	30.81	<b>&lt; 0.001</b>
Region by TP	< 0.01	1	0.17	0.687
Error	0.75	28		
<u>b) Micro</u>				
Region	0.05	1	0.70	0.410
TP	0.89	1	11.58	<b>0.002</b>
Region by TP	0.11	1	1.43	0.243
Error	2.16	28		
<u>c) NaPi</u>				
Region	0.01	1	0.42	0.522
TP	0.54	1	16.99	<b>&lt; 0.001</b>
Region by TP	0.03	1	1.05	0.315
Error	0.90	28		
<u>d) Nano</u>				
Region	< 0.01	1	0.01	0.910
TP	0.67	1	17.65	<b>&lt; 0.001</b>
Region by TP	0.00	1	0.14	0.711
Error	1.06	28		
<u>e) Pico</u>				
Region	0.09	1	1.36	0.253
TP	0.45	1	6.74	<b>0.015</b>
Region by TP	0.11	1	1.68	0.205
Error	1.86	28		

Figure 3 : Total phosphorus-chlorophyll *a* relationships; a) total chlorophyll *a* ; b) Micro; c) NaPi; d) Nano; e) Pico; f) log-log relationships of the Micro, nano, and Pico size fractions with respect to TP. Open circles are Laurentian lakes and dark circles are Eastern Townships lakes. Variable names are defined in Table II.



The main effect of regions (Laurentians and Eastern Townships) and the interaction term (region x TP) were statistically not significant for all size fractions (Table III). In the microphytoplankton size fraction, the highest Chl *a* biomass and TP concentrations were observed in two lakes (Brome and Waterloo: Fig. 2h; Fig 3b) from the Eastern Townships. In general, our results indicated that the responses of total chlorophyll *a* biomass, and the responses of micro-, nano- and picophytoplankton, to changes in total phosphorus concentrations were not strongly influenced by the regional geology in this cross-section of southern Québec lakes.

Although we could not detect a statistically significant effect of watershed geology on TP-Chl *a* relationships, regression models and scattergrams nonetheless suggested a tendency for Eastern Townships lakes to deviate from the overall regression trends for several of the algal size fractions (Figs. 3b-e). This apparent regional deviation appeared to be most evident at TP concentrations  $> 20 \mu\text{g P.L}^{-1}$ . In the more eutrophic environments, lower Chl *a* biomass was found in the NaPi ( $< 20 \mu\text{m}$ ), Nano (3 - 20  $\mu\text{m}$ ), and Pico ( $< 3 \mu\text{m}$ ) size fractions in the Eastern Townships lakes than in the Laurentian lakes, while the inverse pattern was observed for the Micro ( $> 20 \mu\text{m}$ ) size fraction (Figs. 3b-e). Our failure to detect these differences statistically may in part be due to the relatively limited range of total phosphorus concentrations observed in our study lakes (3 to 34  $\mu\text{g.P.L}^{-1}$ ) and the low number of lakes with TP concentrations  $> 20 \mu\text{g.P.L}^{-1}$ . Previous studies reporting significant differences in lake productivity and TP-Chl *a* relationships among geological regions (Duarte and Kalff 1989; Seip et al. 1992; Seip and Goldstein 1994) have been based upon much broader ranges of lake trophic state than in the dataset analysed in the study reported here.

### 3.3.3 Regression models and comparisons with other geographical locations

When all Québec lakes were included in the analysis, the overall regression model describing the relationship between total phosphorus and total chlorophyll *a* (TCHL) was:

$$\log \text{TCHL} = - 1.02 + 1.12 \log \text{TP} \quad (\text{n}=32; \text{R}^2 = 0.75; \text{P} < 0.0001) \quad (2)$$

When compared to other previously models, the relationship between mean summer TP and total chlorophyll *a* (TCHL) in southern Québec lakes presented either a higher slope or a lower intercept than other models established in different regions of

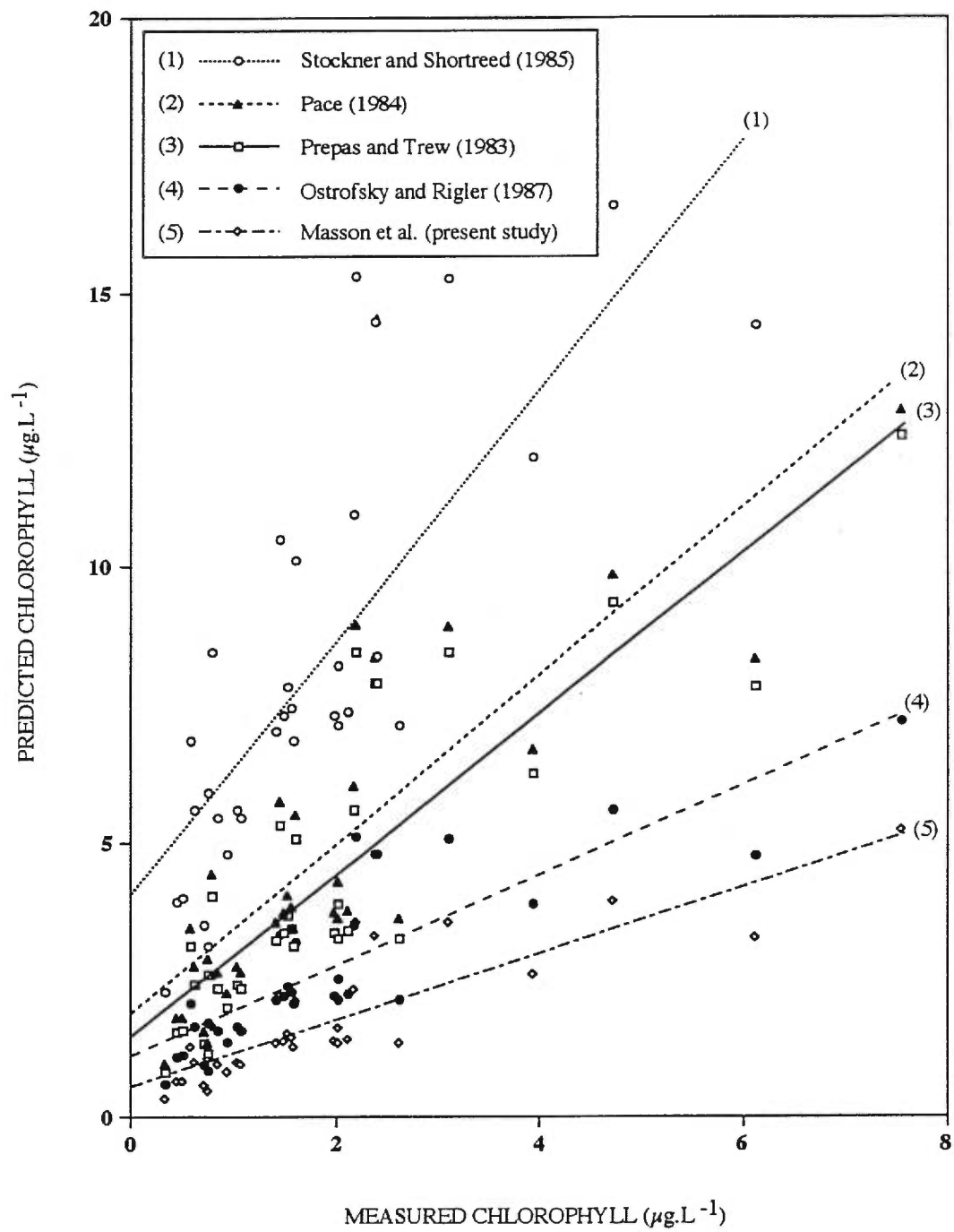
Canada (Table IV). The slope of our model was similar to the slope of the Prepas and Trew's model (1983), but the intercepts were strongly different (Table IV). By comparing chlorophyll *a* values observed in this study, we found that all models developed from lakes located either in sedimentary or igneous watersheds in other Canadian regions overestimated the concentration of total chlorophyll *a* per unit of TP in southern Québec lakes (Fig. 4).

Table IV. Relationships between summer mean total chlorophyll *a* (TCHL;  $\mu\text{g.L}^{-1}$ ), edible (EB < 35  $\mu\text{m}$ ) and inedible (IB > 35  $\mu\text{m}$ ) algae ( $\mu\text{g.L}^{-1}$ , dry weight or wet weight), and summer mean Total Phosphorus (TP;  $\mu\text{g.L}^{-1}$ ) from the literature and range of summer mean TP. \* : biomass evaluated by dry weight; \*\* : evaluated by wet weight. ‡ : from Douglas (1970).

Author	Region (geology ‡)	Model TP - Chl <i>a</i>	R <sup>2</sup>	range of Summer TP $\mu\text{g.L}^{-1}$
<b>total Chlorophyll <i>a</i></b>				
Ostrofsky and Rigler (1987)	Yellowknife (igneous rock)	Log TCHL = - 0.728 + 1.03 Log TP	0.63	7.5 - 63
Prepas and Trew (1983)	Alberta (sedimentary rock)	Log TCHL = - 0.661 + 1.15 Log TP	0.81	9.6 - 158
Stockner and Shortreed (1985)	British Columbia (igneous rock)	Log TCHL = - 0.09 + 0.92 Log TP	0.58	1.1 - 7.4
Pace (1984)	Eastern Townships (sedimentary rock)	Log TCHL = - 0.56 + 1.09 Log TP	0.93	3.7 - 56
This study	Laurentians and Eastern Townships (mainly igneous rock)	Log TCHL = - 1.02 + 1.12 Log TP	0.75	3 - 34
<b>Chlorophyll <i>a</i> size fractions</b>				
Watson and Kalff (1981)	worldwide	* Log EB = 1.24 + 1.28 Log TP * Log IB = 0.94 + 1.67 Log TP	0.93 0.82	3 - 50
Watson and McCauley (1988)	temperate and tropical	** Log EB = 2.28 + 0.41 Log TP ** Log IB = 1.27 + 1.32 Log TP	0.46 0.56	6 - 100

The model of Ostrofsky and Rigler (1987) presented the closest fit to our model because its slope was similar and its intercept was one of the lowest among all models (Table IV). The lowest biomass of chlorophyll *a* per unit of TP predicted by both models

Figure 4 : Relationships between total chlorophyll *a* measured in our study and total chlorophyll *a* predicted with literature models presented in Table V.





(the present study and that of Ostrofsky and Rigler) may be related to their similarity in regional geology, since both sets of lakes are mainly situated on igneous bedrock (Table IV). The lakes located on sedimentary bedrock that were studied by Pace (1984) and Prepas and Trew (1983) both tended to have higher Chl *a* biomass per unit of TP than the southern Québec, and both of their models gave similar predicted chlorophyll levels (Fig. 4; lines 2-3). Consequently, chlorophyll *a* biomass in lakes from similar regional geology appears to respond similarly to water column concentrations of TP.

The apparent effects of watershed geology on the yield of Chl *a* per unit of TP in temperate lakes may reflect variations in chemical (nutrients), biological (herbivory), and physical (thermal stratification) characteristics among the lakes being compared. Among these factors, food web structure may be particularly important. For example, analyses of TP/Chl *a* relationships in lakes of differing trophic state and food web structure has revealed that eutrophic and hypereutrophic lakes, which occur primarily on sedimentary bedrock, often lack large-bodied herbivores. These lakes exhibit roughly four times more Chl *a* per unit of TP than do oligotrophic lakes, which occur primarily on igneous bedrock and typically contain significant populations of large cladoceran herbivores (large *Daphnia* spp.; see Mazumder 1994a, 1994b).

In his study of 12 lakes in the Eastern Townships region that encompassed a slightly broader range of TP concentrations ( $3.37 - 55.7 \mu\text{g}\cdot\text{L}^{-1}$ ) than that reported here, Pace (1984) did not find that total zooplankton biomass or any zooplankton group explained a significant portion of the residual variance in TP-Chl *a* models; however, mean cladoceran body size had a borderline significance. Lakes with higher concentrations of macrozooplankton relative to microzooplankton also have less Chl *a* per unit of TP. Changes in the yield of Chl *a* per unit of TP also appear to be related to the transition from stratified to mixed systems along the TP gradients (Mazumder 1994a). In our data set, the two lakes that deviated the most from our general model for total Chl *a* (Fig. 3a) were Lake Brassard in the Laurentian region and Lake Waterloo in the Eastern Townships region, both of which are mixed systems. However once removed from the model, Lake Brassard did not influence total or micro chlorophyll *a*, while at the opposite the slopes of the small algae size fractions strongly decreased. As we mentioned, the dominance of fish planktivorous species could explain the dominance of small algae.

Although lakes studied by Stockner and Shortreed (1985) are also situated on igneous bedrock, their model predicted the highest Chl *a* biomass per unit of TP. The

tendency for this model to overpredict Chl *a* biomass in southern Québec lakes may be explained by important differences in hydrology and climate, as well in watershed physiography between coastal monomictic lakes in British Columbia and dimictic temperate lakes in Québec. In addition to watershed geology, watershed physiography and topography have been identified as important factors influencing lake water nutrients, dissolved organic carbon and chlorophyll *a* (Rasmussen et al. 1989; D'Arcy and Carignan 1997). In oligotrophic Shield lakes in Québec, models based on watershed characteristics (catchment slope, lake size, percentage of wetlands in the drainage area) explain Chl *a* concentrations in lakes ( $r^2 = 0.70$ ) as well as models based on water quality data (TP and Ca concentrations:  $r^2 = 0.69$ ) (D'Arcy and Carignan 1997).

Typical values of the slope of TP-Chl *a* log-log relationships in lakes worldwide range from 0.7 to 1.6 along TP-range approximately 0.5 to 1000  $\mu\text{g.P.L}^{-1}$  (Sakamoto 1966; Hoyer and Jones 1983; Pridmore et al. 1985; Ahlgreen et al. 1988; Prairie et al. 1989; Seip and Goldstein 1994; Vyhnálek et al. 1994). From the present data set, we obtained regression slopes from 0.93 to 1.22 for a limited TP-range (0 - 34  $\mu\text{g.P.L}^{-1}$ ) either for regressions of total Chl *a* biomass (equation 2) or chlorophyll size fractions (equations 3 to 6 below). In oligotrophic Shield lakes in Québec, D'Arcy and Carignan (1997) obtained a multiple regression slope of  $0.94 \pm 0.19$  for lakes over a TP range of 4.2 - 14.3  $\mu\text{g.P.L}^{-1}$  in their model predicting total Chl *a* as a function of both TP and Ca.

### 3.3.4 Individual TP-Chl *a* relationships for phytoplankton size fractions

Our study is a first attempt to generate a series of new TP-Chl *a* predictive models relating the quantitative responses of four empirical chlorophyll size fractions (Pico: < 3  $\mu\text{m}$ , Nano: 3 - 20  $\mu\text{m}$ , NaPi: > 20  $\mu\text{m}$  and Micro: > 20  $\mu\text{m}$ ) in lake phytoplankton to changes in epilimnetic total phosphorus concentrations. The overall log-log regression models describing the relationships between TP and Chl *a* biomass in each size fraction were (Fig. 3b-e):

$$\log \text{Pico} = - 1.61 + 1.07 \log \text{TP} \quad (\text{n}=32; R^2 = 0.50; P < 0.0001) \quad (3)$$

$$\log \text{Nano} = - 1.21 + 0.82 \log \text{TP} \quad (\text{n}=32; R^2 = 0.46; P < 0.0001) \quad (4)$$

$$\log \text{NaPi} = - 1.05 + 0.91 \log \text{TP} \quad (\text{n}=32; R^2 = 0.58; P < 0.0001) \quad (5)$$

$$\log \text{Micro} = - 1.58 + 1.23 \log \text{TP} \quad (\text{n}=32; R^2 = 0.51; P < 0.0001) \quad (6)$$

As noted in the Introduction, one of the major goals of our study was to test the hypothesis that the regression parameters (the slope and intercept) of the TP-Chl *a* model for each chlorophyll size fractions would differ significantly, and that the slopes of these regression models would increase consistently from the smallest algal size fraction to the largest. The slopes and the intercepts of the TP-Chl *a* relationships indeed were found to differ significantly between the Pico and Micro size fractions ( $P \leq 0.015$ ), and among the NaPi and Micro size fractions ( $P \leq 0.001$ ) (Table V). The comparison established between the Pico and Nano and among Micro and Nano size fractions only showed significant different intercepts ( $P = 0.045$ ).

Table V. Result of ANCOVA to test for difference between parameters of the regression models (TP - Chl *a*) established for the different chlorophyll fractions. Variable names are defined in Table II.

Source	Sum of Square	d.f.	F-ratio	P
<u>a) Pico vs Nano</u>				
Size	0.62	1	4.18	<b>0.045</b>
TP	3.21	1	56.82	<b>&lt; 0.001</b>
Size by TP	0.56	1	3.82	0.089
Error	2.39	60		
<u>b) Pico vs Micro</u>				
Size	1.00	1	5.01	<b>0.010</b>
TP	4.73	1	61.88	<b>&lt; 0.001</b>
Size by TP	1.02	1	5.27	<b>0.015</b>
Error	2.59	60		
<u>c) Nano vs Micro</u>				
Size	0.62	1	4.18	<b>0.045</b>
TP	3.74	1	56.54	<b>&lt; 0.001</b>
Size by TP	0.15	1	2.22	0.141
Error	3.27	60		
<u>d) NaPi vs Micro</u>				
Size	0.72	1	11.63	<b>0.001</b>
TP	4.08	1	66.84	<b>&lt; 0.001</b>
Size by TP	0.69	1	10.45	<b>0.002</b>
Error	2.67	60		

Despite the slope of the regression for the Micro size fraction was significantly greater than that of the three smaller size fractions (Pico and NaPi), there was no consistent increase in the slopes of progressively larger size fractions (Pico = 1.08, Nano = 0.82, NaPi = 0.91 and Micro = 1.23; see equations 3 to 6). Nevertheless, a comparative view of the TP-Chl *a* models for the Pico, Nano and Micro size fractions suggests that nanophytoplankton are more dominant in oligotrophic lakes, while microphytoplankton become increasingly more important as eutrophication proceeds (Fig. 3f).

These trends support the conclusions of previous studies based on direct microscopic phytoplankton counts reporting that summer means of net phytoplankton biomass ( $> 35 \mu\text{m}$ ) increase progressively faster than that of the nanophytoplankton ( $< 35 \mu\text{m}$ ) under enrichment (Gelin and Rippl 1978; Kalff and Knoelchel 1978; Watson et al. 1992). Watson and Kalff (1981) and Watson and McCauley (1988) also found that the slope of the TP-Chl *a* relationships for the net phytoplankton (inedible algae biomass: IB  $> 35 \mu\text{m}$ ) was higher than the slope of the regression model for the pico- and nanophytoplankton (edible algae biomass: EB  $< 35 \mu\text{m}$ ) (Table IV). A similar pattern was observed in our study when considering the slopes of the regressions for the NaPi (edible algae  $< 20 \mu\text{m}$ ; 1.00) and Micro (inedible  $> 20 \mu\text{m}$ ; 1.22) size fractions (see Table Vd, and equations 5 and 6). This implies that at higher TP levels, either microphytoplankton has higher growth rate or nanophytoplankton suffer greater losses, for example by grazing; either of these mechanisms would generate an increase in the relative biomass of microphytoplankton in more productive lakes, as reported by Chow-Fraser et al. (1994) in Canadian lakes over a wide range of trophic states (TP: 1-300  $\mu\text{g.L}^{-1}$ ) and by Mazumder (1994b) in enclosures over a mesotrophic range (TP: 15-30  $\mu\text{g.L}^{-1}$ ).

Our results indicated that the shift in dominance from nanophytoplankton to microphytoplankton in southern Québec lakes occurs at a TP concentration of ca. 8  $\mu\text{g.P.L}^{-1}$  (Fig. 3f). Above this TP threshold, the microphytoplankton size fraction becomes relatively more important than the nanophytoplankton size fraction for any given TP concentration. The Chl *a* biomass of the Pico size fraction, in contrast, was always smaller than that of either the Nano or Micro size fractions at all TP concentrations observed in this data set. A similar threshold has already been identified by Watson et al. (1992) using the Üthermohl method for estimating phytoplankton biomass from direct microscopic counts. They showed that total phytoplankton biomass was dominated by edible algae ( $< 35 \mu\text{m}$ ) at TP concentrations below 8-10  $\mu\text{g.L}^{-1}$ . Above this threshold and

up to  $30 \mu\text{g.P.L}^{-1}$ , they noticed a transition zone where both edible and inedible algal biomasses had relatively similar abundance without any relationship with TP concentrations.

We did not find a significant relationship between TP concentrations and the relative contribution of the Pico, Nano and Micro size fractions to total chlorophyll *a* biomass ( $R^2 < 0.10$ ,  $P > 0.05$ ; Fig. 5). We could not detect any clear pattern of variation in the chlorophyll *a* size structure along the TP gradient in our study lakes, with the exception of a clear dominance of the Micro size fraction at TP level higher than  $24 \mu\text{g.P.L}^{-1}$  as noticed in the TP-Chl *a* model for this size fraction (Fig. 3b). Thus, even if there was different responses of the chlorophyll size fractions along the TP gradient in southern Québec lakes (Fig. 3f), a clear shift in the algae size structure community was difficult to detect due to the limited number of eutrophic lakes in our dataset.

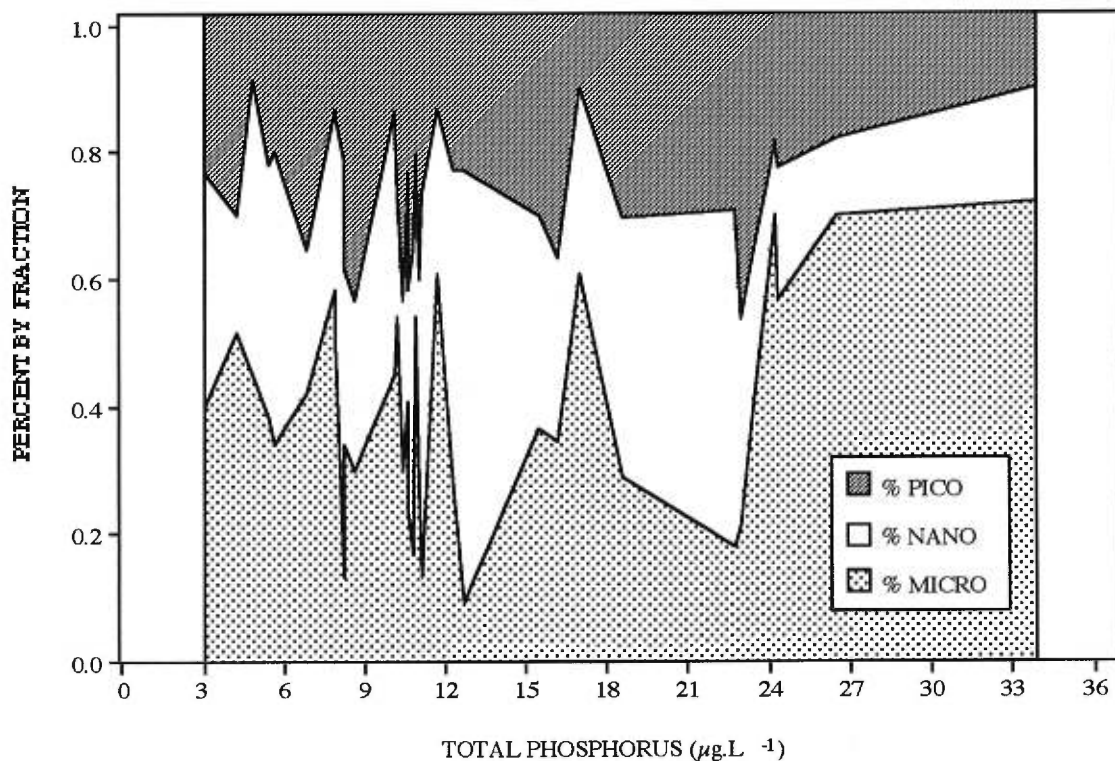


Figure 5: Relative contribution of each chlorophyll *a* size fraction to total chlorophyll *a* biomass along the trophic gradient observed in our lake data set.

### 3.3.5 Effect of other lakes characteristics on TP-Chl *a* relationships

TP-Chl *a* relationships potentially can be affected by many abiotic and biotic factors (Nicholls and Dillon 1978; Ahlgren et al. 1988; Duarte and Kalff 1989; Molot and Dillon 1991; D'Arcy and Carignan 1997). In our study, however, only the inclusion of water alkalinity among chemical variables increased the amount of variance explained by total phosphorus for two size fractions (Table VI). The predictability of Chl *a* biomass in the NaPi and Nano size fractions was increased by adding water alkalinity in the model (Table VI). The effect of alkalinity was not significant for Pico and Micro size fractions, although borderline for the Micro.

Table VI. Multiple regression models for chlorophyll *a* size fractions ( $\mu\text{g.L}^{-1}$ ) including lake characteristics. The cumulative coefficient of determination ( $r^2$ ) of the model as well as the partial  $r^2$  of the coefficients, standard error of the coefficients (SE), F-value (F), and probability of F-test (P) are also listed. For each regression,  $n = 32$ . Variable names are defined in Table II.

Equation	Model	$r^2$	SE	F	P
2	Log NaPi = - 0.71 + 1.09 <b>Log TP</b> - 0.44 <b>Log alkalinity</b>	<b>0.58</b> <b>0.74</b>	0.19 0.05	41.77	< 0.0001
3	Log Nano = - 0.81 + 1.03 <b>Log TP</b> - 0.53 <b>Log alkalinity</b>	<b>0.46</b> <b>0.70</b>	0.21 0.16	33.38	< 0.0001

Similarly, the addition of calcium, magnesium, or pH as independent variables substantially improved multiple regression models of log (Chl *a*) in the Adirondack lakes (Siegfried et al. 1989) and the oligotrophic boreal shield lakes (D'Arcy and Carignan 1997). The effect of water alkalinity that are suggested by these models may reflect changes in plankton community structure along the trophic gradient. Pinel-Alloul et al. (1990a) have already shown that the alkalinity-acidity gradient was the most important abiotic factor related to phytoplankton groups and species distribution throughout 54 Québec lakes located on the Canadian Shield, but their study did not consider Chl *a* size fractions.

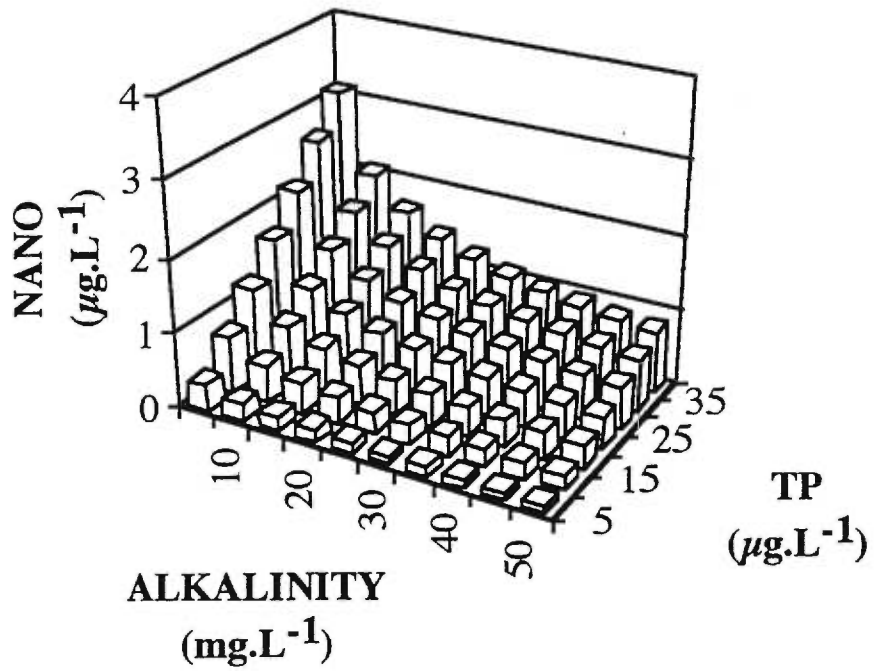
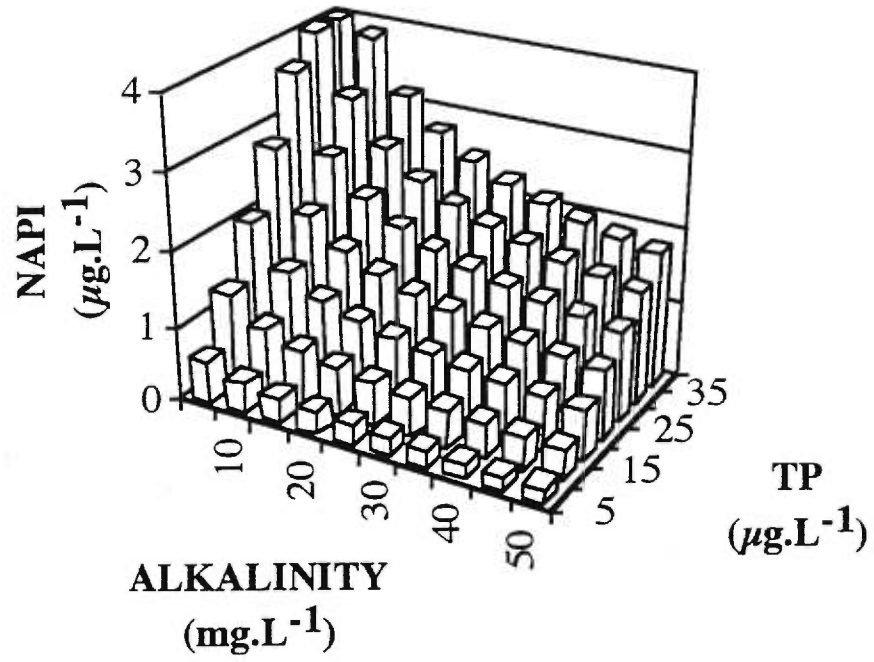
Our study is the first to report an effect of water alkalinity on the relationship between TP concentrations and the chlorophyll content of different algal size fractions. Chl *a* biomass in the NaPi and Nano size fractions decreased with water alkalinity (Fig. 6). Although not significant ( $P = 0.052$ ), the Micro size fraction increased with water alkalinity. There was an interaction of TP and water alkalinity on the responses of chlorophyll *a* size fractions (Fig. 6). The responses of Chl *a* biomass of the small size fractions (Nano and NaPi) to increase in TP was more important at low water alkalinity levels (Fig. 6). The response of Chl *a* biomass in the NaPi size fraction mostly reflected that of the Nano size fraction. Because of their strong covariance with alkalinity, conductivity and pH could be used as surrogate variables in the models to predict Chl *a* biomass in the NaPi and Nano size fractions, and we obtained similar trends in the relationships (positive effect for the Micro size fraction, and negative effects for the Nano, and NaPi size fractions).

The dominance of small algae in lakes of low alkalinity or conductivity has been reported in some studies (Søndergaard 1990; Pinel-Alloul et al. 1996). We hypothesize that the inverse relationships observed between water alkalinity and chlorophyll *a* in the edible size fractions (NaPi, Nano) may reflect a top-down grazing effect of large herbivores on small algae in alkaline lakes. Indeed, a predominant effect of water hardness on composition and size structure of zooplankton communities was detected by Tessier and Horwitz (1990) in 146 lakes in northeastern United States, and by Pinel-Alloul et al. (1990b) in 54 Canadian shield lakes in southern Québec. Pinel-Alloul et al. (1995) also provided evidence that large cladoceran herbivores (*Diaphanosoma*, *Daphnia galeata mendotae*, *Sida crystallina* and *Ceriodaphnia reticulata*) predominate in alkaline lakes whereas small cladocerans (*Bosmina longirostris*) were more abundant in circumneutral and acidic lakes.

To further support this hypothesis, we noted that alkalinity negatively affected small algal size fractions (Nano, NaPi); in contrast, although not significant, alkalinity positively affected the largest size fraction (Micro), which should be less affected by grazing by large herbivores in eutrophic lakes rich in filamentous or colonial phytoplankton (Tailling 1976; McCauley et al 1989). Lake Brassard was a clear example of the low effect of small zooplankton to control algae size fractions. The dominance of planktivorous fish species does not allow the development of large zooplankton species, which could control the small algae. The edible algae (NaPi, Nano, and Picophytoplankton) clearly dominate the phytoplanktonic community in this lake. This

Figure 6 : Joint effects of total phosphorus concentration and alkalinity on NaPi- and Nanoplankton fractions of total chlorophyll *a* .





result highlights the hypothesis that the absence of large zooplankton can lead to small phytoplankton dominance. More detailed investigations of the relationships between zooplankton community structure, lake trophic gradients, and chlorophyll *a* biomass and size structure will be needed to clearly understand the mechanisms by which grazers and nutrients produce variable Chl *a* yields per unit of TP in lakes.

Among water characteristics measured in this study, no other nutrients (e.g. DOC, TN) were retained by the stepwise modelling procedure. A lack of responses of algal biomass to changes in TN has also been observed in oligotrophic Québec shield lakes by D'Arcy and Carignan (1997), suggesting that the lakes in our data set were not N-limited. A similar lack of N-limitation has also been reported for Ontario shield lakes (Molot and Dillon 1991). Smith's (1982) model for total chlorophyll concentrations in subarctic Québec lakes included both TN and TP, but his study considered a much lower range of total nitrogen (61 - 135  $\mu\text{g.L}^{-1}$ ) (Smith et al. 1984).

### 3.4 CONCLUSIONS

We have developed a series of new predictive models relating the quantitative responses of total chlorophyll *a* and four empirical chlorophyll size fractions (Pico: < 3  $\mu\text{m}$ , Nano: 3-20  $\mu\text{m}$ , NaPi: < 20  $\mu\text{m}$  and Micro: > 20  $\mu\text{m}$ ) to changes in epilimnetic total phosphorus concentrations in southern Québec lakes of two regions (Laurentians and Eastern Townships) with contrasting watershed geology. Although our survey covered a limited range of lake trophic conditions (TP: 3 - 34  $\mu\text{g.L}^{-1}$ ; Chl *a* : 0.3 - 7.5  $\mu\text{g.L}^{-1}$ ), the slope of the TP-Chl *a* models developed for total Chl *a* and Chl *a* in size fractions (0.93 - 1.22) fell within the range of typical values reported for TP-Chl *a* models in oligotrophic Québec shield lakes (0.94) over a narrow TP range (4 - 14  $\mu\text{g.L}^{-1}$ ), and in lakes worldwide (0.85 - 1.6) along a large TP-range (0.5 to 1000  $\mu\text{g.L}^{-1}$ ). Our study suggests that TP-Chl *a* relationships were not strongly influenced by the regional variations in watershed geology in southern Québec, although our results suggest a tendency for eutrophic lakes (TP > 20  $\mu\text{g.L}^{-1}$ ) in the Eastern Townships region to deviate from the overall regression models. The overall model describing the relationship between TP and total Chl *a* biomass (TCHL) was:

$$\log \text{TCHL} = -1.02 + 1.12 \log \text{TP} \quad (n=32; R^2 = 0.75; P < 0.0001).$$

When a comparison was made with TP-Chl *a* models established in lakes of different regions and geology in Canada, we found the closest fit with models developed in lakes that exhibit a regional geology and climate that was similar to that in Eastern Canada. Our study also shows that Chl *a* size fractions responded differentially to TP gradients, as has been reported in comparative studies using microscope-derived estimates of algal biomass. The slope of the TP/Chl *a* regression for the largest chlorophyll size fraction (Micro: the inedible fraction) was higher than the slopes for the three small size fractions (Pico, Nano and NaPi: all edible fractions). Our models suggest that nanoplankton are more important in oligotrophic lakes, while the relative proportion of Chl *a* contributed by microplankton increases as eutrophication proceeds in southern Québec lakes. Although no consistent increasing trend was observed in the magnitudes of the slopes of TP-Chl *a* relationships for pico- (slope=1.07), nano- (0.82), and microphytoplankton (1.23), we observed a clear dominance of the Micro size fraction at TP levels greater than 24  $\mu\text{g}\cdot\text{L}^{-1}$ . Our study also is the first to report an effect of water alkalinity on the TP/Chl *a* relationship for different algal size fractions. We suggest that this effect may result from the differences in zooplankton community structure that tend to occur in lakes having contrasting alkalinities: grazing by large herbivores on the nano (3-20  $\mu\text{m}$ ) and edible (< 20  $\mu\text{m}$ ) algal size fractions in low alkalinity lakes may account for the observed interaction between alkalinity and TP.

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## CHAPITRE 4

### AMONG-LAKE AND WITHIN-LAKE SPATIAL VARIATIONS OF ZOOPLANKTON BIOMASS AND SIZE STRUCTURE IN SOUTHERN QUÉBEC LAKES

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## RÉSUMÉ

Cette étude avait pour but de déterminer les facteurs contrôlant la structure en taille de la biomasse zooplanctonique répartie en quatre classes de taille (53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$ , 202-500  $\mu\text{m}$ , > 500  $\mu\text{m}$ ) dans les trois strates limnétiques des lacs du bouclier du sud du Québec. Les différences de biomasse zooplanctonique entre les lacs constituaient la plus grande source de variation, alors que la forte interaction lac-strate observée indiquait que la variation verticale de la biomasse zooplanctonique et de ses composantes de taille n'étaient pas constante d'un lac à l'autre.

La productivité des systèmes aquatiques, qui est principalement reliée à la profondeur des lacs, au taux de renouvellement des eaux et à la concentration en phosphore total, était le facteur le plus important expliquant la variabilité épilimnétique de la biomasse zooplanctonique totale et de ses classes de taille entre les lacs. Cependant, lorsque l'effet de la profondeur des lacs fut enlevé par l'analyse de redondance partielle, la biomasse du gros zooplancton > 500  $\mu\text{m}$  devint fortement influencée à la fois par le gradient de phosphore total et par la prédation des planctivores.

Cette étude démontre que malgré la complémentarité des processus ascendants et descendants sont complémentaires dans la structuration des communautés zooplanctoniques, ces processus peuvent aussi agir de différentes façons sur leurs attributs (biomasse et structure en taille). La biomasse du zooplancton peut être prédite à partir de la trophie des lacs, mais la structure en taille de la communauté n'en dépend pas. Dans les eaux métalimnétiques, les fractions de biomasse zooplanctonique de 53-100  $\mu\text{m}$  et 100-202  $\mu\text{m}$  dépendaient principalement des facteurs abiotiques, alors que les fractions de 202-500  $\mu\text{m}$  et > 500  $\mu\text{m}$  étaient reliées à la fois à la prédation des planctivores et à la concentration du picophytoplancton. Les lacs dont les eaux froides hypolimnétiques étaient bien oxygénées offraient un refuge aux grosses fractions zooplanctoniques (202-500  $\mu\text{m}$  et > 500  $\mu\text{m}$ ) face à la turbulence de surface et à la planctivorie.

## ABSTRACT

Environmental control of zooplankton biomass in four size classes (53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$ , 202-500  $\mu\text{m}$ , > 500  $\mu\text{m}$ ) was investigated in the three limnetic strata of southern Québec Shield lakes. Among-lake differences were the greatest source of variation of zooplankton biomass, whereas the strong lake-by-stratum interaction observed indicated that the vertical variations of zooplankton biomass and its size fractions were not constant from lake to lake.

Productivity of the aquatic systems, which was driven by lake depth, flushing rate and total phosphorus concentration, was the primary factor influencing zooplankton biomass and size structure in epilimnetic waters among lakes. However, when the effect of lake depth was removed by partial redundancy analysis, large zooplankton biomass (> 500  $\mu\text{m}$ ) was strongly influenced by both total phosphorus concentration and fish predation.

This study shows that although bottom-up and top-down forces are complementary in structuring of zooplanktonic communities, they can also act differently on the community attributes (i.e., biomass and size structure). Zooplankton biomass is predictable from lake trophy, but the size structure of zooplankton communities is not dependent on lake trophy. In metalimnetic waters, the 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  zooplankton biomass fractions were primarily dependent on abiotic factors, while the 202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$  biomass were rather controlled by both the planktivory and picophytoplankton concentrations. The well-oxygenated and cold hypolimnetic waters of some lakes offered a refuge from surface turbulence and planktivory to large zooplankton size fractions (202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$ ).

## 4.1 INTRODUCTION

During the last decade, a strong debate in ecology led scientists to consider the relative contribution of resource availability, the physical and geochemical bottom-up (BU) processes (McQueen et al. 1986; Pinel-Alloul et al. 1990) and the top-down (TD)/trophic cascade theory (Carpenter et al. 1985; Mazumder et al. 1990a; Rodriguez et al. 1993) to explain the spatial structure of zooplankton communities in freshwater ecosystems. Carpenter (1988) suggested that the zooplankton community should be perceived as a spatially well-structured and dynamic system which requires a combination of abiotic and biotic factors for a better understanding and more realistic and reliable predictions of its ecology. This postulate corresponds to the recent hypothesis of multiple driving forces (Pinel-Alloul et al. 1995), under which the control of zooplankton structure within lakes includes both abiotic and biotic bottom-up and top-down factors.

Numerous studies have been carried out to assess the relative importance of the physico-chemistry, and morphometry of lakes and the abundance of phytoplankton and fish communities for limnetic zooplankton in Precambrian Shield lakes. Among them, Shaw and Kelso (1992) indicated that lake size, lake location and buffering capacity were ranked as the most important factors explaining zooplankton community structure. As Hanson and Peters (1984) and Pace (1986), Yan (1986) observed that total phosphorus concentration was the best predictor of zooplankton biomass in Canadian Shield lakes among several abiotic (e.g. morphometry, transparency, phosphorus, temperature) and biotic (chlorophyll *a*) factors. At the opposite, Pinel-Alloul et al. (1995) found that water chemistry (30.7%), and especially the acidity gradient, was the main environmental process explaining zooplankton community structure, followed by fish species composition (15.6%) and phytoplanktonic resource (11.2%). However, in that study total phosphorus was not measured, but should be correlated to hardness gradient. Working on the planktonic community of the euphotic zone, Rodriguez et al. (1993) considered potentially confounding effects of abiotic variables (maximum depth, water transparency, and lake volume) and determined that fish species composition was an important factor influencing cladoceran abundance and size structure. Keller and Conlon (1994) noticed that species richness and zooplankton abundance in 60 near-neutral Precambrian Shield lakes strongly varied with morphometric features, mainly lake depth, and among three groups of lakes, relative to fish species composition.

From these studies, it seems difficult to draw a general pattern of the most important factors influencing the zooplankton community structure, for several reasons. First, the number of studied lakes, between 12 and 132, and the areas of survey, from small to large, differed widely among studies. Secondly, the zooplankton sampling strategies were not comparable, in time (e.g., single time point, biweekly or monthly sampling, during spring, summer or autumn) and in space (e.g., one or more vertical hauls of the whole water column or only the epilimnetic or euphotic zone). Thirdly, some studies considered many more biotic and/or abiotic variables for prediction than others, with or without taking fish into account; studies also differed in the dependent variables (e.g., diversity, biomass, abundance, presence or absence of species). Above all, there were major differences in the objectives and hypotheses tested in these studies. On this point, discrepancies arise from lake selection, whereas several authors have eliminated in the goal to answer to their hypotheses, *a priori*, the influences of some lake characteristics known to influence community structure (Shaw and Kelso 1992). When same biotic and abiotic factors are not integrated in the analysis, and divergence in the approaches arise, comparison of results can be complicated.

Both abiotic factors (morphometry, physico-chemistry) and biotic factors, bottom-up (phytoplankton) and top-down (fish), were shown to regulate the zooplankton community structure (Pinel-Alloul et al. 1995). The next goal is now to determine the scale at which each of these factors regulates the populations or communities (Hunter and Price 1992). When environmental heterogeneity is taken into account, one should expect the relative roles of different ecological forces to vary among biological systems, and even within the same system (Karr et al. 1992). Incorporating and measuring that variability will increase our understanding of population and community ecology (Hunter and Price 1992).

All previous studies performed on zooplankton structure communities did not consider within-lake vertical variations. In their extensive regional survey, Pinel-Alloul et al. (1995) suggested that factors operating at the level of the lake, such as within-lake spatial heterogeneity, local effects of abiotic and biotic variables, and species behaviour, can exert an important influence on lake zooplankton structure. Among lake (e.g., Tessier et Horwitz 1990: calcium) and within-lake (e.g., Rodriguez et al. 1993: fish) variations both affect zooplankton size structure and vertical distribution (Brooks and Dodson 1965, Lampert and Taylor 1985, Sommer et al. 1986, Dini and Carpenter 1991). By integrating the water column, the responses of organisms which are organized vertically in relation to

local environmental forces are lost. Vertical heterogeneity has been studied for more than a century through the phenomenon of Diel Vertical Migration (DVM) of pelagic animals (Ringelberg 1993), and its consideration illustrates the importance to take into account this source of variation in among-lake surveys. There are numerous links among pelagic and profundal communities and thus, comparative studies conducted in a variety of habitats are helpful in revealing aspects of community dynamics that are not apparent from studies confined to a single habitat (Lodge et al. 1988). As most biotic and abiotic processes are scale-dependent, it implies the necessity for comprehensive sampling programs incorporate the pertinent spatial scales of physical and biological heterogeneities (Pinel-Alloul 1995).

This study is the first attempt to determine the environmental factors influencing zooplankton structure community among lakes and within lakes (i.e., among limnetic strata), using a large set of biotic variables (i.e., chlorophyll *a* size components and fish species composition) and abiotic variables (i.e., lake morphometry and physico-chemistry). Our primary objective was to quantify the relative importance of among-lake and within-lake sources of variation, and their interactions, in controlling zooplankton biomass and size structure in southern Québec lakes. We tested the hypothesis that environmental characteristics among lakes are the main source of variability in total zooplankton biomass and size fractions. Our second objective was to examine the relationships between the total biomass of zooplankton and the biomass of its size fractions on the one hand, and the environmental characteristics of watersheds and lakes (i.e., morphometric, physico-chemical, and biological factors) on the other hand, at both among lakes and among limnetic strata. In a review of the processes affecting spatial heterogeneity of zooplankton community, Pinel-Alloul (1995) suggested a scaling effect on the relative importance of abiotic and biotic factors in the environmental control of zooplankton community. According to her model, the relative importance of the abiotic processes increases at large scale, while inversely the contribution of biotic processes increases at smaller scales. In that perspective, we hypothesize that abiotic factors mainly regulate the variations of the total zooplankton biomass and the biomass of the four size fractions (53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$ , 202-500  $\mu\text{m}$ , and > 500  $\mu\text{m}$ ) in epilimnetic waters. Because large zooplankters are more vulnerable to fish predation, we further tested the hypothesis that in the meta- and hypolimnion strata, biotic factors control the biomass of the largest zooplankton size fractions (202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$ ), whereas the smallest fractions (53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$ ) are related to abiotic factors.

## 4.2 MATERIALS AND METHODS

### 4.2.1 Description of the Study Lakes

To study a wide range of morphometric, trophic and chemical lake features, we chose 25 lakes in two contrasting regions from southern Québec: the Laurentians (19 lakes) and the Eastern Townships (6 lakes). The Laurentian lakes are located in the southeastern part of the Precambrian Shield, 80 km north of Montréal (46°N, 74°W). The bedrock in this region is mainly gneiss and granite, and is covered by morainic soils and boreal forests. The Eastern Townships lakes are located 100 km south of Montréal (45°N, 72°W) in a well-buffered calcareous region containing mixed crystalline and sedimentary rocks, and covered primarily by deciduous forests. The climate in both regions is temperate.

Morphometric features of the lakes and their respective watershed are presented in Table I. The surface area of lakes ranged from 0.02 to 14.4 km<sup>2</sup>, and their drainage area varied between 0.1 to 1 932.2 km<sup>2</sup>. The maximum lake depth ranged from 3.2 to 45.7 m and the mean lake depth, from 1.8 to 13.3 m. Lake volume varied between 3.6 x 10<sup>4</sup> and 8 743 x 10<sup>4</sup> m<sup>3</sup>. Most of the lakes were dimictic, but 4 lakes (Brome, Desjardins, Triton, Waterloo) did not stratify completely during the summer. The summer total precipitation was 280 mm in 1993 and 511.4 mm in 1994. The flushing rate of lakes (i.e., the number of times per year the lake volume is replaced by flushing) ranged from 0.2 to 18.5 year<sup>-1</sup>. All morphometric and bathymetric parameters were measured on 1:20 000 topographic and bathymetric maps, using a digitizing table. To evaluate the flushing rate of lakes, we used climatic data recorded during the last 25 years for the Laurentians and Eastern Townships area (Environment Canada 1993) with the model of Dillon and Rigler (1975) :

$$\rho = Q \text{ (m}^3 \text{ yr}^{-1}\text{)} / V \text{ (m}^3\text{)}$$

$$\text{where : } Q = A_d \times r + A_o (\text{Pr} - \text{Ev})$$

$\rho$ = the flushing rate	and	$V$ = lake volume
$Q$ = total outflow volume per year	and	$A_d$ = drainage area
$r$ = represents the differences between precipitation and evapotranspiration		
$A_o$ = lake area	and	$\text{Pr}$ = input of water by precipitation
$\text{Ev}$ = output of water by evaporation		



Table I : Morphometric features of the 25 study lakes and their associated watershed.

Lake (year of sampling)	Altitude (m)	Catch- ment area (km <sup>2</sup> )	Drainage area (km <sup>2</sup> )	Drainage density (km km <sup>-2</sup> )	Lake area (km <sup>2</sup> )	Shore- line (km)	Maxi- mum depth (m)	Mean depth (m)	Lake volume (x 10 <sup>4</sup> m <sup>3</sup> )	Epilim- nion volume (x 10 <sup>4</sup> m <sup>3</sup> )	Metalim- nion volume (x 10 <sup>4</sup> m <sup>3</sup> )	Hypolim- nion volume (x 10 <sup>4</sup> m <sup>3</sup> )	Summer precipi- tation (m)	Flushing rate (year <sup>-1</sup> )
<b>Laurentians</b>														
Achigan (93)	207	94.1	88.7	0.7	5.37	19.4	26.8	12.9	6948.1	2969.1	1214.5	2764.5	0.28	0.8
Beaulac (94)	332	5.1	4.2	0.5	0.87	6.5	9.3	5.4	463.5	287.5	105.7	70.3	0.51	0.6
Bonny (93)	360	0.3	0.2	0.0	0.07	1.0	10.7	4.7	32.4	15.9	5.4	11.1	0.28	0.5
Brassard (94)	365	0.2	0.1	0.0	0.04	0.8	6.1	1.8	6.7	4.4	0.9	1.5	0.51	1.3
Brûlé (94)	378	143.9	141.2	0.5	2.68	16.2	24.4	8.4	2259.6	734.7	538.3	986.6	0.51	3.7
Connolly (93)	195	23.3	22.1	1.4	1.21	6.8	20.0	7.9	950.3	424.8	166.2	359.2	0.28	1.4
Corriveau (93-94-95)	325	13.9	13.9	1.4	0.06	1.3	13.7	7.1	43.5	16.6	6.7	20.3	0.35	18.5
Cristal (93)	264	2.2	1.9	1.3	0.29	2.3	18.5	9.5	274.6	128.0	95.2	51.4	0.28	0.5
Cromwell (93)	340	10.2	10.1	1.1	0.11	2.0	10.0	3.1	32.4	19.6	5.4	7.4	0.28	18.2
Desjardins (93)	351	0.3	0.2	0.0	0.06	1.1	4.6	2.1	12.0	12.0	....	....	0.28	1.4
Echo (94)	241	12.0	10.2	1.0	1.76	6.8	9.1	2.5	432.8	368.4	50.0	14.5	0.51	1.6
Marois (93)	299	7.0	6.0	0.9	0.99	6.3	22.7	6.7	660.9	466.9	128.9	65.1	0.28	0.6
Masson (93)	302	34.4	31.7	0.4	2.71	16.5	45.7	10.2	2763.7	658.7	488.2	1616.8	0.28	0.7
Montagne Noire (94)	456	12.8	10.0	0.1	2.81	11.8	33.5	13.3	3729.9	1485.4	882.4	1362.1	0.51	0.2
Ouimet (93-94-95)	302	6.4	5.8	0.5	0.59	6.2	18.3	5.2	309.2	130.8	76.9	101.5	0.35	1.2
Patrick (93)	347	63.2	61.7	0.5	1.51	7.4	30.5	10.8	1625.7	646.2	235.8	743.6	0.28	2.2
Pin Rouge (93-94-95)	332	6.8	6.6	1.7	0.15	2.2	15.2	5.1	76.7	37.0	21.9	17.9	0.35	5.1
Tracy (93)	349	0.2	0.1	0.0	0.08	1.4	24.4	8.9	69.4	38.7	14.2	16.6	0.28	0.2
Triton (93)	340	0.2	0.2	1.0	0.02	0.7	3.2	1.9	3.6	3.6	....	....	0.28	2.9
<b>Eastern Townships</b>														
Brome (94)	196	187.3	172.9	0.6	14.39	20.8	12.2	5.9	8465.4	7650.7	814.7	....	0.44	1.2
D'Argent (94)	248	65.0	64.0	0.6	1.00	4.2	15.6	4.5	446.9	294.2	100.3	52.4	0.44	7.7
Desmarais (94)	279	1.8	1.6	0.1	0.24	4.4	7.0	2.5	60.9	51.2	9.2	0.5	0.44	1.6
Lovering (94)	241	46.2	41.3	0.5	4.94	16.8	22.9	8.8	4351.1	2431.6	844.0	1075.5	0.44	0.6
Magog (94)	193	1950.2	1939.2	?	10.95	30.3	19.2	8.0	8743.0	5230.2	1616.2	1896.7	0.44	11.9
Waterloo (94)	207	33.9	32.5	0.4	1.47	9.2	4.9	3.4	493.4	493.4	....	....	0.44	3.7

The lakes under study cover a wide range of physical, chemical and biological characteristics (Table II). In the summer, water transparency and the euphotic zone ranged from 0.5 to 8.1 m from 2.8 to 17 m, respectively. The mean mixing zone was 3.9 m, but reached 9.5 m in some lakes. The summer values of temperature, oxygen concentration, pH and dissolved organic carbon (DOC) decreased with depth. On the other hand, the mean values of water alkalinity, conductivity, concentrations of nutrients, turbidity and true water color rather increased from the epilimnion to the hypolimnion. These vertical patterns describe the physico-chemical stratification and the sedimentation of algae and particles in deep waters, which both operate during the summer. At the same time, the epilimnetic pH of lakes ranged from 5.5 to 9.1, whereas the phosphorus level varied between 1.1 and 44.5  $\mu\text{g.L}^{-1}$ . However, the summer phosphorus concentration in epilimnetic waters was generally low (i.e., 12.6 on average). The mean concentration of total chlorophyll *a* and of most size fractions increased with depth. The concentration of total chlorophyll *a* in the epilimnetic stratum ranged from 0.1 to 12.7  $\mu\text{g.L}^{-1}$ . The mean concentrations of nano- plus picophytoplankton ( $< 20 \mu\text{m}$ ) were more important than those of the microphytoplankton ( $> 20 \mu\text{m}$ ) in all limnetic strata.

A qualitative description of fish communities was performed in this study (Table III). We classified lakes in three categories: lakes without piscivore species (Brassard, Corriveau, Cromwell, Desjardins, Triton), lakes with 1 or 2 piscivore species (12 lakes), and lakes with 3 or more piscivore species (8 lakes). One interest of this classification is missing or not identifying planktivorous species in some lakes does not affect our classification. The information about the fish composition of lakes was provided by the Ministère de l'Environnement et de la Faune du Québec and by local fishermen. The piscivore species were identified from the list of Post and Kitchell (1997). In our data set, brook trout (*Salvelinus fontinalis*) was considered as a planktivorous species, since this species mainly feeds on zooplankton in presence of non-salmonid competitors (Magnan 1988).

#### 4.2.2 Field sampling

Sampling was carried out once a month from June to August in 11 lakes in 1993 and 11 lakes in 1994 (see Table I). In addition, 3 lakes (Corriveau, Pin Rouge, Ouimet) were monitored during three years (1993 to 1995).

Table II : Summary statistics for summer physical, chemical and biological characteristics of each water column of the study lakes.

Variable	EPILIMNION (25 lakes)				METALIMNION (22 lakes)				HYPOLIMNION (21 lakes)			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Water transparency (m)	3.3	1.7	0.5	8.1	-	-	-	-	-	-	-	-
Euphotic zone (m)	7.9	3.6	2.8	17	-	-	-	-	-	-	-	-
Mixing zone (m)	3.9	1.8	1.5	9.5	-	-	-	-	-	-	-	-
Temperature (°C)	21.7	1.9	18	27	14.9	2.6	10.2	23	6.8	2.7	4	17
Oxygen (mg.L <sup>-1</sup> )	7.5	0.8	5.9	10.7	6.8	3.6	0.2	13	4.2	3.3	0.1	10.4
Alkalinity (mg CaCO <sub>3</sub> .L <sup>-1</sup> )	18.6	12.3	3.5	50.9	19	13.7	3.4	62.8	22	18.3	3.6	98.9
pH	7.3	0.6	5.5	9.1	6.9	0.5	5.6	7.9	6.6	0.5	5.2	8
Conductivity (µmhos.cm <sup>-1</sup> )	76.4	45.2	19	210	77.7	44.9	20	210	88.6	49.6	19	275
Total phosphorus (µg.L <sup>-1</sup> )	12.6	8.3	1.1	44.5	14.3	10.5	1.8	56.4	16.3	17.4	1.6	132.1
Total nitrogen (µg.L <sup>-1</sup> )	246.7	121.8	43.3	727.6	250.1	117.8	23.4	843	307.6	138.5	10.4	793.1
Total dissolved silica (µg.L <sup>-1</sup> )	2555.4	1410.7	12.6	6835.4	3495.8	1755.6	328	10287	4962.2	2068.3	1048.9	10872
Turbidity (NTU)	1.9	1.8	0.5	16.3	2.1	2.6	0.6	22	3.6	3.7	0.6	16.6
True color (mg Pt.L <sup>-1</sup> )	44	34.2	0.5	165	45.9	38.2	2.5	267	56.8	58.3	2.5	395
DOC (mg.L <sup>-1</sup> )	5	2.1	2	12.2	4.4	2.2	1.6	21.8	4.1	1.9	1.5	12.3
Chlorophyll <i>a</i> (µg.L <sup>-1</sup> )												
Total	1.9	1.9	0.1	12.7	3.2	5	0.3	37.2	4.3	11.4	0.1	85.6
micro (> 20 µm)	0.8	1.2	0.002	9.2	1.3	2.3	0.02	18.6	1.1	4.4	0.003	58.5
Nano + pico (< 20 µm)	1.1	1.1	0.05	7.9	1.9	3.2	0.04	19.2	3.1	8.4	0.02	57.6
Nano (3-20 µm)	0.6	0.8	0.01	5.8	1.2	2.2	0.001	15.8	2.2	6.3	0.01	37.6
Pico (< 3 µm)	0.5	0.4	0.002	2.6	0.7	1.3	0.001	10.6	0.9	2.9	0.001	27.2

Table III : Fish community of the study lakes.

Fish species	Brassard	Cornveau	Cromwell	Desjardins	Triton	Beaulac	Bonny	Brdle	Crstal	D'Argent	Desmarais	Marois	M. Notre	Oumet	Patrick	Pinrouge	Tracy	Achigan	Brome	Connelly	Echo	Loving	Magog	Masson	Waterloo
<b>Piscivores</b>																									
Atlantic Salmon																									
Brown Trout																									
Chain Pickerel																									
Lake Charr																									
Largemouth Bass																									
Muskellunge																									
Northern Pike																									
Rainbow Trout																									
Rock Bass																									
Smallmouth Bass																									
Walleye																									
<b>Planktivores</b>																									
Brook Charr																									
Brown Bullhead																									
Central Mudminnow																									
Common Shiner																									
Creek Chub																									
Cutlips																									
Fallfish																									
Fathead Minnow																									
Golden Shiner																									
Lake Chub																									
Northern redbelly Dace																									
Pumpkinseed																									
Rainbow Smelt																									
White sucker																									
Whitefish																									
Yellow Perch																									
<b>Total of species</b>	1	1	6	2	2	9	4	3	1	5	3	4	8	4	6	5	2	7	9	8	5	9	8	8	5
<b>Piscivores number</b>	0	0	0	0	0	2	1	2	2	2	1	2	1	1	2	1	1	6	4	4	3	5	9	3	3

At each sampling date, water transparency was measured using a black and white Secchi disk at the deepest site of each lake. A photometer LI-COR with a spherical quantum sensor (model LI-193SB) was also used to determine the thickness of the euphotic zone (1% of the air-water interface reading). In order to determine the depth of epi-, meta-, and hypolimnion, profiles of temperature and dissolved oxygen were established at 0.5 m intervals with a YSI model 51B electronic temperature/oxygen meter. Thereafter, two or three water samples per stratum were collected at three stations by using a 6 L Van Dorn bottle. These samples were then mixed per stratum per station for further analyses. Water samples for chlorophyll *a* and water physico-chemistry (pH, alkalinity, conductivity, turbidity, true water color, DOC) were mixed and stored in amber and brown polyethylene bottles in a cooler. Bottles were filled to the top to avoid gases exchange between the time of sampling and laboratory analysis. Water for nutrients analyses (TN, Si, and TP) was collected separately in sterilized bottles.

At each sampling date and at the same three stations as the other variables, zooplankton was collected as separate integrated samples through the epi-, meta-, and hypolimnion strata, using a cantilevering towed net (53  $\mu\text{m}$  mesh size) (Masson and Pinel-Alloul 1998). After collection, organisms were immediately narcotized in carbonated water, and preserved in 4% formaldehyde solution with sugar.

#### 4.2.3 Laboratory water analysis

Measurements of pH, conductivity and turbidity were made using a Fisher Acumet model 620 pH meter, a Cole Parmer model 1484 conductivity meter (standardized to 25°C) and a Nephelometer (Hach model 18 900-00), respectively. Alkalinity was determined by titrating a 200 mL water sample at a pH of 4.5 with 0.06 N HCl (APHA 1992). True water color was determined spectrophotometrically at 440 nm (Cuthbert and Del Giorgio 1992) after filtration on 0.45  $\mu\text{m}$  membrane filters and the absorbance values were converted to standard platinum units (Environment Canada 1979). Water samples collected for TP and TN were placed in sterilized 30-mL tubes previously soaked in a HCl acid bath (10% v/v) and rinsed with deionized distilled water. Water samples for Si were filtered through 0.45  $\mu\text{m}$  cellulose membranes and placed in sterilized plastic bottles. Nutrient samples were finally stored at 4°C in a refrigerator until analysis. All nutrients were analysed on an Alpkem autoanalyzer (model RFA 300). Total phosphorus (TP:  $\mu\text{g P.L}^{-1}$ ) was measured using the molybdenum blue colorimetric assay with 10 cm cuvettes after acidic persulfate digestion (Murphy and Riley 1962). Total nitrogen (TN:  $\mu\text{g N.L}^{-1}$ )



was analysed colorimetrically using 2 or 5 cm flow cells following the indophenol blue method (Armstrong et al. 1967) after digestion by alkaline persulfate oxidation. Dissolved silica concentration was measured by the acidic ammonium molybdate method after reduction with  $\text{SnCl}_2$  (Golterman and Clymo 1969). Water samples for DOC (Dissolved Organic Carbon) were filtered through Whatmann GF/F glass-fiber filters that had been precombusted at  $500^\circ\text{C}$ . The DOC samples were stored in 60 mL polyethylene bottles at  $4^\circ\text{C}$ , and analysed within 72 hours. The DOC concentration was determined by conductimetry after persulfate-UV oxidation (Kaplan 1992).

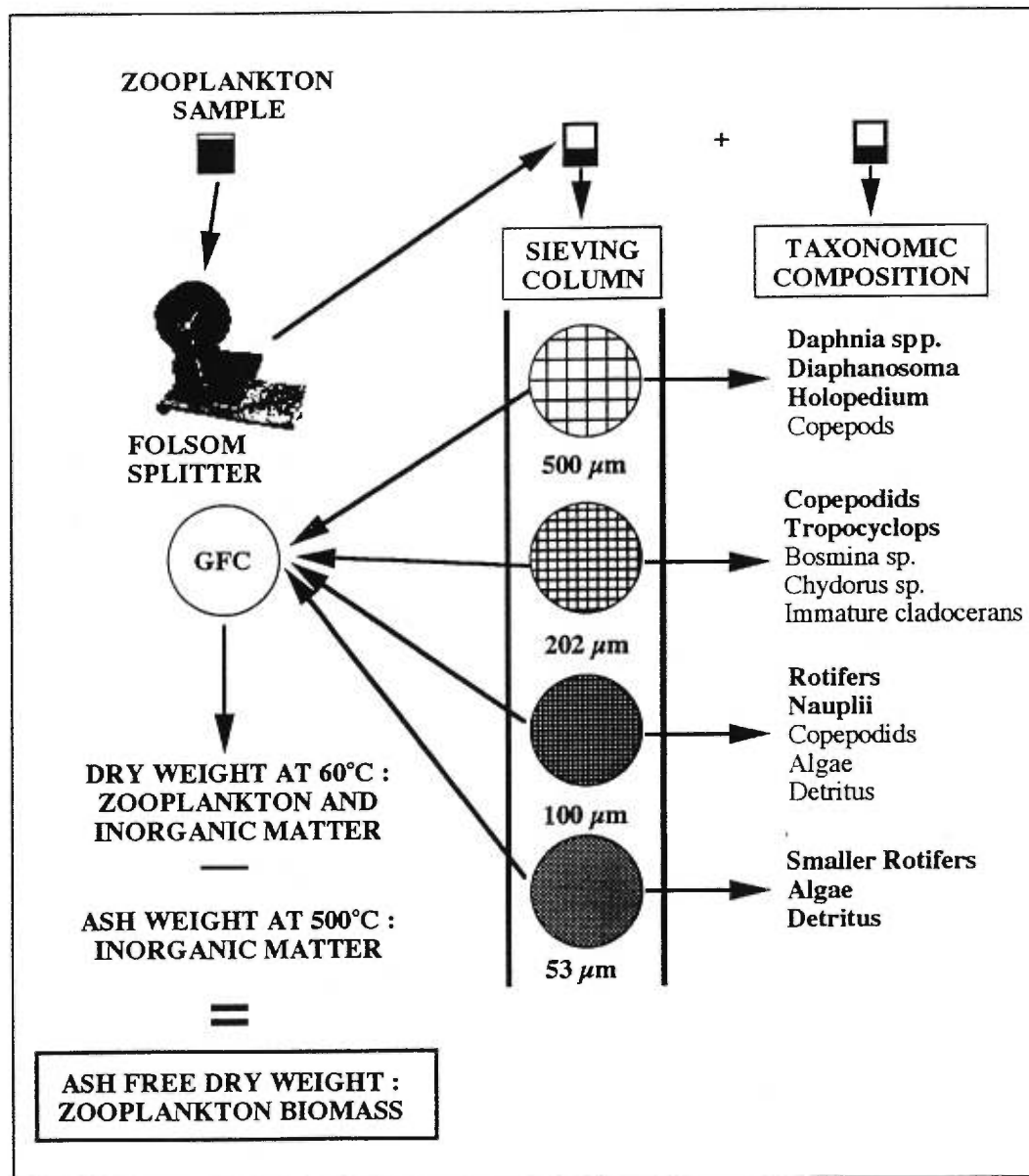
Both the total chlorophyll *a* concentrations and the chlorophyll *a* concentrations in four operationally-defined size fractions (Pico:  $< 3 \mu\text{m}$ , Nano:  $3$  to  $20 \mu\text{m}$ , Nano + Pico "NaPi":  $< 20 \mu\text{m}$ , and Micro:  $> 20 \mu\text{m}$ ) were determined by fluorometry. For measurements of total chlorophyll *a*, 300 mL of epilimnetic water were filtered through  $0.45 \mu\text{m}$  cellulose Millipore™ membranes in subdued light. For the NaPi size fraction ( $< 20 \mu\text{m}$ ), 300 mL of epilimnetic water was sieved through  $20 \mu\text{m}$  mesh Nitex nets before filtration onto  $0.45 \mu\text{m}$  cellulose membranes. Similarly, for the Pico size fraction ( $< 3 \mu\text{m}$ ), 300 mL of epilimnetic water was filtered through  $3 \mu\text{m}$  porosity polycarbonate Nucleopore™ filters at a low vacuum of 10 to 15 cm Hg, and the particles present in this filtrate were captured by filtration onto  $0.45 \mu\text{m}$  cellulose membranes. The chlorophyll concentrations in the two other size fractions were estimated by difference: Chl *a* in the inedible Micro size fraction ( $> 20 \mu\text{m}$ ) was calculated as the difference between the total Chl *a* concentration and that of the NaPi size fraction ( $< 20 \mu\text{m}$ ). Similarly, Chl *a* in the Nano size fraction ( $3 - 20 \mu\text{m}$ ) was calculated as the difference between the Chl *a* concentration of the NaPi size fraction ( $< 20 \mu\text{m}$ ) and that of the Pico size fraction ( $< 3 \mu\text{m}$ ). All systems were rinsed with distilled water between successive filtrations in order to avoid the retention of residual particles smaller than the effective pore size of Nitex nets or polycarbonate filters. We added  $\text{MgCO}_3$  to the samples at the end of filtration to prevent chlorophyll degradation in acidic waters. The membrane filters were then folded and wrapped in an aluminium foil, and stored at  $-20^\circ\text{C}$ . Chlorophyll *a* was extracted in 90% acetone for 24 hrs at  $4^\circ\text{C}$ , and measured using a Turner fluorometer model 10-AU (precision:  $\pm 0.11 \mu\text{g.Chl } a.L^{-1}$ ) after spectrophotometric calibration (Strickland and Parsons 1968). Calibration of the fluorometer was performed using total chlorophyll *a* concentrations in five 300 mL water samples. Chlorophyll *a* concentrations were not corrected for pheopigments.

#### 4.2.4 Laboratory zooplankton analysis

Zooplankton biomass and size structure were estimated using a quick but accurate technique for determining the carbon biomass of total zooplankton ( $> 53 \mu\text{m}$ ) and four size fractions ( $53\text{-}100 \mu\text{m}$ ,  $100\text{-}202 \mu\text{m}$ ,  $202\text{-}500 \mu\text{m}$ ,  $> 500 \mu\text{m}$ ), derived from McCauley (1984) and Seda and Dostalkova (1996). Although direct microscopic methods are commonly used to estimate zooplankton density and biomass (e.g., Bottrell et al. 1976, McCauley 1984), the laboratory procedures involved in these measurements are time consuming and expensive, and require qualified personnel in zooplankton taxonomy. The either size fraction or total of fresh, dry, and ash weight biomass estimations of zooplankton are used as an alternative procedure of counting and sizing individual animals. This method is reliable, convenient and much faster to perform, especially when a very large number of zooplankton samples are to be analysed as it was the case in this study. These techniques have been used in the evaluation of spatial or temporal variations of planktonic communities in relation to environmental characteristics in both marine and freshwater systems (e.g., Dumont et al. 1975, Maranda et Lacroix 1983, Lindley et al. 1994, Schneider et al. 1994).

In this study, zooplankton biomass and size structure were estimated using organic carbon biomass of ash-free dry weight. Zooplankton samples were split in two halves with a Folsom splitter, and one half was used for estimation of zooplankton carbon biomass (Fig. 1). Ash-free dry weight was preferred to dry weight because of possible underestimation of the zooplankton biomass due to losses of filter pieces during the drying procedure. To estimate the zooplankton biomass and size structure, samples were filtered through Nitex sieves of 500, 202, 100 and  $53 \mu\text{m}$  mesh size, which provided four size fractions:  $53$  to  $100 \mu\text{m}$ ,  $100$  to  $202 \mu\text{m}$ ,  $202$  to  $500 \mu\text{m}$ , and  $> 500 \mu\text{m}$ . Zooplankton in each sieve was back-washed, filtered onto precombusted ( $500^\circ\text{C}$ , 24 h) 25 mm Whatmann GFC glass fiber filters, dried at  $60^\circ\text{C}$  for 24 hours, and weighted using a Cahn microbalance (mean  $\pm 0.1 \mu\text{g}$ ) to obtain dry-weight estimates. Finally, dry samples on filters were burned at  $500^\circ\text{C}$  for 24 hours and weighted again to obtain the ash weight. Zooplankton biomass in each size fraction (organic carbon biomass:  $\mu\text{g.C}$  weight) was obtained by subtracting the ash weight from the dry weight. In boreal shield lakes, total zooplankton carbon biomass correlates to total zooplankton biomass and density estimated by classical taxonomic approaches (Pinel-Alloul and Méthot 1998). This method was used in the identification of the abiotic and biotic factors influencing the spatial distribution of zooplankton biomass size fractions in a bog lake (Masson and Pinel-

Figure 1: Zooplankton size fractionation method for ash free dry weight measurements.



Alloul 1998). Based on species size and microscopic examination of organisms retained on each sieve (Fig. 1), we found that the size fraction  $> 500 \mu\text{m}$  was composed of large cladocerans and, in a lesser extent, by some copepods; the 202-500  $\mu\text{m}$  size fraction was rather dominated by calanoid and cyclopoid copepods and their instars and, to a lesser importance, by small cladocerans and immatures; the 100-202  $\mu\text{m}$  size fraction was represented by the nauplii of calanoids and cyclopoids and some copepodid stages (C1-C3), and by the most rotifer species; the 53-100  $\mu\text{m}$  size fraction was constituted by smaller rotifers. More details of the taxonomic composition of the four size fractions is given in the Results section. For small fractions ( $< 202 \mu\text{m}$ ), ash free dry weights included various amounts of particulate organic matter such as phytoplankton and detritus. However, algae and detritus were apparent mainly in the 53-100  $\mu\text{m}$  size fraction.

#### 4.2.5 Statistical analyses

Although the sampled lakes were located in two different regions, geology was not considered as a source of variation in the productivity of lakes (Duarte and Kalff 1989), which might indirectly influence the biomass and size structure of zooplankton community. The absence of difference in the ratio of chlorophyll *a* per unit to total phosphorus between Laurentians and Eastern Townships lakes (Masson, Pinel-Alloul and Smith, unpublished data) justified this statement. We have also eliminated the temporal sources of variation (i.e., month and year) from further analyses, to concentrate on the spatial sources of variation described below. This was justified after preliminary ANOVAs using the spatio-temporal model and testing procedures of Dutilleul and Pinel-Alloul (1996) had detected no temporal effect in our data. Thus, lake and stratum were the two factors retained for investigating the variation of total zooplankton biomass and its size fractions, with stations within a lake as replicates. Therefore, mean values per stratum per station within a lake were calculated for 21 lakes in which all three limnetic strata could be identified. These mean values were used in the ANOVAs described below. Based on normality tests performed on raw data and transformed data, the  $\log_{10}$  transformation of the zooplankton biomass data was performed prior to the ANOVAs.

The among-lake and within-lake sources of variation of the total zooplankton biomass and its four size fractions were analysed by ANOVA. The lake main effects represent the purely among-lake source of variation, whereas the stratum main effects represent a purely within-lake source of variation. The lake and stratum factors being crossed, their interaction, if it exists, represents the lack of constancy of the within-lake

source of variation over lakes. For a given station within a lake, the vector of three zooplankton biomass mean values corresponding to the three limnetic strata defines a profile vector of spatial repeated measures (Dutilleul 1998a). This type of data requires an appropriate statistical analysis (Crowder and Hand 1990). With lake considered as a random factor crossed with depth as a fixed factor, the ANOVA model is that a mixed two-way ANOVA with spatial repeated measures. We followed Dutilleul (1998b) for its statistical analysis. In particular, the ANOVA *F*-tests were modified in order to take into account the autocorrelation and heteroscedasticity of the spatial repeated measures at the three depths (Greenhouse and Geisser 1959). The ANOVAs were performed with procedure GLM, option REPEATED of SAS version 6 (SAS Institute Inc. 1989).

To evaluate the effects of environmental factors on total zooplankton biomass and its size fractions, we chose a total of 36 potential independent (i.e., explanatory) variables grouped in three matrices. For the morphometric data set, we used a total of 14 variables mainly related to lake morphometric features (Table I). For the physico-chemical data set, we also used 14 variables (Table II), whereas 8 variables (i.e., total chlorophyll *a* and its size components, fish species composition) were retained for the biological matrix (Tables II and III). We used multivariate statistical methods to test the explanatory power of environmental factors. Because of the complex inter-relationships of environmental factors regulating the lake zooplankton community (Pinel-Alloul et al. 1995, Pinel-Alloul 1995), we performed Principal Component Analysis (PCA) and Canonical Redundancy Analysis (RDA) to identify the variables or sets of collinear variables which contribute the most to the variation in total zooplankton biomass and its size fractions. Thus, the PCA of log<sub>10</sub>-transformed data (i.e., dependent and independent variables, except pH) was performed for exploring the relationships between the independent variables and the total zooplankton biomass, for each of the three limnetic strata separately. The equilibrium circle of descriptors was drawn in the biplot of first and second principal axes of each PCA. Variables falling close to this circle were identified as variables contributing the most to the total variation in the reduced space (Legendre and Legendre 1998).

The RDA, also known as constrained PCA (van den Wollenberg 1977), is a statistical method designed for direct gradient analysis of multivariate data tables. Hereafter, we followed three distinct approaches: **1-** independent, **2-** additive and **3-** co-variable. The RDAs were performed on log<sub>10</sub>-transformed data because a linear model is assumed for all relationships between independent variables (i.e., morphometric, physico-chemical, and biological characteristics in this study) and dependent variables

(i.e., biomass of the four zooplankton size fractions here) (ter Braak 1987, 1988). In the independent approach, we performed the RDA on each set of explanatory variables (morphometric, physico-chemical, and biological matrices) separately for the epi-, meta- and hypolimnetic strata.

After the most important variables from each set of morphometric, physico-chemical and biological variables were identified, we carried out the additive approach by performing the RDA on these predominant variables in order to identify parsimoniously the factors in structuring the zooplankton biomass community. This analysis allowed us to evaluate the interactions between abiotic and biotic factors influencing zooplankton biomass in the three limnetic strata.

Because maximum depth was identified as the most important variable influencing zooplankton biomass in this study (see the Results section), we also following a co-variable approach based on partial redundancy analysis, by performing the RDA on the variables identified in the independent approach after removal of the effect of maximum depth. The maximum depth strongly influenced water physico-chemistry, phytoplankton and zooplankton communities structure and was consequently strongly correlated with some important variables might differently explain the variations of the zooplankton size structure in lakes. By removing the influence of maximum depth on all the other variables, the physico-chemical and biological mechanisms explaining the changes of the zooplankton biomass size structure with environmental processes could be better described in the three limnetic strata.

For all RDAs, the forward procedure of CANOCO version 3.1 (ter Braak 1988, 1990) was used with a significance level of 0.1. Thus, although some of the environmental factors retained in the RDA forward procedure might not be statistically significant at the 0.05 level, they could be ecologically plausible as explanatory factors of zooplankton biomass response. The statistical significance of the environmental variables was evaluated by Monte Carlo permutation tests of the sum of all eigenvalues, as implemented in CANOCO. To avoid multicollinearity problems, we chose the least collinear factors among those selected by the forward procedure and kept the inflation factor below 2 in most of the final models. Ordination scores for zooplankton biomass size fractions and environmental variables were used to draw biplots in order to visualize the relationships between those sets of variables (additive and co-variable approaches). In the RDA, as in the PCA, the angle between environmental and zooplankton size fractions arrows and the length of arrows can be used jointly to infer the direction of size

fractions responses to environmental variables (ter Braak 1987). Thus, an angle near  $0^\circ$  between a zooplankton biomass size fraction arrow and an environmental variable arrow indicates a strong positive correlation. An angle near  $90^\circ$  indicates the absence of a relationship, whereas an angle near  $180^\circ$  indicates a strong negative correlation. Furthermore, zooplankton biomass size fraction arrows pointing in different directions indicate differences among individual size fractions in their response to environmental variables.

### 4.3 RESULTS

#### 4.3.1 Zooplankton carbon biomass, size structure and species composition

During the growing season, the mean epilimnetic total zooplankton biomass was  $108.8 \pm 97.6 \mu\text{g.L}^{-1}$  and ranged from 17.3 to  $690 \mu\text{g.L}^{-1}$  (Table IV). The mean total biomass decreased with depth but in some lakes, maximum values in the hypolimnion ( $775.3 \mu\text{g.L}^{-1}$ ) were more important than one registered in the epilimnion ( $690 \mu\text{g.L}^{-1}$ ). The total zooplankton biomass strongly varied from lake to lake (Fig. 2). Mean total biomass was ranked by ascending values observed in epilimnetic waters and ranged from  $40.1 \pm 17.1 \mu\text{g.L}^{-1}$  (Lake Lovering) to  $388.6 \pm 167.5 \mu\text{g.L}^{-1}$  (Lake Desjardins). The lakes presenting the highest zooplankton biomass were either unstratified (lakes Desjardins and Waterloo) or were the most productive (lakes Desjardins, Waterloo, Cromwell and Pin Rouge).

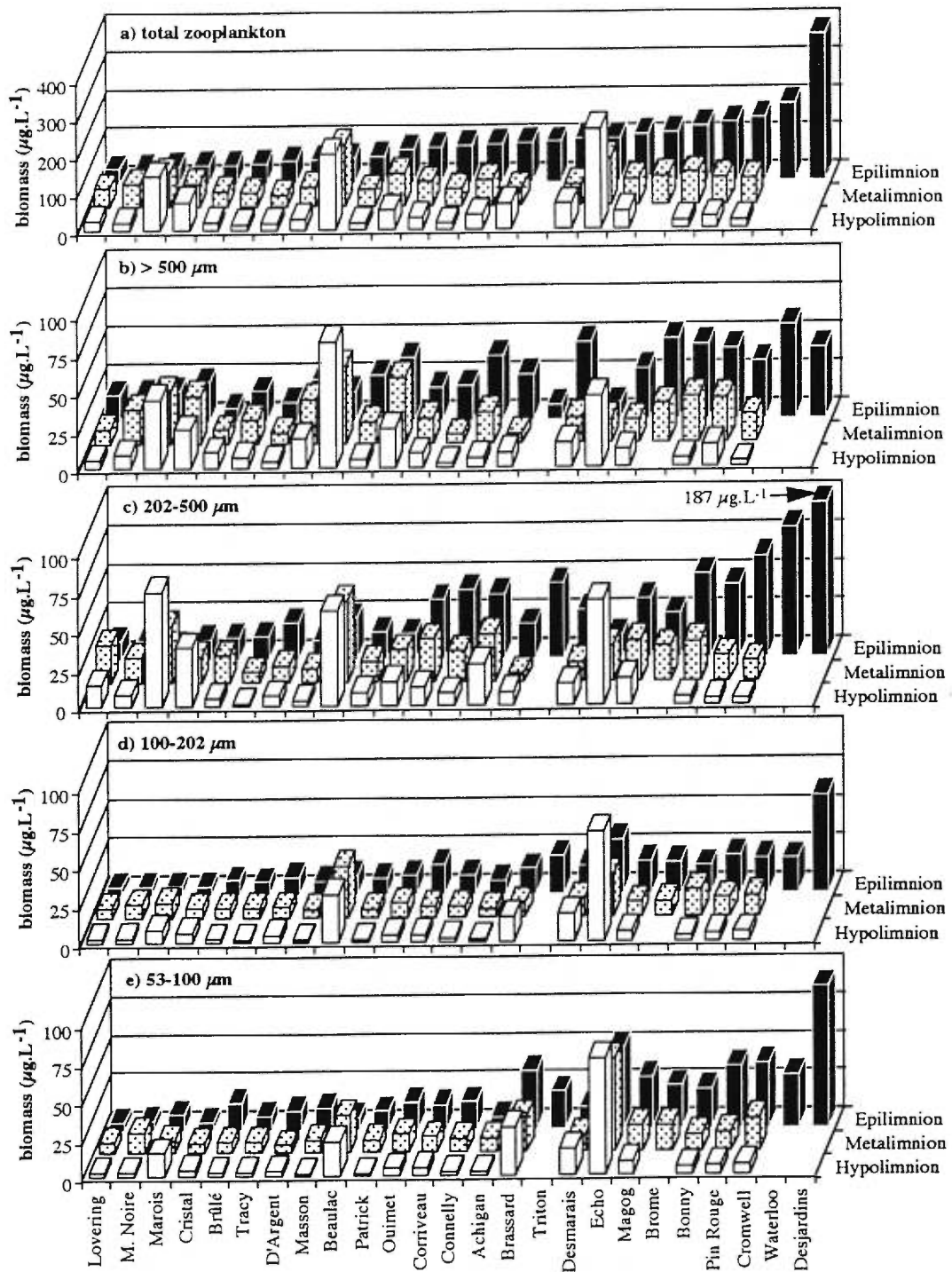
At the opposite, lakes with the lowest zooplankton biomass were rather the deepest (lakes Lovering, Montagne Noire and Brûlé) or the least productive and the clearest (lakes Marois, Tracy, Cristal). The total biomass decreased with depth (Fig. 2a), but this trend cannot be generalized. Some lakes presented the highest biomass in the metalimnion (lakes Lovering, Montagne Noire and Ouimet), whereas others lakes showed a more important biomass in the hypolimnion (lakes Marois, Cristal, Beaulac, and Echo).



Table IV : Summary statistics for biomass of total zooplankton and its size fractions in the three limnetic strata and species composition of the four size fraction.

	Statistic	Total ( $\mu\text{g.L}^{-1}$ )	> 500 $\mu\text{m}$ ( $\mu\text{g.L}^{-1}$ )	202-500 $\mu\text{m}$ ( $\mu\text{g.L}^{-1}$ )	100-202 $\mu\text{m}$ ( $\mu\text{g.L}^{-1}$ )	53-100 $\mu\text{m}$ ( $\mu\text{g.L}^{-1}$ )
Epilimnion	Mean	108.8	31.3	36.1	17.1	23.4
	SD	97.6	29.6	41	18.4	31.4
	Min	17.3	0.9	2.4	2.2	2
	Max	690	193.7	295.9	177.8	245.4
Metalimnion	Mean	68.7	23.3	20.9	10.8	13.7
	SD	42.2	19.5	16.1	9.1	15.9
	Min	6.5	0.7	1.2	1.4	2.5
	Max	320.7	112.1	118.8	80	155.8
Hypolimnion	Mean	51.7	16.5	17.3	8.4	9.5
	SD	75.5	23.1	25.8	17.5	18.7
	Min	2.9	0.2	0.3	0.5	0.5
	Max	775.3	180	202.5	187.1	205.7
Species composition						
(dominant zooplankton in bold characters)						
		<b>CLADOCERANS</b>	<b>CLADOCERANS</b>	<b>CLADOCERANS</b>	<b>COPEPODS</b>	<b>ROTIFERS</b>
		<i>Diaphanosoma</i> sp.	<i>Bosmina</i> spp.	<i>Bosmina</i> spp.	<b>nauplii</b> of calanoids	<i>Gastropus</i> sp.
		<i>Daphnia ambigua</i>	<i>Ceriodaphnia</i> sp.	<i>Ceriodaphnia</i> sp.	and cyclopoids and	<i>Keratella</i> spp.
		<i>D. catawba</i>	<i>Chydorus</i> spp.	<i>Chydorus</i> spp.	some copepods	<i>Polyarthra vulgaris</i>
		<i>D. dubia</i>	cladocerans immature			
		<i>D. galeata</i>	<b>COPEPODS</b>	<b>COPEPODS</b>	<b>ROTIFERS</b>	
		<i>D. pulex</i>	<i>Tropocyclops prasinus</i>	<i>Tropocyclops prasinus</i>	<i>Ascomorpha</i> sp.	
		<i>Holopedium gibberum</i>	instars of calanoids	instars of calanoids	<i>Conochilus</i> sp.	
			and cyclopoids	and cyclopoids	<i>Kellicottia</i> sp.	
		<b>COPEPODS</b>			<i>Keratella</i> spp.	
		<i>Cyclops scutifer</i>			<i>Lecane</i> sp.	
		<i>Epichuracustris</i>			<i>Trichocerca</i> spp.	
		<i>Leptodiaptomus</i> spp.			<i>Synchaeta</i> sp.	
		<i>Mesocyclops</i> sp.				
		<i>Skistodiaptomus</i> sp.				

Figure 2: Among-lake and within-lake spatial variations of total zooplankton biomass and its four size fractions in the 25 lakes.



In the epilimnion, the 202-500  $\mu\text{m}$  biomass ( $36.1 \pm 41 \mu\text{g.L}^{-1}$ ) was more important than the  $> 500 \mu\text{m}$  biomass ( $31.3 \pm 29.6 \mu\text{g.L}^{-1}$ ), whereas the 53-100  $\mu\text{m}$  biomass ( $23.4 \pm 31.4 \mu\text{g.L}^{-1}$ ) was higher than 100-202  $\mu\text{m}$  biomass ( $17.1 \pm 18.4 \mu\text{g.L}^{-1}$ ) (Table IV). As for the total, the general tendency of all size fractions was a decrease from the epilimnion to the hypolimnion. At the opposite to the epilimnion, the  $> 500 \mu\text{m}$  biomass ( $23.3 \pm 19.5 \mu\text{g.L}^{-1}$ ) in the metalimnion was more important than the 202-500  $\mu\text{m}$  biomass ( $20.9 \pm 16.1 \mu\text{g.L}^{-1}$ ). In hypolimnion, the relative importance of the four size fractions followed the pattern observed in the epilimnion. We also noted that the mean maximum biomass were always lower in the metalimnion, while those registered in the epi- and hypolimnion were both large for most size fractions. Based on lake to lake description, the size fractions in some extent increased from lake Lovering to Lake Desjardins at the exception of the  $> 500 \mu\text{m}$  biomass which presented a more variable pattern (Fig. 2b-e). For the more productive or unstratified lakes (Desjardins, Waterloo, Cromwell, Pin Rouge and Bonny), the 202-500  $\mu\text{m}$  biomass was more important than the  $> 500 \mu\text{m}$  biomass, while the opposite held for the less productive, clearer and deeper lakes (Lovering, Montagne Noire, Marois and Cristal). As for the total, the four size fractions biomass decreased with depth for most lakes. Particularities observed with total biomass (biomass more important in meta- or hypolimnion) were also detected within most size fractions distributions. We also noted that in lake without piscivore species (Brassard, Corriveau, Cromwell, Desjardins, Triton), the  $> 500 \mu\text{m}$  biomass was not the zooplanktonic fractions that dominated the epilimnetic waters.

The taxonomic analysis revealed that the biomass  $> 500 \mu\text{m}$  was mainly constituted by large cladocerans such as *Daphnia* spp. represented by five species, *Diaphanosoma* sp. and *Holopedium gibberum*, and is a lesser importance, by five adult copepod species (Table IV). The copepods rather dominated the 202-500  $\mu\text{m}$  fraction and was composed by instars of the five copepods species identified in the  $> 500 \mu\text{m}$  fraction and by adults *Tropocyclops prasinus*. The cladocerans was not as important in the 202-500  $\mu\text{m}$  fraction, but were well represented by *Bosmina* spp., *Ceriodaphnia* sp., *Chydorus* spp. and by immatures of cladocerans identified in the  $> 500 \mu\text{m}$  fraction. The two later fractions 100-202  $\mu\text{m}$  and 53-100  $\mu\text{m}$  were mainly dominated by different rotifers species (Table IV). However, the 100-202  $\mu\text{m}$  presented important densities of copepodids and nauplii.

### 4.3.2 Sources of variation

Among-lake differences are the greatest source of variation for total zooplankton biomass and most size fractions (Table V;  $\geq 36.5\%$  of total variation,  $P = 0.0001$ ). Strata-related effects (i.e., strata main effects and lake-by-strata interaction) were highly significant for total zooplankton biomass and its four size fractions; the least significant strata-related effect was observed for the 202-500  $\mu\text{m}$  fraction and the strata main effects ( $P = 0.0139$ ; Table V). The strata-related effect was the least important source of variation ( $\leq 19.9\%$ ; Table V). The relative lake-by-strata zooplankton biomass variation was as important as lake variation for total and size fractions 202-500  $\mu\text{m}$  and  $> 500 \mu\text{m}$  (Table V). The highly significant lake-by-strata interaction ( $P = 0.0001$ ; Table V) indicates that vertical variations of total zooplankton and its size fractions were not constant from lake to lake.

### 4.3.3 Correlation structure of environmental characteristics and zooplankton biomass

The Principal Component Analysis applied on all environmental variables ( $n=36$ ) allowed us to either obtain a picture of the overall links existing between morphometric, physico-chemical and biological characteristics of our data set or identify the main environmental processes explaining variations of the total zooplankton biomass. The first two PCA axes of the epilimnetic environmental data explained 61.9% of the variance (Fig. 3a). The dominant environmental gradients associated with the total zooplankton biomass was identified on the first axis. This axis explained 35.6% of the variance and contrasted lakes of higher productivity presenting high concentrations of nutrients (TP, TN, COD), chlorophyll *a* (total and all size fractions) and total zooplankton biomass against lakes of lower productivity with high maximum depth and high water transparency. The second axis explained 26.3% of the variance, and contrasted lakes and watershed of large area, with an high alkaline pH and having 3 or more piscivore fish species against small acidic lakes without piscivore and situated at high altitude level.

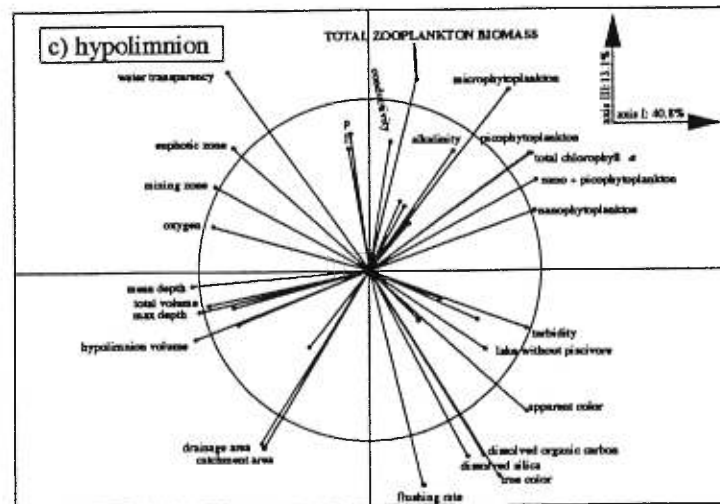
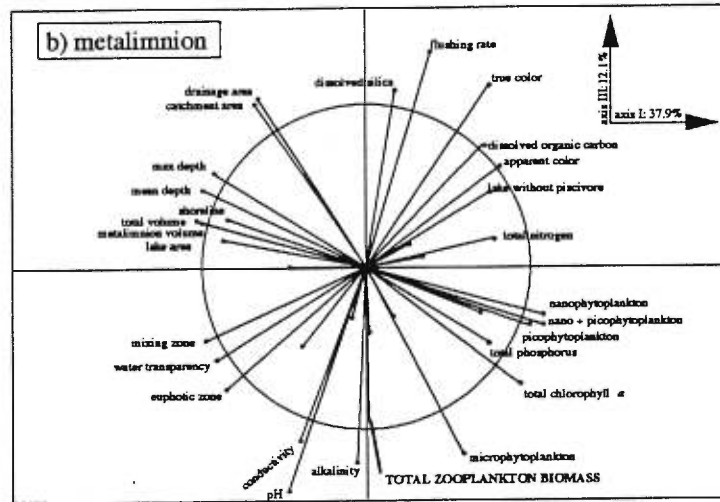
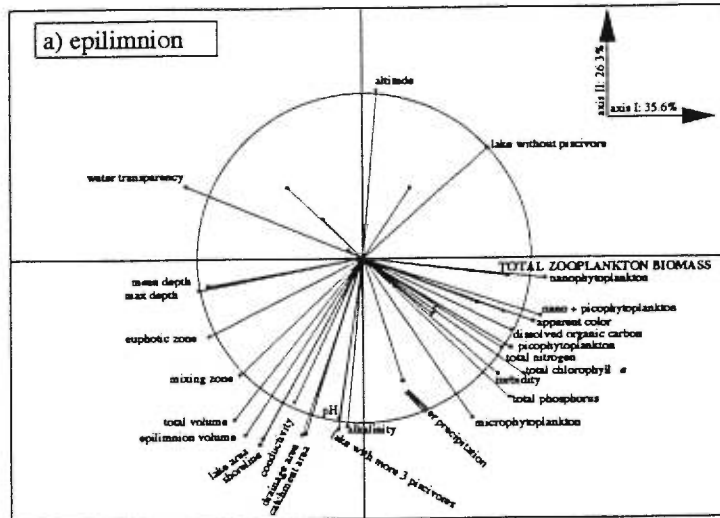
Table V. Results of the ANOVA  $F$ -tests ( $\dagger$ ) for among-lake and within-lake variations of total zooplankton biomass and its size fractions.

Source	Mean square	d.f.	$F$ observed	P	% of variation
Zooplankton total					
Lake	1.6537	20	63.84	0.0001	39.3
Strata	8.1758	2	10.91	0.0003	19.5
Lake x strata	0.7496	40	28.94	0.0001	35.6
Epsilon = 0.9097					
Zooplankton > 500 $\mu$ m					
Lake	2.2198	20	34.75	0.0001	38.8
Strata	9.6071	2	9.43	0.0005	16.8
Lake x strata	1.0188	40	15.95	0.0001	35.6
Epsilon = 0.9953					
Zooplankton 202-500 $\mu$ m					
Lake	2.2214	20	51.79	0.0001	36.5
Depth	7.0052	2	5.00	0.0139	11.5
Lake x depth	1.4005	40	32.65	0.0001	46.1
Epsilon = 0.9200					
Zooplankton 100-202 $\mu$ m					
Lake	3.0276	20	89.61	0.0001	53.4
Strata	10.1166	2	15.17	0.0001	17.8
Lake x strata	0.6667	40	19.73	0.0001	23.5
Epsilon = 0.8785					
Zooplankton 53-100 $\mu$ m					
Lake	3.7903	20	140.55	0.0001	55.0
Strata	13.0376	2	16.82	0.0001	19.9
Lake x strata	0.7749	40	28.74	0.0001	22.5
Epsilon = 0.9350					

$\dagger$  The ANOVA  $F$ -tests were modified in order to take into account the autocorrelation and heteroscedasticity of the spatial repeated measures at the three strata (Greenhouse and Geisser 1959).

Figure 3: Principal component analysis ordinations of the total zooplankton biomass and all environmental variables for (a) epilimnion, (b) metalimnion, and (c) hypolimnion.





The environmental gradients observed for the epilimnion data were also identified in the metalimnion and the hypolimnion, but the greatest variations of the total zooplankton biomass were expressed on the third axis (Fig. 3b-c). The first and the third PCA axes explained together 50% and 53.9% of the variance of environmental data for the metalimnion and the hypolimnion, respectively. The first axis, which explained 37.9% and 40.8% of the variance for the metalimnion and the hypolimnion, opposed larger, deeper and clearer lakes against small colored lakes of high productivity (high concentration of nutrients, chlorophyll *a*) without piscivore species. The third axis explained 12.1% and 13.1% of the variance for the metalimnion and the hypolimnion, respectively. In these strata, the total zooplankton biomass was more important in lakes of higher alkalinity, transparency, and concentrations of microphytoplankton. At the opposite, the zooplankton biomass was less important in the meta- and hypolimnion of colored lakes presenting high flushing rate and large drainage area.

#### **4.3.4 Zooplankton size fractions responses to environmental factors**

Canonical redundancy analysis (RDA) was firstly used to determine the main factors within each of the three variable matrices (morphometric, physico-chemical, and biological) that explained the variation of the four zooplankton size fractions in the three limnetic water strata (independent approach) (Table VI). Thereafter, a second serie of RDA was realized to determine the relative importance of these abiotic and biotic variables in structuring the zooplankton biomass size fractions in the three limnetic strata (additive approach) (Figs. 4a,c,e). Finally, the same analyses were performed by removing the effect of the maximum depth (co-variable) in the goal to better identify the mechanisms explaining variations of the four size fractions in the three limnetic strata (co-variable approach) (Figs. 4b,d,f).

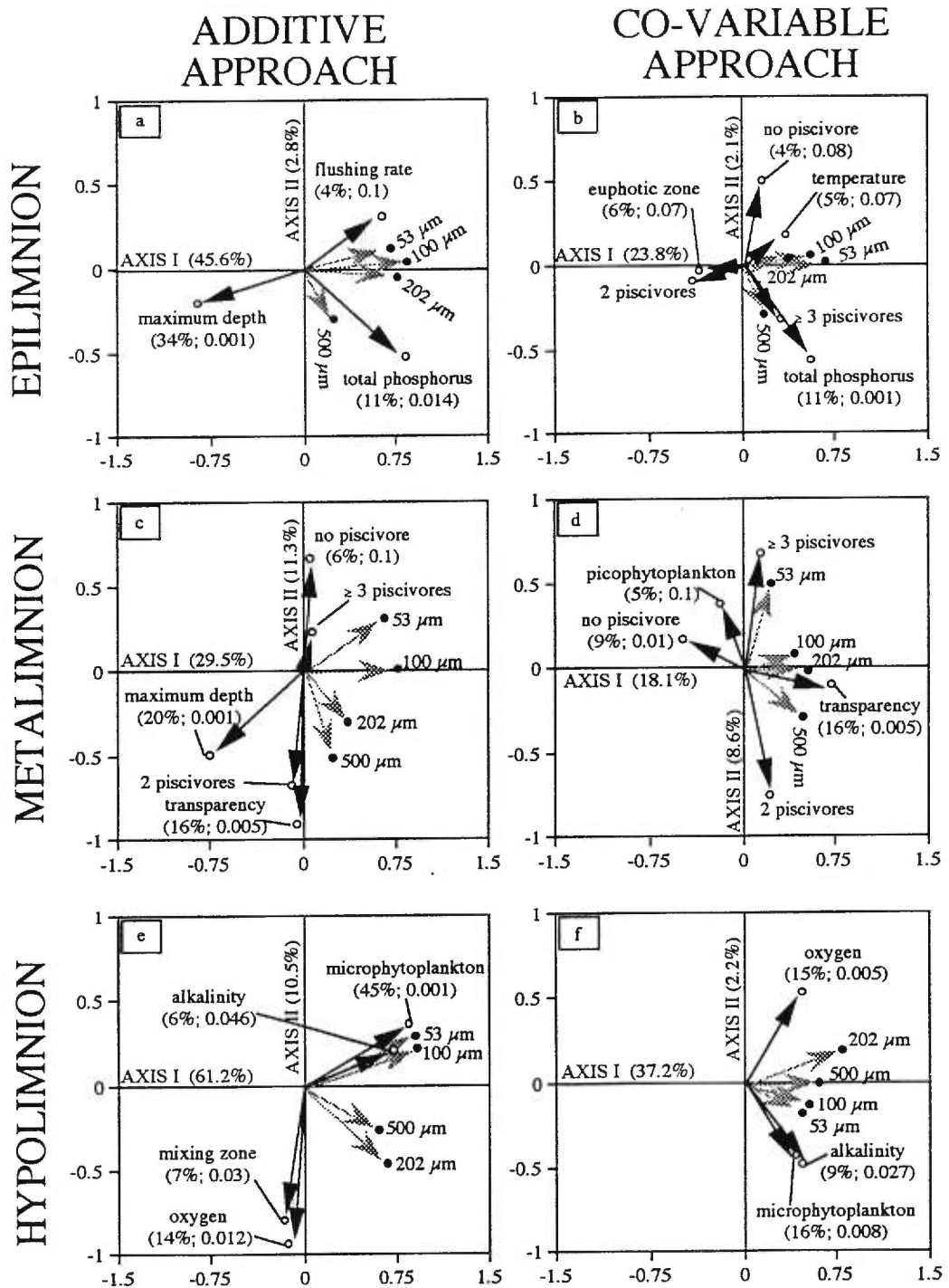
Among the three variable matrices, the physico-chemical factors were the most important in explaining variation of the zooplankton biomass size fractions in the three limnetic strata (Table VI). In the epilimnion, the physico-chemical factors explained 56% of the variations compared to 42% and 46% for the morphometric and biotic factors respectively. In the meta- and hypolimnion, the physico-chemical factors explained 35% and 67% respectively, compared to 31% and 63% for the biotic factors and 30% and 46% for the morphometric factors. In term of total variance explained, the morphometric factors were the less important in the three limnetic strata.

Table VI. Ordination scores for zooplankton biomass size fractions in redundancy analyses (RDA) for the three limnetic strata with the significant abiotic and biotic variables as predictors.

Variable	EPILIMNION		METALIMNION		HYPOLIMNION	
	% of variance explained	<i>P</i> -value	% of variance explained	<i>P</i> -value	% of variance explained	<i>P</i> -value
<u>Morphometric</u>						
Maximum depth	0.34	0.001	0.20	0.001	0.32	0.002
Flushing rate	0.08	0.068				
Metalimnetic volume			0.10	0.063		
Total volume					0.14	0.031
<b>Total variance explained</b>	<b>0.42</b>		<b>0.30</b>		<b>0.46</b>	
<u>Physico-chemical</u>						
Total phosphorus	0.32	0.001				
Euphotic zone	0.17	0.001				
Water transparency			0.12	0.036		
Mixing zone					0.20	0.002
Temperature	0.07	0.036	0.14	0.001		
Oxygen					0.14	0.017
Dissolved silica			0.09	0.05		
Alkalinity					0.33	0.001
<b>Total variance explained</b>	<b>0.56</b>		<b>0.35</b>		<b>0.67</b>	
<u>Biotic</u>						
Microphytoplankton	0.08	0.064			0.45	0.001
Nano + picophytoplankton					0.18	0.001
Nanophytoplankton	0.30	0.001				
Picophytoplankton			0.19	0.01		
No piscivore	0.08	0.05	0.06	0.09		
2 or ≥ 3 piscivores			0.06	0.11		
<b>Total variance explained</b>	<b>0.46</b>		<b>0.31</b>		<b>0.63</b>	

However, when we examined the percentage of variance explained by each factor within each variable matrix, the maximum depth was one of the most important factors influencing the zooplankton biomass size fraction among all abiotic and biotic factors in the epi-, and metalimnion. In the epilimnion, maximum depth explained 34% of the zooplankton size structure variation, while the total phosphorus and the nanophytoplankton concentrations explained 32% and 30% respectively. In the metalimnion, the maximum depth explained 20% of the zooplankton size structure variation, compared to 14% for the water temperature and 19% for the picophytoplankton concentration. The maximum depth was not the most important factor explaining the variation of the zooplankton size structure in the hypolimnion (32%), whereas microphytoplankton explained 45% and water alkalinity 33%.

Figure 4: Ordination biplots of the epilimnetic, metalimnetic, and hypolimnetic waters of zooplankton size fractions and environmental variables for additive (a,c,e) and co-variable approaches (b,d,f). Values in parentheses are the percentages of variance explained by the variables followed by probabilities. Zooplankton biomass 53  $\mu\text{m}$ : 53-100  $\mu\text{m}$ ; 100  $\mu\text{m}$ : 100-202  $\mu\text{m}$ ; 202  $\mu\text{m}$ : 202-500  $\mu\text{m}$ ; 500  $\mu\text{m}$ : > 500  $\mu\text{m}$ .



Many other factors were retained by the forward procedure of the RDA in the three variable matrices, but their importance in structuring zooplankton communities in lakes was better identified in the additive and co-variable approaches (Figs. 4a-f). Details of these analyses are presented in Table VII.

The maximum depth (34%), the flushing rate (4%) and the concentration of total phosphorus (11%) explained together 49% of the variation of the zooplankton biomass size fraction in the epilimnion (Fig. 4a). The 53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$  and 202-500  $\mu\text{m}$  biomass were more important in shallow lakes of high flushing rate and high total phosphorus concentrations. The > 500  $\mu\text{m}$  biomass only responded to positive increase of total phosphorus concentrations. These results indicated that the epilimnetic zooplankton biomass of the four size fractions increased with the systems productivity. After removing the maximum depth effect, the explained variance decreased from 49% (Fig. 4a) to 26% (Fig. 4b), indicating a strong influence of the lake depth on the variation of the zooplankton biomass size fraction. This later analysis allowed to either confirm the influence of the total phosphorus (11%) on the variation of the zooplankton biomass or identify three new variables, such as euphotic zone (6%), water temperature (5%) and fish community (4%). Thus, the 53-100  $\mu\text{m}$ , 100-202  $\mu\text{m}$  and 202-500  $\mu\text{m}$  biomass increased in epilimnetic waters of lakes of high temperature and shallow euphotic zone, but decreased in lakes presenting 2 piscivore species. This later result was directly related to the predation influence of planktivorous species on > 500  $\mu\text{m}$  biomass. This fraction increased in lakes of high concentration of total phosphorus, but also decreased in lakes without piscivore species. Thus, the absence of piscivore (greater predation on > 500  $\mu\text{m}$  fraction) allows a more important biomass of the small zooplankton size fraction (< 500  $\mu\text{m}$ ) in epilimnetic waters.

In the metalimnion (Fig. 4c), 41% of the variation of the four size fraction zooplankton biomass was explained by the maximum depth (20%), the water transparency (16%) and the fish community (6%). The 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass were low in metalimnion of deep lakes, whereas the 202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$  slightly increased in this stratum. These two fractions were rather influenced by the water transparency and by the fish predation. In clearer lakes with 2 piscivore species, their biomass increased but decreased in lakes without piscivore in whose the 53-100  $\mu\text{m}$  biomass was favored. When we removed the maximum depth effect, the explained variance decreased from 41% (Fig. 4c) to 30% (Fig. 4d). This diminution was less important than one observed in the epilimnion, indicating that maximum depth had less

Table VII. Ordination scores for zooplankton biomass size fractions in redundancy analyses (RDA) for the three limnetic strata with the additive and co-variable approaches.

<b><u>EPILIMNION</u></b>				
Variable	<u>Additive</u>		<u>Co-variable</u>	
	% of variance explained	<i>P</i> -value	% of variance explained	<i>P</i> -value
Maximum depth	0.34	0.001		
Total phosphorus	0.11	0.014	0.11	0.001
Flushing rate	0.04	0.101		
Euphotic zone			0.06	0.07
Temperature			0.05	0.07
Absence of piscivore			0.04	0.08
<b>Total variance explained</b>	<b>0.49</b>		<b>0.26</b>	
<b><u>METALIMNION</u></b>				
Maximum depth	0.20	0.001		
Water transparency (Secchi)	0.16	0.005	0.16	0.005
Absence of piscivore	0.06	0.099	0.09	0.013
Picophytoplankton			0.05	0.092
<b>Total variance explained</b>	<b>0.45</b>		<b>0.30</b>	
<b><u>HYPOLIMNION</u></b>				
Microphytoplankton	0.45	0.001	0.16	0.008
Oxygen	0.14	0.012	0.15	0.005
Alkalinity	0.06	0.046	0.09	0.027
Mixing zone	0.07	0.034		
<b>Total variance explained</b>	<b>0.72</b>		<b>0.40</b>	

influence on metalimnetic zooplankton size structure. The concentration of picophytoplankton (5%) was a new variable added to the model explaining variation of the zooplankton biomass size structure, when the water transparency (16%) and the fish community (9%) still occurred in this analysis. The 202-500  $\mu\text{m}$  and  $> 500 \mu\text{m}$  biomass were important in lakes of higher transparency having two piscivore species and strongly decreased in metalimnion of lakes without piscivore species. However, these two fractions were less important in this stratum when the concentration of picophytoplankton was high, indicating a possible control of this algae size fraction by grazing. The 53-100  $\mu\text{m}$  biomass was more important in lakes having either more than 3 piscivore species or high picophytoplankton concentration. This positive correlation with picophytoplankton could be due to the fact that the 53-100  $\mu\text{m}$  biomass was more contaminated by phytoplanktonic items relatively to the size fractionation method used in this study. Thus, the fish predation and the phytoplankton resource seemed both the main factors control the biomass of the zooplankton size structure in the metalimnetic waters of lakes.

In the hypolimnion (Fig. 4e), more than 70% of the zooplankton biomass size structure variation was explained by the microphytoplankton (45%) and oxygen (14%) concentration, by the mixing zone depth (7%) and by the water alkalinity (6%). At the opposite to 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass, more the mixing zone was deep and the hypolimnion oxygenated, more the 202-500  $\mu\text{m}$  and  $> 500 \mu\text{m}$  biomass were important in this stratum. Thus, the hypolimnetic waters seemed offer a refuge for large zooplankton fractions from turbulence and fish predation occurring in surface layers. The 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass were more important in hypolimnion of lakes having high concentrations of microphytoplankton and high water alkalinity, as for the large fractions  $\geq 202-500 \mu\text{m}$  but in a lesser extent. This strong correlation between small zooplankton fractions ( $\leq 100-202 \mu\text{m}$ ) with microphytoplankton concentration (inedible algae) could reflect a more important contamination of the algae in these hypolimnetic fractions. Once removing the effect of maximum depth, the explained variance decreased from 72% (Fig. 4e) to 40% (Fig. 4f) by retaining the microphytoplankton (16%) and oxygen (15%) concentrations and the water alkalinity (9%). This strong diminution could lead to the conclusion that maximum depth also strongly influence zooplankton biomass in hypolimnetic waters, but we observed that microphytoplankton and oxygen concentrations and mixing zone were highly correlated with maximum depth ( $r > 0.66$ ;  $P \leq 0.001$ ). Furthermore, the maximum depth did not really influenced the zooplankton biomass in hypolimnion because either it was not chosen in the additive RDA or the same relationship occurred after removing its effects.



## 4.4 DISCUSSION

### 4.4.1 Source of variation of the zooplankton biomass

Spatial and temporal variability are essential considerations in the study of aquatic organisms. Traditionally, these two sources of variability are treated separately although they occur concurrently in natural systems (Haury et al. 1978, Resh and Rosenberg 1989). In our study, the temporal variability (year and month) was not a significant source of variation in zooplankton data. The importance of among-lakes spatial variations over the temporal effects was observed in several studies conducted on phytoplankton (Pinel-Alloul et al. 1996), zooplankton (Betsill and Van Den Avyle 1994, Pinel-Alloul and Méthot 1998, Patoine and Pinel-Alloul unpublished data, present study), fish communities (Pierce et al. 1994; Rundle and Jackson 1996) and trophic parameters (Larsen et al. 1995, and references therein). Temporal variations generally predominates in studies conducted at within-lake scale where the seasonal and/or the inter-annual scales provide more variability than spatial horizontal scales (i.e. among-site) in relation to succession processes (e.g. Evans and Sell 1983, Sommer et al. 1986, Sarvala et al. 1994). Our preliminary analyses showed that temporal variation could be important in some lakes (strong significant lake-by-month interaction). Indeed, the variance found in any given study depends upon duration and frequency of data collection (Carpenter and Kitchell 1987). As we realized, it is essential to evaluate the importance of both sources of variations (spatial and temporal) before eliminating temporal variability by aggregation-averaging data (Resh and Rosenberg 1989), because these both sources of variation could provide an explanation factor causing the patterns observed and then may elucidate underlying mechanisms.

As for phytoplankton (Pinel-Alloul et al. 1996), the greatest source of variation in our zooplankton data was observed at among-lake scale. This result supports our first hypothesis which stipulates that environmental changes among lakes are the main source of variability in total zooplankton biomass and size fractions. Our results and those of Pinel-Alloul et al. (1996) indicate that importance of spatial variation increases with the scale of observation. As the space over which a study is done increases, variability is more pronounced. This argument is supported by the scale-continuum concept defined by Haury et al. (1978) for marine zooplankton. When the scale of observation (temporal and spatial) increases, the zooplankton biomass variability increases too. Across a large spatial scales, the important environmental processes that influence zooplankton

community structure are probably at the origin of this variability (Carter et al. 1986, Tessier and Horwitz 1990, Pinel-Alloul et al. 1995, this study). By revealing the spatial and (or) temporal scales at which significant variation occurs in the community, we obtain a more informative picture of the data (Rundle and Jackson 1996). Thus, mechanistic explanations of the causes of the zooplankton biomass size fractions variations of this study may be explored at the scales at which variations occur and then may be more successfully identified.

Important lake-to-lake and within-lake variations (i.e. lake-by-strata interaction) observed in this study reflect the local influence of physico-chemical and biological factors on zooplankton biomass size community. In their large scale study on zooplankton spatial structure in Québec lakes, Pinel-Alloul et al. (1995) suggested that 44% of their unexplained variation could be due to factors operating at lake scale such as within-lake spatial heterogeneity, local effects of abiotic and biotic variables, and species behaviour. Although not inconsiderable, the strata was not an important source of variation for zooplankton biomass compared to the lake effect, but variations between strata from lake-to-lake were very important and reasons of this must be explored. Our study take account of this source of variation and attempt to identify factors influencing the total zooplankton biomass and its size fractions variations at among-lake and within-lake scales.

#### **4.4.2 Primacy of the abiotic environmental control of the zooplankton biomass**

By examining the literature it is obvious that the perception that we have of the biological structuring of the communities in lakes will change with the scale of observation. Wiens (1986) clearly argued that the most vociferous disagreements among ecologists arise from differences in their choice of scale. Those who study the long-term dynamics of a particular community at a single site often reach very different conclusions from those reached by individuals conducting short-term studies of similar communities at many different sites distributed over a large area. In this paper we tested three hypotheses relative to the zooplankton biomass heterogeneity from two scales of observation, among- and within-lakes.

We first tested that abiotic environment (morphometry and physico-chemistry) is the primarily factor explaining the spatial heterogeneity of zooplankton community among

lakes in epilimnetic waters. As we hypothesized, the independent, additive and co-variable approaches showed that abiotic environment, especially either maximum depth or total phosphorus concentration, was the primary factor influencing the zooplanktonic size structure at among-lake scale. Our results agree with the Pinel-Alloul's model (1995), which implies a predominance of abiotic forces in the environmental control of the zooplanktonic communities at large spatial scales. The primacy of the abiotic environment also confirms that physical processes *sensu lato* constitute the first step of the hierarchy of processes controlling ecosystems and influencing biological sub-systems while, conversely, physical processes are little influenced by biological systems (Allen and Star 1982, Amanieu et al. 1989). However, in specific situations, biological systems can influence physical and chemical processes (see Pinel-Alloul et al. 1998 for a review). Results of this study also support the multiple driven forces hypothesis which implies an interactive effect of both abiotic factors (lake depth, residence time, phosphorus, oxygen and transparency), and biotic (chlorophyll *a* size structure) bottom-up and top-down (fish communities) factors in the control of heterogeneity of zooplankton within Québec shield lakes (Rodriguez et al. 1993; Pinel-Alloul et al. 1995). Although abiotic bottom-up factors have strong effects on zooplankton biomass levels, biotic bottom-up and top-down factors contribute to the modification of the size structure of zooplankton community depending on the limnetic strata concerned (discussed below). Thus, although these forces are complementary in structuring zooplanktonic communities, they can also act differently on the community attributes (biomass and size structure).

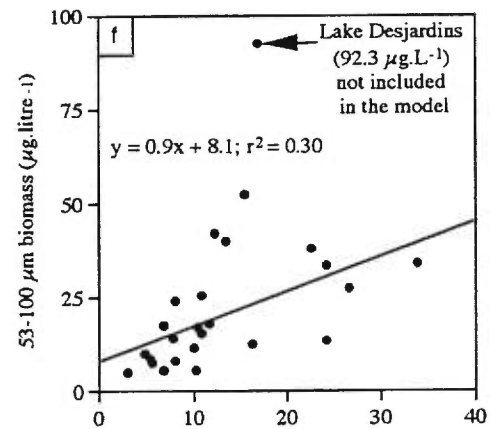
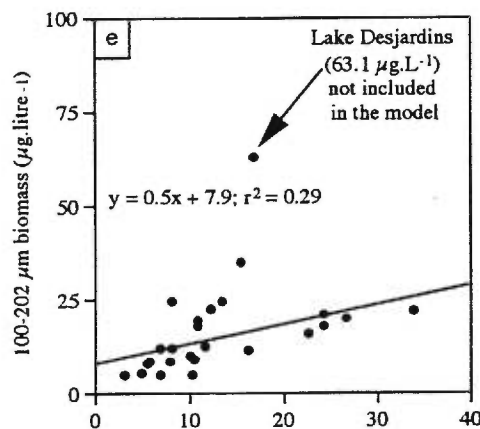
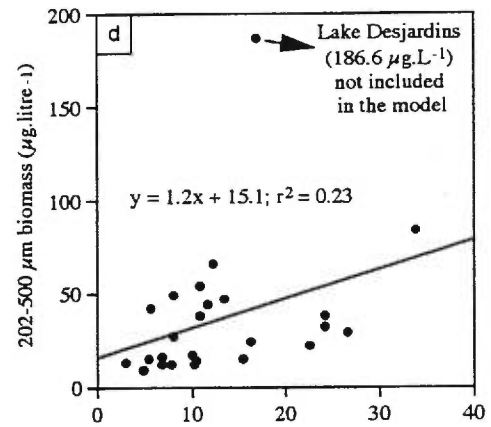
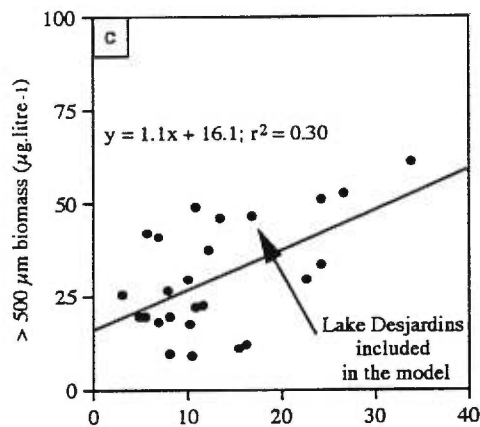
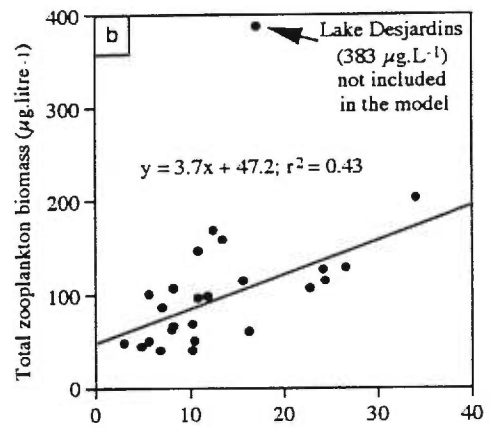
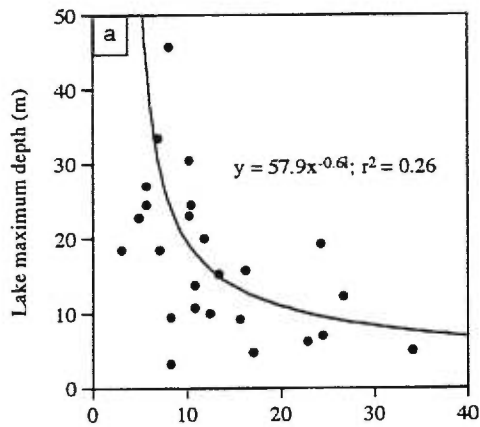
#### **4.4.3 Epilimnetic control of the total zooplankton biomass and its size structure**

The epilimnetic zooplankton biomass was primarily influenced by the lake trophic state. The negative correlations between depth and either TP or flushing rate, reflect the commonly observed relationship between lake productivity and lake maximum depth. The lake maximum depth (or mean depth) had a strong negative effect on the zooplankton biomass as detected in some studies (e.g. Hanson and Peters 1986, Yan 1986, Quiros 1991). The deepest lakes are generally recognized as less productive system compared to shallow lakes (Riley and Prepas 1985, Keller and Conlon 1994) due to the limitation of the nutrient in epilimnion during the stratification period (Gaillard 1995). Shallow lakes are associated with either high flushing rate (this study; Chow-Fraser 1991) or low water residence (retention) time (Meybeck 1995) and consequently to high level of phosphorus because phosphorus retention (high loss) in lakes increases with increasing water

residence time (D'Arcy and Carignan 1995). Keller and Conlon (1994) indicated that lake depth emerged as the best correlate with either species richness or environmental variable (e.g. TP, transparency, DOC) suggesting that lake depth is a key factor as we observed in this study. Depth is closely linked to other important lake characteristics such as general trophic status, degree of thermal stratification, occurrence and extent of anoxia, and fish community composition. The influences of depth on zooplankton communities may, however be manifested as both direct and indirect effects (Keller and Conlon 1994). In our study, the lake maximum depth indirectly determined the epilimnetic zooplankton biomass amount by establishing the potential of productivity of lakes. However, although shallow lakes generally present higher TP concentration than deeper lakes, the relationship between TP and maximum depth is not linear (Fig. 5a). Many factors affect lake productivity and consequently lake water residence time such as the latitude, the precipitation, the drainage area, the ratio drainage area/lake area, the watershed slope and the lake volume (D'Arcy and Carignan 1995, Hakanson and Peters 1995, Meybeck 1995).

The total zooplankton biomass and the four size fractions responded positively to TP concentration as observed in several studies (Hanson and Peters 1986, Pace 1986, Yan 1986). However, strong variations were observed at low TP level in the relationships between TP and either total zooplankton biomass or the four size fractions (Figs. 5b to 5f). Some morphometric, physico-chemical and biotic factors could confound these relationships. Once removed the lake maximum depth influence, the biomass of small zooplankters ( $\leq 202\text{-}500\ \mu\text{m}$ ) was less important in colder and clearer lakes, while the biggest zooplankters ( $> 500\ \mu\text{m}$ ) were not influenced by these confounding factors. They rather negatively responded to the presence of planktivorous fish community (no piscivore species) and positively to high phosphorus concentration. The combined effect of these factors on the phosphorus-zooplankton biomass relationships could thus explained discrepancies observed in the literature about responses of size structure of zooplankton communities faced to phosphorus gradient. Bays and Crisman (1983) argued that only small zooplankters biomass increased with lake trophic, while Quiros (1991) and Pace (1986) found that both small and large zooplankters increased with lake trophic refuting the hypothesis that relative biomass changes with lake trophy. Although Pace (1986) indicated that the disparity could be related to difference either in climate of study areas or methodological approaches, all these studies (including Quiros' one) did not consider morphometric, physico-chemical and biotic confounding factors as we did. The influence of abiotic factors on zooplankton

Figure 5: Relationships between total phosphorus concentration and lake maximum depth (a), total zooplankton biomass (b),  $> 500 \mu\text{m}$  biomass (c), 202-500  $\mu\text{m}$  biomass (d), 100-202  $\mu\text{m}$  biomass (e), 53-100  $\mu\text{m}$  biomass (f). All relationships used average but raw data.



TOTAL PHOSPHORUS GRADIENT ( $\mu\text{g.litre}^{-1}$ )

biomass have already been detected in some studies (see Yan 1986 for a brief review). Fish predation was also identified as an important factors regulating zooplanktonic communities size structure (e.g. Brooks and Dodson 1965, Zaret 1980, Rodriguez et al. 1993). In the study lakes, the predation plays an important role in structuring zooplankton size structure. Our results support Pace (1986) who argued that while biomass of zooplankton is predictable from lake trophic state, the size structure of zooplankton communities is independent of lake trophic state. It was rather partly related to fish predation. Quiros (1991) indicated that lake with planktivorous fish showed lower macrozooplankton biomass when lake trophic state was reduced to a common denominator. The most obvious example of the predation effect was detected in Lake Desjardins which is unstratified, the most productive system in Laurentians and characterized by the absence of piscivore species. The zooplankton biomass in this lake is largely dominated by small zooplankton ( $\leq 202\text{-}500\ \mu\text{m}$ ) due to the strong predation by planktivorous species on large zooplankton  $> 500\ \mu\text{m}$ . As in Lake Desjardins, these large zooplankters, mainly represented by *Daphnia* sp., *Diaphanosoma* sp. and *Holopedium gibberum*, were not dominant in all lakes without piscivore species (Brassard, Corriveau, Cromwell, Triton). This predation effect allowed to improve the competitive advantage of smaller zooplankton (e.g. *Bosmina* sp., *Chydorus* sp., and copepods sp.) (Rodriguez et al. 1993, and references therein). These small organisms overdominated the zooplankton community compared to other lakes with the same level of TP, and then provides, especially for Lake Desjardins, strong discrepancies in the TP - zooplankton biomass relationships (Figs. 5b to 5f). The fish predation pressure, total phosphorus concentration, and thermal stratification (lake depth) are thus dominant gradient in structuring zooplanktonic community size structure (Keller and Conlon 1994, Stemberger and Lazorchak 1994, Hessen et al. 1995, this study). However at the opposite to all previous studies, our results were obtained from epilimnetic waters, while in other strata zooplankton biomass size structure can be affected by the identical or different mechanisms.

#### **4.4.4 Meta- and hypolimnetic environmental control of the zooplankton biomass**

We further hypothesized that the size fractions respond differently in both meta- and hypolimnetic waters to environmental variables, whereas either the biotic factors control the biomass of the largest zooplankton size fractions ( $202\text{-}500\ \mu\text{m}$  and  $> 500\ \mu\text{m}$ )

or the smallest fractions (53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$ ) are rather better related to abiotic factors. These hypotheses were confirmed in the metalimnion, where the 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass still negatively responded to lake maximum depth. On the other hand, the 202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$  biomass rather increased in metalimnion of lake of high transparency with 1 or 2 piscivore species or decreased in lakes without piscivores. The larger organisms were more susceptible to the visual predation than smaller ones and thus were primarily influenced by fish predation (Brooks and Dodson 1965, Zaret 1980). The > 500  $\mu\text{m}$  biomass responded positively to maximum depth in the metalimnion and as suggested by Rodriguez et al. (1993), this relationship could be related to a relative decrease in the intensity of competition, predation or could be due to the resource heterogeneity.

By removing the effect of maximum depth, we observed that the > 500  $\mu\text{m}$ , 202-500  $\mu\text{m}$  and 100-202  $\mu\text{m}$  were negatively correlated with the picophytoplankton concentration. The negative correlation was stronger for the > 500  $\mu\text{m}$  biomass suggesting a possible grazing effect on these small algae. As observed in enclosure experiments, the picophytoplankton concentration was higher in lakes with planktivorous species (no piscivore) and where low biomass of large zooplankton > 500  $\mu\text{m}$  occurred (Mazumder et al. 1988, Mazumder et al. 1990b). Large zooplankters are recognized for their highest efficiency to graze on broader range (1 to 50  $\mu\text{m}$ ) of organisms and particles (Stockner and Porter 1988). However, nanophytoplankton seem to be more readily grazed by macrozooplankton than are picophytoplankton and it would appear that predation by flagellates may be an extremely important step in the transfer of picophytoplankton carbon to larger metazoans. This statement could explain the positive relationship between 53-100  $\mu\text{m}$  and picophytoplankton since grazing efficiency of small zooplankton is less important due to their highest selectivity (Mazumder et al. 1990b). However, this positive association could also be related to the fact that either small species are too insufficient filterers to survive in low phytoplankton concentrations in presence of larger ones (Gliwicz 1977) or because this fraction (53-100  $\mu\text{m}$ ) was contaminated by algae and detritus according to our size fractionation methodology and then partly responded as an algae fraction.

In hypolimnetic waters, our hypothesis of biotic or abiotic control was partly rejected since 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass were highly correlated to biotic factors, such as microphytoplankton concentration, while 202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$  biomass were rather more important in hypolimnion of lakes with deep mixing zone and



more oxygenated waters. As we mentioned for the metalimnion and in the result section, we believe that strong correlation between 53-100  $\mu\text{m}$  and 100-202  $\mu\text{m}$  biomass with either microphytoplankton or alkalinity could be partly the result of the presence of algae in these small fractions due to our size fractionation methodology. The contamination by detritus and algae seemed more important in hypolimnetic samples. On the other hand, rotifer species, which are the main organisms of the 53-100  $\mu\text{m}$  and 100-202 fractions (Table IV), were also dominant in hypolimnion of lakes with both anoxic waters and shallow mixing depth. These two characteristics strongly regulate hypolimnetic occurrence of these organisms (Stemberger 1995, and references therein). The more important 202-500  $\mu\text{m}$  and > 500  $\mu\text{m}$  biomass in hypolimnion could be traduced as an avoidance behaviour for these fractions face to planktivorous. The hypolimnetic waters, especially well oxygenated, offer a refuge for large zooplankton fractions from surface turbulence and fish predation occurring in surface layers (Pinel-Alloul et al. 1988, Tessier and Horwitz 1990, Wright and Shapiro 1990). The hypolimnion is a region of low light intensity and low temperature that are inhabitable by herbivores but not by their predators (Shapiro 1990). These results agree with Masson and Pinel-Alloul (1998) who used this fractionation methodology and showed that the vertical distribution of the zooplankton biomass size structure is function to both either avoidance of potential predators or occupation of the best physico-chemical environment. Thus, large zooplankton may persist in the presence of abundant planktivores when a spatial or visual refuge exists (Wright and Shapiro 1990). The > 500  $\mu\text{m}$  fraction was mainly dominated by *Daphnia* species and these organisms are recognized to migrate vertically, whereas the depth and the patterns of migration depend on the intensity of planktivory in stratified lakes (Lampert and Taylor 1985, Dini and Carpenter 1991).

#### 4.5 CONCLUSIONS AND FUTURES PERSPECTIVES

The presence and distribution of species could not be only explained by surface water quality, since water quality parameters in lakes are seldom uniform from top to bottom, organisms that are mobile and can sense the condition of their environment can move to more favourable areas (Havas and Rosseland 1995). The organization of the zooplanktonic size communities in the water column varies according to multiple abiotic and biotic factors. Productivity is probably the most important process regulating zooplankton biomass in Shield lakes (lake depth and phosphorus concentration), but other abiotic and biotic forces, especially planktivory and food resource, regulate the size

structure of communities and their vertical distribution. This study provide evidence that interaction between zooplankton and abiotic and biotic bottom-up and top-down forces varied with scale of observation, but did not consider microbial food web. Future works should consider bacterial and flagellate communities because either they has been identified as important component in the food webs of shield lakes or their abundance is also scale dependent (Gasol et al. 1995). Our results was also realized on a narrow range of lake productivity (seasonal mean : 3-34  $\mu\text{g.L}^{-1}$ ). Wider range of phosphorus concentration must be explored, since fish predation becomes increasingly important in determining zooplankton species composition in meso- to eutrophic lakes (Hessen et al. 1995). Important changes also occur in the size structure and species composition of algae and fish as eutrophication proceeds (Persson et al. 1988, Watson and McCauley 1988, Masson, Pinel-Alloul and Smith, unpublished data). Although we worked at three stations, horizontal variability was not strongly investigated, whereas for instance aggregation phenomena, Diel Horizontal Migration (DHM) and habitat heterogeneity may occur (Pinel-Alloul et al. 1988, Masson and Pinel-Alloul 1998, and references therein). Thus, relationships between zooplankton communities with the suite of limnological conditions, both biotic and abiotic, as well as the suite of prey resources available are necessarily complex and must be investigated at different spatio-temporal scales.

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## 5.0 DISCUSSION GÉNÉRALE ET PERSPECTIVES

Depuis les années 1960, la majorité des travaux portant sur les communautés zooplanctoniques ont permis de reconnaître que la plupart des organismes étaient distribués en amas, nuées, essais ou agrégats (Pinel-Alloul 1995). Plusieurs études ont été menées afin d'identifier, d'évaluer et/ou de prédire de telles structures spatiales selon diverses échelles d'observations (Downing et al. 1987; Downing 1991 et Horne et Schneider 1995). Ces estimations de l'hétérogénéité, faisant référence à l'hétérogénéité mesurée (Smith 1972), ont ainsi permis aux écologistes de se doter d'outils ayant pour but, d'une part de maximiser l'échantillonnage et l'estimation des densités zooplanctoniques, et d'autres part de comparer les écosystèmes lacustres entre eux selon diverses échelles d'observation. Cependant, ces outils ne permettent en rien de comprendre les processus générateurs sous-jacents qui induisent les différents patrons de répartition des organismes. C'est plutôt l'hétérogénéité fonctionnelle (Smith 1972), qui permet de faire le lien entre les facteurs environnementaux et la répartition spatiale des organismes planctoniques. Bien que l'hétérogénéité fonctionnelle est biologiquement plus pertinente, elle a été beaucoup moins explorée jusqu'au début des années 1990 (Pinel-Alloul 1995). Ainsi des travaux comme ceux réalisés au cours de cette thèse apportent de l'information complémentaire et indispensable à la compréhension des phénomènes induisant l'hétérogénéité spatiale des organismes planctoniques.

Les objectifs de ce projet étaient de (1) déterminer l'hétérogénéité spatiale de la biomasse et de la structure en taille des communautés planctoniques aux échelles intra- et inter-lacs et (2) d'évaluer la contribution relative ou individuelle des facteurs environnementaux ascendants "Bottom-Up" et/ou descendants "Top-Down" à l'origine de cette hétérogénéité. On sait déjà d'une part, que l'hétérogénéité spatiale du zooplancton se manifeste à des échelles spatiales hiérarchiques (Haury et al. 1978; Imboden 1990; Pinel-Alloul et Pont 1991) et que d'autre part, les forces abiotiques et biotiques sous-jacentes de l'environnement cascaded des plus grandes à des plus petites échelles spatiales (Mackas et al. 1985; Barry et Dayton 1991; Pinel-Alloul 1995). Suivant ces deux concepts, les processus générateurs de l'hétérogénéité spatiale des communautés planctoniques différeront définitivement selon l'échelle d'observation (Malone et McQueen 1983; Pinel-Alloul et Pont 1991).

A l'échelle intra-lac, les travaux de Pinel-Alloul et al. (1988) et de Pinel-Alloul et Pont (1991) ont clairement établi que le maximum d'hétérogénéité spatiale du zooplancton

survenait sur l'axe vertical (colonne d'eau). Cependant, en travaillant à de plus grandes échelles spatiales horizontales que celles étudiées dans nos travaux, on se rend compte que l'hétérogénéité horizontale peut être aussi importante sinon plus importante que l'hétérogénéité verticale. L'échantillonnage de 30 stations réparties sur l'ensemble du lac Geai, a permis de constater que la distribution de la biomasse zooplanctonique et de ses 4 classes de taille ( $> 500 \mu\text{m}$ ;  $202 \text{ à } 500 \mu\text{m}$ ;  $100 \text{ à } 202 \mu\text{m}$ ;  $53 \text{ à } 100 \mu\text{m}$ ) était aussi hétérogène sur l'axe horizontal que sur l'axe vertical (**Chapitre 1**). Le même phénomène a été observé pour la distribution des daphnies et des copépodes du lac Annecy étudiée au cours d'un cycle nyctéméral (**Chapitre 2**). Dans ce lac sub-alpin, de grandes variations spatiales horizontales ont été observées à l'échelle du kilomètre.

De tels patrons de répartitions sont assez contrastants avec l'idée que le maximum d'hétérogénéité spatiale s'observe sur l'axe vertical. Cependant, cette forte hétérogénéité horizontale a été détectée parce que les études aux lacs Geai et Annecy ont été conduites à de grandes échelles spatiales horizontales. A l'échelle de quelques stations, et selon les méthodes d'échantillonnage conventionnelles, il est difficile d'identifier de tels patrons. Nos travaux permettent de réaliser l'importance de l'hétérogénéité horizontale dans l'étude des phénomènes spatiaux des communautés planctoniques, d'identifier les phénomènes en cause, et appuient les arguments selon lesquels la réponse des organismes face aux facteurs environnementaux dépend de l'échelle d'observation (Malone et McQueen 1983; Pinel-Alloul 1995).

Considérant les deux sources spatiales de variabilité (**Chapitre 4**), soit intra- (entre les strates) et inter-lacs (entre les lacs), on constate que les différences de biomasse zooplanctonique entre les lacs constituent la plus grande source de variation. Cependant, des fortes interactions lac-strate indiquent que les variations verticales de la biomasse zooplanctonique ne sont pas constantes d'un lac à l'autre. La diminution de la biomasse zooplanctonique de la strate épilimnétique vers l'hypolimnion n'est pas nécessairement une généralité des écosystèmes lacustres étant donné que les plans d'eau diffèrent selon leurs caractéristiques abiotiques et biotiques. Ces résultats, ainsi que ceux obtenus aux lacs Geai et Annecy, supportent l'hypothèse que la variation spatiale de la biomasse ou de la densité planctonique augmente avec l'échelle d'observation (Haury et al. 1978; Pinel-Alloul et al. 1996). La détermination des principales sources de variations de la biomasse planctonique est une étape cruciale dans l'étude des communautés planctoniques puisqu'elle permet d'une part, d'obtenir une meilleure description du dynamisme des communautés et d'autre part, de maximiser l'identification des mécanismes impliqués aux

échelles pertinentes (Resh et Rosenberg 1989; Lewis et al. 1996; Rundle et Jackson 1996). Imhof et al. (1996) mentionnent d'ailleurs que pour toute échelle d'observation, il est nécessaire de regarder dans un premier temps à de plus grandes échelles spatiales pour comprendre le contexte, et dans un deuxième temps à de plus petites échelles spatiales pour déterminer les mécanismes sous-jacents.

Plusieurs contradictions au sujet du contrôle "Bottom-up" ou "Top-Down" des communautés aquatiques dans la littérature proviennent du fait que l'interprétation des patrons et des processus originent de diverses échelles d'observation (Wiens et al. 1986; Frost et al. 1988). Un des défis actuels pour les écologistes n'est donc pas de déterminer quels sont les forces "Bottom-Up" et/ou "Top-Down" qui influencent les communautés planctoniques, mais bien à quelles échelles l'ensemble de ces forces prédominent (Hunter et Price 1992), et quelle est leur contribution relative. Les forces "Top-Down" semblent les plus importantes dans le contrôle de la structure en taille et de la répartition des communautés planctoniques à l'échelle intra-lac. La densité et la structure en taille des prédateurs invertébrés (*Chaoborus* spp.) du lac Geai ont été identifiés comme les principaux facteurs de régulation de la répartition spatiale horizontale et verticale de la biomasse zooplanctonique (**Chapitre 1**). Cependant, la physico-chimie des eaux (conductivité, oxygène, température) influencent de façon complémentaire et non indépendante les forces "Top-Down" dans le contrôle de la répartition horizontale et verticale des organismes, tel que maintenant reconnu dans la littérature (Carpenter 1988; Hunter et Price 1992; Power 1992; Arnott et Vanni 1993; Pinel-Alloul 1995; Pinel-Alloul et al. 1995).

Bien que les facteurs abiotiques n'ont pas été considérés dans l'étude de la répartition horizontale et verticale du zooplancton réalisée dans le lac Annecy, nos résultats indiquent que les patrons de distribution du zooplancton observés au cours du cycle nycthéral pourraient être influencés par ceux des poissons (**Chapitre 2**). La réponse des organismes face à la prédation s'est traduit à la fois par des migrations journalières verticales (DVM), ainsi que par des migrations horizontales à grandes échelles. Plusieurs travaux ont reconnu à juste titre l'importance de la prédation comme facteur de contrôle de la structure en taille et de la répartition du zooplancton lacustre (Brooks et Dodson 1965; Zaret et Suffern 1976; Kairesalo 1980; Kerfoot 1987; Gliwick et Rybowska 1992; Ringelberg 1993).

A l'échelle inter-lacs, les travaux réalisés au cours des dernières décennies indiquent que la biomasse algale est dépendante des effets "Bottom-Up", soit principalement via la concentration en phosphore (ex: Vollenweider 1968; Dillon et Rigler 1974; Dillon et al. 1988; Seip 1990; Chow-Fraser et al. 1994; Pinel-Alloul et al. 1996; **Chapitre 3**). Cependant, cette relation peut être influencée par de nombreux facteurs physiques, chimiques et/ou biologiques (ex: Nicholls et Dillon 1978; Ahlgren et al. 1988; Seip et Goldstein 1994; Mazumder 1994a,b). La géologie est un de ces facteurs (Dillon et Kirchner 1975; Gliber et Silberbauer 1985; Duarte et Kalff 1989) et notre étude montre que les lacs du bouclier canadien présentent effectivement des concentrations en chlorophylle *a* moins importantes pour une même concentration de phosphore que les lacs d'autres régions géologiques (**Chapitre 3**).

Bien que les effets "Bottom-Up" expliquent les variations en chlorophylle *a* à l'échelle inter-lacs (phosphore et géologie), la complémentarité des effets "Bottom-Up" et "Top-Down" (broutage) sur la productivité des lacs s'observe non pas au niveau de la biomasse totale, mais plus spécifiquement au niveau de la structure en taille de la communauté algale ( $> 20 \mu\text{m}$ ;  $< 20 \mu\text{m}$ ;  $3\text{-}20 \mu\text{m}$ ;  $< 3 \mu\text{m}$ ). Tel que démontré dans notre étude (**Chapitre 3**) et par Watson et Kalff (1981) et Watson et McCauley (1988), les algues de grandes tailles prédominent à de fortes concentrations en phosphore, tandis que les algues de petite taille sont plus importantes en milieu oligotrophe. Cette dominance des grosses algues dans les lacs plus productifs implique soit un taux de croissance plus élevé, soit un contrôle des petites algues par le broutage zooplanctonique (Chow-Fraser et al. 1994; Mazumder 1994b). L'identification de l'alcalinité comme variable complémentaire à nos modèles de prédiction (TP-Chl *a* pour les algues  $< 20 \mu\text{m}$  et pour le nanophytoplancton) permet de proposer la seconde hypothèse. On observe une diminution graduelle des petites algues en relation avec l'augmentation de l'alcalinité des eaux. Plusieurs travaux reconnaissent la dominance des gros herbivores dans les milieux plus alcalins et l'abondance des petits cladocères dans les lacs plus acides ou près de la neutralité (Tessier and Horwitz 1990; Pinel-Alloul et al. 1990; Pinel-Alloul et al. 1995). Ainsi, le gros zooplancton herbivore plus abondant dans les lacs alcalins et productifs influencerait la structure en taille de la communauté algale. Un tel contrôle "Top-Down" sur la biomasse algale suivant un gradient de phosphore a été proposé dans la littérature, plus spécifiquement au niveau de la biomasse algale totale (chlorophylle *a* totale) (Mazumder 1994ab, Taylor et Carter 1997), mais pas au niveau de la structure en taille de la communauté tel que suggéré dans ce travail (**Chapitre 3**).

La prédominance des facteurs "Bottom-Up" à l'échelle inter-lacs sur le contrôle des communautés planctoniques est également applicable au zooplancton (**Chapitre 4**). La productivité des systèmes aquatiques, qui est principalement reliée à la profondeur des lacs, au taux de renouvellement des eaux et à la concentration en phosphore total, est le facteur le plus important expliquant la variabilité épilimnétique de la biomasse zooplanctonique totale et de ses classes de taille à l'échelle inter-lac. Bien que les facteurs abiotiques "Bottom-Up" influencent la biomasse zooplanctonique, les facteurs biotiques "Top-Down" (prédation par les poissons) contribuent à modifier la structure en taille de la communauté et sa distribution verticale dans les lacs. Ces résultats permettent d'appuyer les arguments de Pace (1986) qui conclut que bien que la biomasse zooplanctonique est positivement reliée à l'augmentation du phosphore, les variations de la structure en taille de la communauté n'en dépend pas. Ainsi, la structure en taille à l'échelle inter-lacs est contrôlée par les poissons, tel qu'également observé par Rodriguez et al. (1993) et Pinel-Alloul et al. (1995). L'absence de poisson piscivore (abondance de planctivores) dans les eaux lacustres implique une dominance de la biomasse microzooplanctonique, une pression de prédation plus importante sur le macrozooplancton et leur migration en eaux méta- et hypolimnétique. Étant moins influencé par la prédation, le microzooplancton répond davantage aux variations physico-chimiques tels qu'observé dans les eaux métalimnétiques. Ainsi la réponse du zooplancton est dirigée à la fois par les forces "Bottom-Up" et "Top-Down" et varie selon le type de communauté zooplanctonique (micro ou macrozooplanctonique).

Globalement (**Chapitres 1, 2, 3 et 4**), l'ensemble de nos travaux appuient fortement le modèle de Pinel-Alloul (1995) impliquant un contrôle dominant des facteurs biotiques (prédation) à petites échelles (intra-lac, inter-strates) et la suprématie des facteurs abiotiques (physico-chimie et morphométrie) à grandes échelles (inter-lacs). On constate également la complémentarité des facteurs abiotiques et biotiques "Bottom-Up" et biotiques "Top-Down" dans le contrôle et la biomasse et de la structure en taille des communautés planctoniques quelle que soit l'échelle d'observation, appuyant ainsi l'hypothèse du contrôle multiple des communautés planctoniques (Pinel-Alloul et al. 1995). Les deux études menées à l'échelle inter-lacs (**Chapitres 3 et 4**), permettent également d'établir que les facteurs Bottom-up contrôlent la biomasse planctonique (algue et zooplancton), tandis que les facteurs Top-Down influencent leur structure en taille. Ces interactions entre effets "Bottom-Up" et "Top-Down" ont largement été explorées en milieux contrôlés (biomanipulation dans les plans d'eau et expériences en enclos) (ex: Carpenter et al. 1987; Vanni 1987; Leibold 1989; Mazumder et al. 1988; Mazumder et al.

1990abc; Lazzaro et al. 1992; Mazumder et al. 1992; Mazumder et Lean 1994; Elser et al. 1995; Pérez-Fuentetaja et al. 1996), mais peu d'études se sont attardées à évaluer l'influence relative de ces forces en milieux naturels (Rodriguez et al. 1993; Gasol et al. 1995; Pinel-Alloul et al. 1995; cette thèse). Power (1992) indique que l'efficacité relative des forces "Top-Down" et "Bottom-Up" dépend en partie de la capacité avec laquelle les consommateurs peuvent exploiter leurs proies. L'hétérogénéité des environnements lacustres fournit diverses possibilités aux organismes d'échapper à la prédation (migration littoral-pélagique, migration verticale, agrégations ou dispersion, développement saisonnier des communautés, etc...) et ainsi limiter la prédiction des réponses des organismes aux changements abiotiques et biotiques. Ces comportements ne peuvent pas être considérés dans des expériences contrôlées.

Bien que les hypothèses des modèle "Bottom-Up"- "Top-Down" et des interactions trophiques en cascade aient été appuyées récemment (Brett et Goldman 1996,1997), la réponse des effets "Top-Down" au niveau des producteurs primaires demeure assez variable. De plus, les réponse du phytoplancton et du zooplancton à l'addition des nutriments ne suivent pas les prédictions théoriques selon le nombre de niveaux trophiques. La difficulté d'obtenir des réponses claires aux modèles actuels vient en partie du fait que l'on considère encore la biomasse totale des groupes planctoniques au lieu d'utiliser la structure en taille des communautés. Selon Mazumder et al. (1992), les impacts de la prédation aux niveaux du zooplancton et du phytoplancton sont plus importants au niveau de leur taille qu'au niveau de leur biomasse totale. Suivant les indicateurs "TD" que nous avons retenus, notre étude montre d'ailleurs les rôles respectifs que jouent les forces "Bottom-Up" (biomasse) et "Top-Down" (structure en taille) dans les variations des communautés planctoniques (zooplancton et phytoplancton). McQueen et al. (1989) concluaient que les effets en cascade de la prédation ne permettaient pas de prédire les changements des communautés planctoniques (biomasse du zooplancton et chlorophylle *a* totale) et la transparence des eaux du lac St-Georges, et que ce résultat pourrait être relié aux effets des nutriments, de la composition et de la structure en taille du zooplancton. Les interactions entre les communautés planctoniques et leurs réponses à diverses caractéristiques environnementales, tant biotiques qu'abiotiques, dépendent initialement de la structure en taille des individus. Comme l'indique Hunter et Price (1992), ce ne sont pas toutes les plantes qui sont ingérables, les herbivores ne sont pas tous dommageables, les prédateurs ne sont pas tous efficaces et les environnements ne sont pas tous hospitaliers. Cependant, toutes ces variables interagissent entre elles et dépendamment de la structure des communautés, la réponse des organismes sera variable.

La taille des organismes planctoniques est particulièrement importante dans le recyclage (taux et ratio N:P) ou le piégeage des nutriments (ex: Elser et al. 1988; Sterner 1990; Sterner et al. 1992). Le recyclage des nutriments (via le zooplancton et les poissons) est d'ailleurs un des phénomènes qui pourraient expliquer la réponse des communautés phytoplanctoniques aux effets "Top-Down" (Vanni et Layne 1997; Vanni et al. 1997). L'étude des interactions trophiques et de l'impact des forces "Bottom-Up" et "Top-Down" passe donc par une bonne compréhension des interactions se déroulant au niveau de la structure des communautés planctoniques.

La chaîne microbienne a été jusqu'à maintenant peu incorporée dans les études portant sur les relations trophiques et le rôle des forces "Bottom-Up" et "Top-Down" sur les communautés planctoniques (ex: Weisse 1991; Gasol et Vaqué 1993; Gasol 1994; Pace et Cole 1994). Son rôle dans le fonctionnement des écosystèmes limnétiques est de plus en plus reconnu (Riemann 1985; Porter et al. 1988; Stockner et Porter 1988; Pace et al. 1990; Arndt 1993; Porter 1996). Plusieurs travaux ont d'ailleurs démontré l'importance des flagellés hétérotrophiques, des ciliés et rhizopodes dans la composition de la biomasse planctonique (Berninger et al. 1991; Jürgens et Güde 1991; Arndt et Mathes 1991). Selon Caron et Goldman (1990), les protistes hétérotrophiques joueraient un rôle crucial non seulement dans la régulation de l'abondance des bactéries, mais également dans le recyclage des nutriments que ces organismes accumulent. Récemment Gasol et al. (1995) indiquaient que l'importance absolue et relative des facteurs abiotiques et biotiques dans la prédiction de l'abondance des flagellés hétérotrophes était fonction de l'échelle d'observation et relevaient l'impact du macrozooplancton sur l'abondance de ces organismes. Ces résultats démontrent la complexité des écosystèmes lacustres et des interactions qui s'y déroulent. Le couplage entre la chaîne microbienne et le réseau pélagique semble cependant négligeable en absence de daphnies (Lyche et al. 1996). Le zooplancton joue un rôle clé dans le transfert de l'énergie vers les niveaux trophiques supérieurs. L'étude des relations entre ce maillon et la chaîne microbienne est donc primordiale à une meilleure compréhension des forces "Bottom-Up" et "Top-Down" dans le contrôle des communautés biologiques selon différentes échelles d'observation. La complexité des relations trophiques et leurs fluctuations face aux caractéristiques environnementales requièrent ainsi une approche multidisciplinaire (Carpenter et al. 1987; Dunson et Travis 1991) qui devrait être dirigée à définir, d'une part les interactions à différents niveaux de la chaîne trophique (Hunter et Price 1992), et d'autre part les concepts à des échelles spatiales et temporelles appropriées (Power 1992).



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## 7.0 APPENDICES

### Appendice 1. Contributions scientifiques

#### 1.1 *Articles de collaboration et autres publications.*

DUTILLEUL, P., S. MASSON, and B. PINEL-ALLOUL. A statistical procedure for assessing the covariance separability of spatio-temporal environmental data. *Environmetrics*. (sous analyse).

MAZUMDER, A., and S. MASSON. Zooplankton stoichiometry in relation to lake eutrophic gradient and zooplankton community (sous analyse).

MICHARD, V., MASSON, S., and B., PINEL-ALLOUL. Étude du contrôle environnemental de la structure en taille de la communauté zooplanctonique des lacs des Laurentides (Québec) déterminée par analyseur optique de plancton (OPC). (en préparation).

AVOIS, C., P. LEGENDRE, S. MASSON, and B., PINEL-ALLOUL. 1998. To what extent may the sampling strategy interfere with the study of spatio-temporal variation of zooplankton communities ? (bientôt soumis à Ecology).

MASSON, S., B. PINEL-ALLOUL, G. MÉTHOT and N. RICHARD. Comparison of nets and pump sampling gears to assess zooplankton vertical distribution in stratified lakes. (en préparation).

MASSON, S., G. DESROSIER, et C. RETIÈRE. 1995. Périodicité d'alimentation du polychète Nereis diversicolor (O.F. Müller) selon les caractéristiques de la marée. *Écoscience* 2 (1) : 20-27.

MIRON, G., G. DESROSIERS, C. RETIÈRE et S. MASSON. 1992. Variations in time budget of the polychaete *Nereis virens* as a function of density and acclimation after introduction to a new burrow. *Marine Biology*, Vol. 114, pp. 41-92.

### ***1.2 Rapports de recherche et autres documents produits.***

MASSON, S., B. PINEL-ALLOUL, P. EAST, P. MAGNAN, G. HOGUE, et A. BARABÉ. 1999. Plan de gestion et de surveillance écologique des écosystèmes lacustres du Parc National de la Mauricie. Développement d'indicateurs de l'intégrité écologique des écosystèmes aquatiques du Parc National de la Mauricie. Pour le Service de la conservation des ressources naturelles. Parc Canada. (dépôt Mars 1999).

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- MASSON, S., B. PINEL-ALLOUL, M. LAPOINTE, P. MAGNAN, G. HOGUE, et A. BARABÉ. 1997. Typologie des caractéristiques biophysiques, des communautés de poissons, et des aspects sociologiques des écosystèmes lacustres du Parc National de la Mauricie. Rapport d'étape pour le Service de la conservation des ressources naturelles. Parc Canada.
- MASSON, S. et B. PINEL-ALLOUL. 1994. Étude limnologique du lac Cristal. Rapport de recherche présenté à l'association des propriétaires du lac Cristal, St-Calixte, prov. de Québec, 18 pages.
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### 1.3 *Communications avec jury.*

- MASSON, S, B. Pinel-Alloul, N. Angeli and J. Guillard. Janvier 1997. Distribution spatio-temporelle de la densité zooplanctonique et de la biomasse ichtyaire dans un lac subalpin. Cinquième Conférence Internationale des Limnologistes d'Expression Française (CILEF V), Namur - Belgique (7 - 11 Juillet, 1997).
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#### 1.4 Communications sans jury.

- MASSON, S., N. Angeli, J. Guillard, et B. Pinel-Alloul. 1997. Contrôle environnemental de la répartition spatio-temporelle du zooplancton dans un lac sub-alpin. Conférence du Groupe d'Écologie des Eaux Douces, Univ. de Montréal.
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