UNIVERSITÉ DU QUÉBEC À MONTRÉAL

BIODIVERSITÉ DU ZOOPLANCTON CRUSTACÉEN DANS LES LACS: LES RÔLES DE L'HÉTÉROGÉNÉITÉ DU PHYTOPLANCTON ET DE LA DIVERSITÉ FONCTIONNELLE

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CRUSTACEAN ZOOPLANKTON BIODIVERSITY IN LAKES: ROLES OF PHYTOPLANKTON RESOURCE HETEROGENEITY AND FUNCTIONAL DIVERSITY

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RÉSUMÉ

L'objectif principal de cette étude était d'examiner comment la biodiversité du zooplancton est affectée par le phosphore total et les changements de l'hétérogénéité des ressources et de l'abondance relative du phytoplancton. Les études empiriques montrent assez clairement que la diversité des espèces de zooplancton est plus importante lors d'un niveau intermédiaire de production par le phytoplancton. Les études théoriques ont généré un certain nombre d'hypothèses pouvant expliquer le fait que cette relation existe. La présente étude a pour but de tester deux de ces hypothèses : soit les hypothèses « resource ratio » et « spatial resource heterogeneity ». Un objectif additionnel de cette étude était d'observer comment les patrons de richesse spécifique et de diversité fonctionnelle répondent à des gradients environnementaux.

Dans le chapitre 1, j'ai effectué une revue de littérature des 50 dernières années sur le zooplancton d'Amérique du Nord et j'ai examiné la possibilité d'utiliser la diversité fonctionnelle dans les études de zooplancton. Un dendrogramme des communautés régionales d'espèces communes de zooplancton du nord-est de l'Amérique du Nord a été généré pour montrer le contraste entre les regroupements taxonomiques des espèces et ceux effectués en utilisant des traits fonctionnels. Bien que dans la littérature, les données fonctionnelles ne soient pas complètes, une combinaison des traits fonctionnels de la littérature et de ceux pouvant être mesurés sur le terrain a été utilisée pour décrire les niches fonctionnelles des espèces de zooplancton.

Dans le chapitre 2, les traits mesurés au laboratoire, ainsi que ceux obtenus de la revue de littérature effectuée au chapitre 1, ont été utilisés pour mesurer la diversité fonctionnelle de 18 lacs de l'Estrie. Une relation curvilinéaire a été trouvée entre la diversité fonctionnelle et la distribution spatiale des algues bleues-vertes, permettant ainsi de supporter l'hypothèse « spatial resource heterogeneity ». Bien qu'une relation curvilinéaire entre la diversité fonctionnelle du zooplancton et le ratio des algues brunes sur les algues bleues-vertes ait été observée, une plus petite proportion de la variation dans la diversité fonctionnelle du zooplancton était expliquée comparativement à celle expliquée par la distribution spatiale des algues bleues-vertes. De façon générale, les mesures de diversité fonctionnelle étaient plus fortement reliées à les variables indépendantes environnementales qu'à la richesse spécifique.

À travers les résultats obtenus, il est possible de conclure que l'abondance et la distribution des ressources jouent un rôle important dans la structure des communautés de zooplancton, et que les mesures de diversité fonctionnelle seront bénéfiques à la recherche écologique portant sur la biodiversité des lacs.

ABSTRACT

The main objective of this study was to investigate how zooplankton biodiversity is affected by total phosphorus concentration and the associated differences in phytoplankton resource heterogeneity and relative abundance. Empirical studies show overwhelmingly that zooplankton species diversity is highest at an intermediate rate of phytoplankton production. Theoretical studies have generated a number of hypotheses to explain why this general relationship exists. Of these, the current study tested two hypotheses: the spatial resource heterogeneity and the resource ratio hypothesis. An additional objective in this study was to observe how patterns of species richness and functional diversity respond to gradients of productivity, resource ratios, and resource heterogeneity.

In Chapter I, I reviewed the literature of North American zooplankton from the past 50 years and examined the feasibility of using functional diversity measures in zooplankton studies. While data was lacking for cyclopoids, data for cladoceran species was more abundant. A regional community dendrogram for common northeastern North American zooplankton species was generated to demonstrate the contrast between taxonomic species groupings and those made using functional traits. While functional data in the literature is not complete, a combination of functional traits from the literature and those that can be measured in the field could be used to generate functional niches of zooplankton species.

In Chapter II, traits measured in the lab and obtained from the review in Chapter I were used to measure the functional diversity of 18 lakes in the Eastern Townships of Quebec. I found a curvilinear relationship between functional diversity and blue-green algal spatial distribution, supporting the spatial resource heterogeneity hypothesis. While a curvilinear relationship between zooplankton functional diversity and the ratio of brown to blue-green algae was observed, a smaller proportion of the variation in zooplankton functional diversity was explained than that explained by blue-green algal spatial distribution. In general functional diversity measures were more strongly related to their environmental explanatory variables (TP, phytoplankton heterogeneity, and relative abundance) than to species richness.

On the basis of these results, I conclude that resource abundance and distribution play an important role in structuring zooplankton communities, and that functional diversity measures will be beneficial to ecological research on biodiversity in lakes.

INTRODUCTION

Les activités humaines ont conduit à des changements considérables dans les dynamiques communautaires des écosystèmes entraînant des pertes ou des invasions d'espèces, avec des effets subséquents sur la façon dont les écosystèmes fonctionnent (Hooper *et al.*, 2005). Ces changements dans la fonctionnalité des écosystèmes (Symstad & Tilman, 2001) comprennent la rétention des nutriments et du carbone, la productivité, et la respiration communautaire (Naeem & Wright, 2003) ainsi que la capacité à conserver ces fonctions lors de perturbations de modifications dans les conditions environnementales (résilience) (Walker, Kinzig, & Langridge, 1999). Afin de chercher à maintenir certaines fonctionnalités d'un écosystème, il est important de comprendre les facteurs augmentant ou diminuant biodiversité. La présente étude vise à expliquer la biodiversité du zooplancton dans les lacs en utilisant des variables environnementales locales.

Cette étude se concentre, en particulier, sur les effets de la variabilité et des abondances relatives des ressources (soit le long du profil de profondeur d'un lac) sur la diversité du zooplancton. Il a été démontré que la structure verticale des lacs et le régime de mélange, qui y est associé, sont des facteurs importants influençant la structure communautaire du biote, particulièrement le plancton (Harris, 1999). Bien que nous sachions que les lacs se stratifient fortement en été (c'est-à-dire qu'il existe une formation de gradients de températures), peu est connu sur l'influence des différentes formes de cette stratification (par exemple la force, la durée, la forme) sur le développement des communautés. Les activités humaines altèrent les régimes de mélange directement avec les changements climatiques (Lehman, 2002) mais aussi indirectement à travers des changements dans la pénétration de la lumière due à l'eutrophisation (Interlandi & Kilham, 2001; Fairchild, Anderson, & Velinsky, 2005) ou bien à travers des changements dans les bassins-versants (Northcote *et al.*, 2005), comme lors de déforestation ou d'altérations des zones humides. Avec ces changements dans le mélange des lacs, des modifications dans la composition et la distribution du phytoplancton sont prévisibles (Reynolds, Wiseman, & Clarke, 1984). Ainsi, il est à envisager que les propriétés physico-chimiques des lacs, qui influencent les régimes de mélange et la structure de la thermocline, devraient en retour affecter la structure communautaire du zooplancton. Plus précisément, cette étude examinera comment la biodiversité du zooplancton est affectée par le phosphore total et ainsi l'hétérogénéité et l'abondance relative du phytoplancton.

La principale question posée par cette étude est donc la suivante : comment les changements dans l'abondance et la distribution des ressources de phytoplancton affectent-ils la diversité des espèces de zooplancton?

Diversité dans les lacs

Une approche courante pour expliquer la diversité dans les lacs est celle basée sur la théorie de l'équilibre biogéographique des îles de MacArthur & Wilson (1967). Lorsque les lacs sont considérés comme des îles, les plus grands lacs devraient posséder des taux d'extinction plus bas, des taux d'immigration plus élevés, une plus grande hétérogénéité dans les habitats, ou une probabilité plus importante de trouver un plus grand nombre d'espèces dû à un effet d'échantillonnage. Un des tests les plus communs de cette théorie est la courbe « species-area », telle que proposée pour le zooplancton de 13 lacs de New York par Browne (1981). D'autres études supportent aussi l'idée que les plus grands lacs sont plus diversifiés (Fryer, 1985; Dodson, 1991; Dodson, 1992; O'Brien *et al.*, 2004). Dodson (1992) a cependant poussé davantage cette idée en montrant une relation significative entre la diversité du zooplancton, la superficie du lac, le nombre de lacs dans les 20 kilomètres aux alentours et le taux moyen de photosynthèse (une estimation de la productivité). Ces trois variables expliquaient 75% de la variation de la richesse spécifique (en log). Les deux variables les plus importantes pour l'explication de cette relation étaient la superficie du lac (linéaire) et sa productivité (parabolique), et il a été supposé que l'hétérogénéité de l'habitat (verticale, à travers la stratification, et horizontale, à travers les habitats littoraux) étaient les facteurs prédominants de cette relation.

L'étude de Dodson (1992) a fourni un support pour la courbe « species-area », ainsi que pour la courbe « species-productivity », et un appui additionnel pour une relation unimodale entre la diversité du zooplancton et la productivité primaire a été trouvé (Leibold, 1999; Waide *et al.*, 1999; Dodson, Arnott, and Cottinghamn, 2000). Cependant, lorsque les lacs sont séparés selon les catégories développées et non-développés (l'aire des developement et agriculture a cote de le lac), la courbe « species-area » ne fut retrouvée que pour les lacs développés (Hoffman & Dodson, 2005). La relation « species-productivity » était significativement positive pour les lacs non-développés mais significativement négative, avec un faible puissance pour les lacs développés. Ainsi, lorsque la courbe « species-area » et les courbes « species-productivity » sont prises en compte, la force relative de ces relations peut être affectée par d'autres facteurs tel que le degré d'influence anthropogénique.

Bien que ces études fournissent un aperçu de l'explication de la biodiversité de façon à émettre des hypothèses futures, elles ne sont pas explicatives de façon mécanistique. Une courbe « species-area » suggère la possibilité d'une plus grande hétérogénéité dans l'habitat, ou peut-être un effet de l'échantillonnage, mais n'indique pas directement quels facteurs, locaux ou régionaux, sont les facteurs prépondérants de diversité. Cependant, la relation « productivity-diversity » possède 4 hypothèses explicatives pour cette relation unimodale : « paradox of enrichment », « resource heterogeneity », « resource ratio », et « keystone predator » (Leibold, 1999).

Ainsi, bien que des études empiriques aient démontré à la fois l'hypothèse « productivity-diversity » et l'hypothèse « diversity-area », les mécanismes à l'origine de ces relations sont encore inconnus. La présente étude se concentre sur deux des hypothèses mentionnées précédemment : soit les hypothèses « resource ratio » et « resource heterogeneity » qui seront donc discutées plus en détail dans les pages suivantes.

Hypothèse « Resource Ratio »

Selon l'hypothèse « resource ratio », la diversité est affectée par les abondances relatives des ressources primaires et secondaires (Huisman & Weissing, 1995). En assumant que les espèces diffèrent pour des concentrations seuils d'une ressource donnée, le nombre d'espèces pouvant être supporté augmentera avec l'augmentation de la concentration de cette ressource (Schoener, 1976). Cependant, si certaines espèces ne dépendent pas uniquement de cette ressource primaire, mais dépendent aussi d'une ressource secondaire, alors la diversité sera maximisée lors d'un ratio intermédiaire de ressources primaire et secondaire (Huisman & Weising, 1995). Bien qu'il soit connu que l'abondance relative des algues bleues-vertes augmente avec l'augmentation de la productivité (Smith, 1983; Watson, McCauley, & Downing, 1997), nous ne savons pas si ces changements de l'abondance relative des ressources affectent la diversité du zooplancton. De plus, bien que certaines études aient expérimentalement démontré les préférences alimentaires du zooplancton en utilisant des cultures de phytoplancton et de bactéries (Bogdan & Gilbert, 1982; Richman & Dodson, 1983), peu est connu sur la façon dont les concentrations de larges groupes de phytoplancton dans les lacs pourront affecter la composition et l'abondance des espèces de zooplancton.

Hypothèse « Spatial Resource Heterogeneity »

L'hypothèse « spatial resource heterogeneity » souligne comment les ressources fluctuent dans le temps et l'espace. L'hétérogénéité de l'habitat dans l'espace et le temps a été une solution d'Hutchinson (1961) au « paradoxe du plancton ». L'explication de cette hypothèse est basée sur la supposition d'une exclusion compétitive selon laquelle il est à prévoir qu'une espèce devrait surpasser toutes les autres jusqu'à ce qu'une monoculture soit atteinte (Hardin, 1960). L'hypothèse « intermediate disturbance » (IDH) constitue la base de l'hypothèse « spatial resource heterogeneity ». En se référant à l'IDH, Connell (1978) suggéra que la richesse spécifique serait plus importante à un niveau intermédiaire d'hétérogénéité ou de perturbations. L'IDH est basée sur la supposition que les espèces subiront des substitutions en réponse à l'abondance et le type de ressources disponibles; certaines espèces seront compétitivement supérieures lors d'un certain ensemble de conditions environnementales alors que d'autres espèces seront compétitivement supérieures lorsqu'un autre ensemble de conditions environnementales sera présent (Abrams, 1984). Les fluctuations de ces conditions environnementales créeront donc des niches spatio-temporelles et ainsi réduiront les effets de l'exclusion compétitive dans les communautés (Tilman, 1994). À travers cette étude, je me concentrerai sur l'hypothèse « spatial resource heterogeneity » le long d'un gradient vertical de distribution du phytoplancton dans les lacs. Bien que l'IDH ait été confirmée dans des communautés de pâturages (Walker *et al.*, 1999), dans des communautés expérimentales de phytoplancton (Flöder & Burns, 2005) et dans des études sur des clones génétiques de *Daphnia* (Weider, 1992), l'IDH n'a pas encore été testée en référence avec l'hétérogénéité spatiale des ressources de communautés de zooplancton.

Qu'est-ce que la diversité?

Les patrons de diversité du zooplancton ont été traditionnellement expliqués par des études comparatives de lacs utilisant la richesse spécifique comme variable de réponse à l'environnement (Dodson, 1992; Dodson *et al.*, 2000; Jeppesen *et al.*, 2000). Cependant, en considérant comment les espèces répondront à des gradients environnementaux, on pourrait s'attendre à une mesure de la diversité prenant en considération la façon dont les espèces diffèrent écologiquement ou fonctionnellement afin de fournir plus d'informations. Des études utilisant des végétaux et portant sur la relation entre la diversité et la fonction d'un écosystème ont toutes abouti à une conclusion similaire, soit l'observation que les mesures fonctionnelles de la diversité expliquent un pourcentage plus important de la variation dans la fonctionnalité d'un écosystème (e.g. la productivité primaire, la retention des nutriments) que les mesures taxonomiques traditionnelles (Walker, 1991; Hooper & Vitousek, 1997; Tilman *et al.*, 1997; Walker *et al.*, 1999). De plus, l'utilisation de mesures de diversité fonctionnelle a été suggérée pour tester l'IDH, les hypothèses d'assurance et les renversements alternatifs d'état stable dans les lacs (Weithoff, 2003). La présente étude fera appel à une nouvelle approche en observant comment les patrons de richesse spécifique et de diversité fonctionnelle répondent à des gradients de productivité, des ratios de ressources, et l'hétérogénéité des ressources.

Hypothèses & vue d'ensemble

Chapitre I

Dans le chapitre I, une revue de la littérature des 50 dernières années sera effectuée afin de déterminer l'étendue des connaissances actuelles permettant une classification des niches fonctionnelles du zooplancton. La faisabilité d'appliquer des mesures de diversité fonctionnelle à des communautés de zooplancton de lacs sera examinée grâce à une recherche de littérature approfondie afin de résumer l'état actuel des connaissances sur les rôles fonctionnels du zooplancton. Les études fournissant des informations concernant le mode et le type d'alimentation, la croissance, la préférence d'habitat et les stratégies pour éviter la prédation sont discutées et résumées dans des tableaux. Ceux-ci pourront être utilisés pour l'élaboration de niches fonctionnelles d'espèces de zooplancton, en utilisant des méthodes telles que la diversité fonctionnelle (Petchey & Gaston, 2002) et la variance des traits (Norberg, 2004).

Hypothèse : Les différences taxonomiques entre les espèces ne refléteront pas les différences fonctionnelles entre les espèces. Certaines espèces de zooplancton qui devraient être hautement différentes basées sur leur taxonomie seront fonctionnellement similaires selon leurs traits fonctionnels étudiés. Inversement, certaines espèces seront plus dissemblables fonctionnellement que lorsque seule la taxonomie est utilisée.

Chapitre II

Dans le chapitre II, les données obtenues au Chapitre I ainsi que des données obtenues sur le terrain seront utilisées pour évaluer la diversité fonctionnelle des communautés de zooplancton retrouvées dans les lacs de l'Estrie. Cette mesure de la diversité fonctionnelle est comparée avec la richesse spécifique dans sa relation avec la productivité environnementale, les ratios de ressources limitantes et l'hétérogénéité spatiale des ressources.

1) L'hypothèse « Resource Ratio » : Les changements dans la productivité affectent la diversité des espèces en altérant les ratios relatifs des ressources primaires et secondaires. En se basant sur cette hypothèse, nous nous attendons à ce que la diversité du zooplancton soit plus importante lors d'un ratio intermédiaire d'une ressource primaire de phytoplancton sur une ressource secondaire.

2) L'hypothèse « Resource Heterogeneity » : La principale hypothèse à être explorée est que l'augmentation de l'hétérogénéité verticale à travers un coefficient de variation (CV) plus important de chlorophylle totale, d'algues vertes, d'algues bleues-vertes, de diatomées et chrysophytes, ou de cryptophytes permettra à un nombre plus important d'espèces de zooplancton de co-exister. Ainsi, il est à prévoir qu'une augmentation du CV de l'abondance de phytoplancton résultera en une augmentation de la diversité du zooplancton. En se basant sur l'IDH, nous nous attendons à ce que la diversité du zooplancton soit maximisée lorsqu'un niveau intermédiaire d'hétérogénéité de phytoplancton est présent.

3) Supposition de réponses divergentes des espèces : Puisque ces hypothèses sont basées sur la supposition que les espèces vont différer dans leurs réponses fonctionnelles à l'abondance d'une ressource, nous nous attendons à ce que l'abondance des espèces soit affectée différemment par la concentration ou le type de ressource. Par exemple, alors que certaines espèces seront plus abondantes dans les lacs contenant une importante abondance d'algues bleues-vertes, d'autres espèces seront plus abondantes dans les lacs contenant une faible abondance d'algues bleues-vertes.

4) L'hypothèse « Functional Species » : Finalement si la diversité fonctionnelle est une mesure reflétant plus les rôles écologiques des espèces, alors nous nous attendrions à ce que la diversité fonctionnelle du zooplancton soit reliée plus fortement à des influences environnementales.

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CHAPITRE I

FUNCTIONAL DIVERSITY OF CRUSTACEAN ZOOPLANKTON COMMUNITIES: TOWARDS A TRAIT-BASED CLASSIFICATION

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Abstract

While studies of terrestrial plant communities have increasingly emphasized the use of functional traits in ecological research, few studies have applied this approach to aquatic communities.

This study reviews the literature on zooplankton and provides a series of functional trait tables for freshwater North American zooplankton species, collected from a large number of laboratory and observational studies on feeding and life history characteristics. The qualitative and quantitative trait tables can be used to identify areas of paucity of data and provide insight into which types of studies will be most beneficial to filling in knowledge gaps of zooplankton niche utilization. Data was most complete for the cladocera across most traits, while feeding information for cyclopoids was most sparse. Qualitative data that distinguishes between species within a genus was lacking for most groups. A table of regressions used to predict important zooplankton functions such as feeding, growth and excretion rates was also compiled.

A regional community dendrogram for common northeastern North American zooplankton species was generated and shows that taxonomic differences between species do not necessarily imply functional differences based on the traits used in this study. The data collected here, combined with readily measurable species attributes, can be used to generate a multivariate measure of the functional niche of each species found in a community. Armed with this information, relationships that are useful for ecological studies of lake ecosystems can be more easily determined.

1.1 Introduction

The human proclivity towards classification of nature has led us to the definition and cataloguing of species in communities based traditionally on morphological, and more recently, on genetic descriptors. While this classification scheme has proved useful for studies of nature, it may not be the most appropriate scheme for all ecological applications. For example, many studies on the relationship between biodiversity and ecosystem function have concluded that it is the ecological roles of those species present that are important, and not necessarily simply the number of taxonomic species (Hooper & Vitousek, 1997; Symstad, Siemann & Haarstad, 2000; Tilman *et al.*, 1997; Walker, Kinzig & Langridge, 1999; Walker, 1991). Thus, there have been calls recently for the use of functional diversity measures - descriptors of communities based on a new type of classification scheme inspired by previous strategies (e.g. Grime, 1977; Reynolds, 1980) that is applicable to many ecological questions (Mason *et al.*, 2005; Mouillot *et al.*, 2005; Norberg, 2004; Petchey & Gaston, 2002).

Earlier attempts by Reynolds (1980) to functionally classify phytoplankton stemmed from the desire to classify phytoplankton communities in a manner that would reflect the environmental conditions of the lake, and the sensitivity of that community to environmental change. Phytoplankton species that were found to co-exist and that were correlated in abundance were placed into 14 functional groupings. Reynolds *et al.* (2002) built upon the previous study by showing that species placed into functional groupings had similar morphological characteristics. Additionally, the importance of the functional traits of species became recognized in studies linking biodiversity to ecosystem function (e.g. Walker *et al.* 1999; Tilman *et al.*, 1997; Hooper & Vitousek, 1997). Furthermore, more quantitative measures that use functional traits to develop indices of functional diversity have been developed. These functional diversity indices measure the diversity of characterestics of organisms that serve to structure their environment, or that limit their abundance and growth in some environments.

Functional diversity is a biodiversity measure based on functional traits of the species present in a community. Functional traits are those that define species in terms of their ecological roles – how they interact with their environments and with other species (Diaz & Cabido, 2001). These traits may include tolerances to environmental conditions, rates of biomass production, and consumption (Reynolds *et al.*, 2002), as well as nutrient utilization and uptake (Walker & Langridge, 2002). Functional traits pertain to the traits that species have that will either affect certain characteristics of an ecosystem they are found in (effect traits), or that will be affected by environmental changes (response traits). In order to take a functional approach and to use these new measures however, descriptors of the functional groups present in a community must exist.

In order to obtain a measure of the functional diversity of a community, it is necessary to define the traits of species present. Traits can been classified as "hard" or "soft" (Walker & Langridge, 2002). Hard traits are attributes of an organism that directly determine the role of a species in a community such as filtering or phosphorus excretion rates in zooplankton. Soft traits are morphological traits that are known to be correlated with hard traits (e.g. body size affects many physiological functions in a predictable way based on allometry theory (Peters, 1983). Since hard traits are sometimes difficult to obtain as they may require detailed experimental study, soft traits that are more readily measurable (e.g. body size, filtering apparatus mesh size for zooplankton) can be used as surrogates (Walker & Langridge, 2002).

The effects of environmental changes on ecosystem properties are thought to be largely determined from the bottom up by the biological processes carried out by the suite of species present in the community (Reynolds, 2002). Studies that focus on whether biodiversity affects the functioning of an ecosystem (e.g. productivity, total biomass) have yielded results that suggest a link between the functional roles of species within a community and the total community responses to environmental changes. For example, Tilman *et al.* (1997) found that functional diversity measures were more strongly related to ecosystem response variables (e.g. productivity, soil NO_3, soil NH_4) than were traditional species diversity measures in a plant community. In another study, Walker *et al.* (1999) observed that minor, functionally redundant species in ungrazed grasslands increased in abundance in heavily grazed communities, providing support for the insurance hypothesis (McNaughton, 1977; Yachi & Loreau, 1999), whereby seemingly redundant species contribute to ecosystem resilience when environmental conditions change. Functional traits of species describe how they respond to the environment, and if we know what functional traits are present in a community, then we should be able to better predict how communities will shift as environmental conditions change and thereby more fully understand the role of biodiversity (Norberg, 2004).

A functional classification of species should greatly enhance our ability to predict how the pulsed and gradual changes of environmental conditions will affect communities. For terrestrial plant species, a classification strategy has recently been proposed to predict changes in vegetation in response to environmental change (Lavorel *et al.*, 1997). A similar strategy has also been proposed for phytoplankton to be applied to ecological questions such as the intermediate disturbance hypothesis, insurance hypothesis, and alternative stable state shifts in lakes (Weithoff, 2003). For example, the intermediate disturbance hypothesis predicts the highest diversity of species at intermediate magnitude or frequency of disturbance by permitting species with different strategies and competitive advantages to coexist (Connell, 1978). Weithoff (2003) asserts that this hypothesis relies on the assumption that species are functionally dissimilar in responses to disturbance. For a greater understanding of the catastrophic shift from a vegetation dominated clear state to an algae dominated turbid one with eutrophication, a functional approach can be used to determine the gradual changes in attributes of the algal community in response to nutrient addition leading up to a shift to an alternative state (Weithoff, 2003). Finally, the use of functional diversity for testing the insurance hypothesis provides insight into the potential roles of seemingly minor or redundant species in lake communities (Weithoff, 2003) as well as in terrestrial ones (Walker *et al.* 1999). Therefore, the use of functional diversity enhances our understanding of these important ecological phenomena.

In aquatic environments, crustacean zooplankton play an important role in structuring phytoplankton communities (McCauley & Briand, 1979; Sterner, 1989), and in mediating energy flow to higher trophic levels in pelagic habitats (Gliwicz & Pijanowska, 1989). Until now, no thorough examination of the potential for functional classification of zooplankton has been attempted. We explore the possibility of determining functional grouping strategies for zooplankton using a review of the extant literature. We develop here, a functional classification tree for common North American zooplankton and show that taxonomic relationships are often insufficient surrogates for questions of how crustacean zooplankton communities function (i.e. community grazing rate, biomass production for planktivorous fish, algal bloom suppression, as well as functional responses to environmental influences such as phytoplankton abundance and distribution). The data reviewed and collected here will be useful both to expand our understanding of response (i.e. traits of response to environmental gradients, changes, or perturbations) and effect (traits that effect ecosystem functions like total zooplankton biomass production) traits of crustacean zooplankton, and to determine where future studies can focus their efforts in order to achieve a more robust classification method of functional diversity to help predict the function of ecosystems.

1.2 Methods

We conducted an extensive search of the primary literature for articles providing information on freshwater zooplankton functional traits. Emphasis was on studies that focused on traits that related to food type, feeding rate, growth rate, life history, and predator aversion strategies. These traits were chosen because they describe both an organism's *response* to environmental conditions (e.g. life history, predator aversion, food availability), and their potential *effects* on ecosystem processes (e.g. feeding rate).

The search was focused on traits for zooplankton species found in northeastern North America, in order toe be able to relate the results to our own field studies. However, traits for many other common North American species were included in the final analysis. Searches were initiated using online databases: Biological Sciences (1960-2005) and ISI's Web of Science (1981-2005) using keywords "zooplankton", "feeding", "growth" or simply the genus names of each species. The reference sections of papers found in this manner were also used to further the search for data in older published studies.

Only feeding rates measured in the lab at temperatures between 15-20°C were included in results tables in order to represent feeding rates in Quebec at the mean summer lake temperature. Feeding rate traits, such as ingestion, clearance, and filtration rates are separately reported as means and standard deviations. Clearance rate is defined as "the volume of water from which the predator removed prey per unit time" (Packard, 2001, while ingestion rate is a measure of the dry mass of prey ingested per unit time (DeMott, 1982), and filtering rate is the volume of water filtered per animal per unit time (Burns and Rigler, 1967). Mean values were computed when traits were measured for the same species under slightly different laboratory conditions (e.g. different phytoplankton concentrations or species). Whenever possible, trait measures were converted into equivalent units. Information found in the text of studies that provided qualitative information, such as habitat preference, qualitative food preferences, or presence/absence of a defensive strategy was also included. All data were compiled into tables and separated into qualititative and quantitative data tables. As well as compiling tables of quantitative and qualitative traits, a table of regression equations that can be used to predict important zooplankton functions like feeding, growth and excretion rates, using morphological characteristics, was also compiled.

1.2.1 Community Dendrogram

Qualitative and quantitative traits that were found for a sufficient number of species (length, habitat, trophic level, and feeding type) were used to generate a functional dendrogram for the regional species pool of northeastern North American lake zooplankton. In addition to the full functional dendrogram based on the four characteristics, a functional dendrogram using only body length was generated for comparison of what information can be gleaned using a very limited estimate of species functional traits. Qualitative measures were entered as ranked categories (i.e. from herbivore to carnivore, and from more passive forms of filtering type to raptorial feeding).

There are several methods for calculating functional diversity of a community, all of which are intended to generate an estimate of the diversity of functional traits in multiple dimensions. Recent methods include Functional Attribute Diversity (FAD), as used in a study of Australian rangelands by Walker *et al.* (1999) and Functional Diversity (FD) proposed more recently by Petchey and Gaston (2002) as a more suitable method than FAD. Trait variance, measured as the width of a trait distribution, has been proposed by Norberg (2004). Beyond simply measuring diversity, Mason *et al.* (2005) proposed also estimating functional richness, functional evenness, and functional divergence to enable descriptions of niche utilization, and competitive interactions in communities. Since the current study focuses on obtaining functional traits of crustacean zooplankton, Petchey and Gaston's (2002) measure of funtional diversity (FD) were used to illustrate the applicability of functional diversity measures. Although other measurements of functional diversity such as functional evenness and functional divergence have been recently developed (Mason *et al.*, 2005), there has been more work using FD as a measure of community function than for other measures (e.g. Blackburn *et al.*, 2005; Petchey, Hector & Gaston, 2004).

Petchey and Gaston (2002) highlight four main steps to calculating FD. First, obtain a trait matrix listing the traits of each species from a region. Traits can be binary, continuous or categorical, though categorical traits must reflect a ranking. In any case, the trait matrix should be standardized to have a mean of 0 and a standard deviation of 1. Second, convert the trait matrix to a distance matrix, where standardized Euclidean distances between each species is shown. Third, use average linkage clustering and unweighted pair groupings to generate a dendrogram from the distance matrix for the region (see Krebs 1999 for clustering information). Finally, add up the vertical branch lengths of all species in a community and do not include the branch lengths of those species not found in that lake. All FD measures were calculated using R 2.20 and code obtained from O. Petchey's website, which included a refinement to the means by which total branch lengths were computed (Petchey and Gaston 2006): that the branch lengths required to connect all species are summed, but branch lengths connecting species to the root of the dendrogram is not included. FD can be considered as a quantitative measure of the richness of functional traits, or the degree of complementarity within a community (Petchey & Gaston, 2002).

1.3 Results

The life history information presented was collected from 66 sources spanning Fryer (1957) to Nandina & Sarma (2003). The majority of references are from the primary peer-reviewed literature, while some data, particularly qualitative data were taken from Great Lakes Copepod key from USGS Great Lakes Science Center (http://www.glsc.usgs.gov/), and taxonomic keys (e.g. Pennak, 1989; Hebert, 1995). While information on more traits were found, traits presented here were those for which information on greater than 15% of the total number of species was found. A complete list of the primary literature used to generate trait tables is given in Appendix 1.

1.3.1 Quantitative Traits Defined

Quantitative traits are listed in Table 1 (a-b). Feeding rate was divided into three types of measurements; clearance rate, filter feeding rate, and ingestion rates. The maximum clearance rate was the highest recorded clearance rate found in the literature. Food size range represented the smallest and largest size of prey ingested. Clutch size, age at first clutch, and total offspring estimated an organism's reproductive capacity, and the time required for an organism to reach a reproductive state. Mesh size is a measure of the size of the filtering apparatus of cladocerans, and therefore is an estimate of the size of the smallest particle an organism is capable of capturing. Finally, threshold food density is the density of food below which an organism cannot grow or reproduce, and thus, it is the lower resource limit of its reproductive capabilities.

1.3.2 Quantitative Data Results

The quantitative trait table is most complete for traits such as length and feeding rates (Table 1 a-b). For other traits, information is more complete for some taxonomic groups than for others. For example, estimates of minimum and maximum food sizes of cladocerans and calanoids was almost complete owing to two studies (Geller & Müller, 1981; Sterner, 1989), but severely deficient for cyclopoids. On the other hand mean clutch size and total offspring values were lacking for cladocerans and calanoids but sufficient for cyclopoids. Clearance rates ranged from 15 µl ind^{-1} hr^{-1} in *Alona affinis* to 4417 µl ind^{-1} hr^{-1} for the predatory *Skistodiaptomus pallidus* feeding on rotifers. Filtration rates were found for four *Daphnia* species and ranged from 166 µl ind^{-1} hr^{-1} (*Daphnia longispina*) to 942 µl ind^{-1} hr^{-1} (*Daphnia hyalina*). Ingestion rates were only found in comparable units for *Chydorus sphaericus* (16.7 mg ind^{-1} day^{-1}) and *Alona affinis* (16.4 mg ind^{-1} day^{-1}) (Table 1 a-b). Overall, there was much less information available for the clearance rates, ingestion rates, or food size preferences for cyclopoid copepods. The age of first clutch was only found a few cladocerans and one calanoid (*Eurytemora. affinis*), but values were found for cyclopoids.

Table 1.1a

Quantitative functional traits of cladoceran zooplankton for 26 species including sources in superscript (See Appendix 1). C, F and I represent average Clearance rates (µl animal^{-1} hr^{-1}), Filtration rates (µl animal^{-1} hr^{-1}), and Ingestion rates (mg dry weight animal^{-1} day^{-1}) respectively. An asterisk (*) indicates that the average and standard deviation were calculated from the published range using a statistical technique first described in Hozo *et al.* (2005). Trait attributes obtained by generalization of a group is indicated with a "†"

Species	Average Length (mm)	Feeding Rate (units, see caption)	Max Clearance Rate (µl ind $^{-1}$h^{-1})	Food Size Range (µm)	Age at First Clutch (days)	Mesh Size (µm)	Threshold Food Density (cells ml $^{-1}$)*10 ^{5}
Alona affinis Leydig	0.408[15]	14.90 ± 17.94 (C)*[15] 16.68 ±15.10 (I)*[15]	56.25[15]				
Alona rectangula Sars	0.400[16]						0.019[20]
Eubosmina corregoni Baird	0.578[22]'			1.6 - 15[19,44]		0.68-1.6[19]	
Bosmina longispina Leydig	0.420[5]						
Bosmina longirostris Müller	0.460[11]	72.15 ± 74.93 (C)* [4,3,32,52,53]					
Ceriodaphnia dubia Richard							0.028[20]
Ceriodaphnia reticulata Jurine	0.590[20]				5.0[20]		
Ceriodaphnia lacustris O.F.M.	0.495[25]'	74.43 ± 19.40 (C)[3]*	320.83[61]	0.4 - 7[19,44]		0.24-0.4[19]	
Chydorus sphaericus Müller	0.264[15]	35.63 ± 41.50 (C)*[15] 16.42 ± 15.44 (I)*[15]		0.4 - 3.5[19,44]		0.24-0.4[19]	
Chydorus brevilabris Frey							

Table 1.1a (continued)

Species	Average Length (mm)	Feeding Rate (units, see caption)	Max Clearance Rate (□l ind^{-1}h^{-1})	Food Size Range (µm)	Age at First Clutch (days)	Mesh Size (µm)	Threshold Food Density (cells ml^{-1})*10^{5}
Daphnia ambigua Scourfield	0.910[11]				5.5[20]		
Daphnia cucullata Sars	0.820[22']		21.80[22']	0.5 - 15[19,44]	5.6[20]	0.23-0.45[19]	
Daphnia galeata Sars	1.167[11,7]			1.1 - 20[19,44]	5.5[20]	0.32-1.0[19]	
Daphnia hyalina Leydig	1.690[21']	942.08 ± 681.30 (F)[50]		2 - 30[19,44]	6.2[20]	0.56-1.8[19]	
Daphnia laevis Birge							0.020[20]
Daphnia longispina Müller	2.400[5]	166.20 ± 54.46 (F)[7]					
Daphnia magna Straus	2.440[40]			0.65 - 45[19,44]		0.24-0.64[19]	
Daphnia pulex Linnaeus	1.16[36,33*]	290.75 ± 118.62 (F)[41,35]			5.9[20,33+]		
Daphnia pulicaria Forbes	0.870[36]			1.5 - 30[19,44]	6.2[45]	0.45-1.4[19]	
Daphnia rosea Sars	1.064[36,7]	195.83 ± 45.96 (F)[7] 713.33 ± 68.6 (C)[14]	1066.67[60]			0.9-22[19]	
Diaphanosoma brachyurum Liéven	0.600[36,22']	291.32 ± 82.10 (C)[3]		0.25 - 5.00[19,44]		0.16-0.24[19]	0.050[20]
Holopedium gibberum Zaddach	0.650[11]		4979.17[60]	4.0 - 25[19,44]			
Leydigia quadrangularis Schödler							
Sida crystallina Müller	1.304[15]	2746.88 ± 3139.28(C)[*15]	9929.17[15]	4.5 - 25[19,44]			
Polyphemus pediculus Linnee			20 000[46]				

Table 1.1b

Quantitative functional traits of 17 copepod species obtained from a primary literature search including sources in superscript (See Appendix 1). C, F and I represent Clearance rates (µl animal^{-1} hr^{-1}), Filtration rates (µl animal^{-1} hr^{-1}), and Ingestion rates (mg animal^{-1} day^{-1}) respectively. An asterisk (*) indicates that the average and standard deviation were calculated from the published range using a calculation from Hozo *et al.* (2005). Trait attributes obtained by generalization of a group is indicated with a "†".

Species	Average Length	Feeding Rate	Max Clearance Rate	Food Size Range	Age at First Clutch	Average Clutch Size	Total offspring
	(mm)	(units, see caption)	(µl ind^{-1}h^{-1})	(µm)	(days)		(#/lifetime)
Cyclopoida							
Acanthocyclops robustus Sars	0.930^{25*}					76.8^{25}	1049.8^{25}
Cyclops vernalis Fischer							
Cyclops scutifer Sars	0.900^{5}	45.00 (C)^{5*}					
Cyclops vicinus Ulianine	1.525^{25*}					49.6^{25}	225.9^{25}
Diacyclops bicuspidatus thomasi Forbes	0.630^{36}	6666.67 (C)^{30} 0.9 (*Synchaeta* h^{-1}) (I)^{59}		150 - 600^{51}			
Eucyclops speratus Lilljeborg							
Mesocyclops edax Forbes	0.620^{36}	697.77 ± 550.85 (C)^{42}					
Tropocyclops prasinus Fischer	0.390^{36}					16.9^{37}	
Thermocyclops crassus Fischer	0.785^{25*}		19.67^{25*}			61.2^{25*}	52.6^{25}
Calanoida							
Epischura lacustris Forbes	0.780^{29}						
Eurytemora affinis Poppe					8.650^{1*}	56.3^{1*}	
Onychodiaptomus birgei Marsh	1.440^{12}			10 - 50^{44†}			
Diaptomus gracilis Sars	0.997^{11}			10 - 50^{44†}			
Leptodiaptomus minutus Lilljeborg	0.770^{36}	762.5 ± 288.73 (C)^{8*}		10 - 50^{44†}			
Leptodiaptomus sicilis Forbes	0.900^{36}			10 - 50^{44†}			
Skistodiaptomus oregonensis Lilljeborg	0.720^{11}		808.33^{60}	10 - 50^{44†}		12.6^{45}	
Skistodiaptomus pallidus Herrick	0.720^{11}	4416.67 ± 2825.05 (C)^{48}					
Skistodiaptomus reighardi Marsh							

1.3.3 Qualitative Traits Defined

Qualitative traits found in sufficient quantities to include in Table 2 (a-b) are predatory escape response (Cladocera), habitat, trophic level, optimal productivity conditions, food size (Cladocera), helmet forming capacity (Cladocera), feeding type and selectivity. Predatory escape response characterized how a species evades an attack from a predator. The habitat each organism was most likely to be found in was categorized as either littoral or pelagic. Trophic level was divided into the traditional herbivore, omnivore and carnivore categories with the addition of herbivore-omnivore, and carnivore-omnivore. This addition was used to distinguish between copepods such as *Mesocyclops edax* that has more carnivorous tendencies than *Tropocyclops prasinus* that is more herbivorous. Optimal productivity conditions characterized the lake trophic status at which optimal competitive ability is achieved by each species. For example, chydorids are more successful competitors in lakes with high productivity while daphnids are generally more successful in low productivity lakes with high quality food (Table 2 a-b). Qualitative food size was used to describe what relative size of phytoplankton food each species feeds on more frequently or more efficiently. The ability to produce a helmet in Cladocera was also included as a trait as it plays a role in the ability of cladocerans to avoid predators.

Feeding type is the manner in which species or groups obtain their food. Cladocerans have been divided into four classes; 1) daphnid-type (D-type) where filtering is from a stationary position with filtering apparatus on the third and fourth legs, 2) sida-type (S-type) similar to D-type with the exception that the filtering apparatus is located on the first five legs, 3) bosmina-type (B-type) characterized by a horizontal active swimming and less developed filtering apparatus on thoracic appendages, and 4) chydorid-type (C-Filtration) where the organism feeds by scraping algal particles from periphyton. Raptorial predators like cyclopoids actively capture and kill prey, while stationary suspension feeders are more passive with less frequent swimming. Finally *Epischura lacustris* is differentiated from both raptorial and stationary suspension feeding as it swims continuously while creating feeding currents thus being characterized as a "current cruiser".

Table 1.2a

Quantitative functional traits of 24 cladoceran species obtained from a primary literature search including sources in superscript (See Appendix 1). Traits marked with an asterisk (*) are personal observations. Trait attributes obtained by generalization of a group is indicated with a "†"

Species	Predatory escape response	Habitat	Trophic Level	Optimal Productivity Conditions	Food Size	Helmet	Feeding Type	Selectivity
Alona affinis Leydig		Littoral[15]	Herbivore[15]			No*	C-Filtration*	
Alona rectangua Sars								
Eubosmina corregoni Baird	Reduced swimming[51,35]†	Pelagic[38]†	Herbivore[14]†		Large[44]	No*	B-Filtration[13]†	Moderate[14,2]†
Bosmina longispina Leydig	Reduced swimming[51,35]†	Pelagic[38]†	Herbivore[14]†		Large[44]	No*	B-Filtration[13]†	Moderate[14,2]†
Bosmina longirostris Müller	Reduced swimming[51,35]†	Pelagic[38]†	Herbivore[14]†	High[18]	Large[44]	No*	B-Filtration[13]†	Moderate[14,2]†
Ceriodaphnia dubia Richard	Rapid swimming[35]†	Pelagic[17]†	Herbivore[38]†			No*	D-Filtration[13]†	
Ceriodaphnia reticulata Jurine	Rapid swimming[35]†	Pelagic[17]†	Herbivore[38]†			No*	D-Filtration[13]†	
Ceriodaphnia lacustris Birge	Rapid swimming[35]†	Pelagic[17]†	Herbivore[38]†		All[44]	No*	D-Filtration[13]†	
Chydorus sphaericus Müller		Pelagic[66]	Herbivore[15]	High[55]†	Small[44]	No*	C-Filtration*	
Chydorus brevilabris Frey		Littoral[17]	Herbivore[38]†	High[55]†	Large[44]	No*	C-Filtration*	

Table 1.2a (Continued)

Species	Predatory escape response	Habitat	Trophic Level	Optimal Productivity Conditions	Food Size	Helmet	Feeding Type	Selectivity
Daphnia ambigua Scourfield	Rapid swimming[35†]	Pelagic[38†]	Herbivore[18]	Low[41,40,18]		Yes[24]	D-Filtration[13†]	Low[14,2†]
Daphnia cucullata Sars	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]	Small[44]	Yes[24]	D-Filtration[13†]	Low[14,2†]
Daphnia galeata Sars	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]	Medium[44]	Yes[24]	D-Filtration[13†]	Low[14,2†]
Daphnia hyalina Leydig	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]	Medium[44]	Yes[57]	D-Filtration[13†]	Low[14,2†]
Daphnia laevis Birge	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]		Yes[24]	D-Filtration[13†]	Low[14,2†]
Daphnia longispina Müller	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]		Yes[57]	D-Filtration[13†]	Low[14,2†]
Daphnia magna Straus	Rapid swimming[35†]	Ponds[24]	Herbivore[38†]	Low[41,40]	Small[44]	No[24]	D-Filtration[13†]	Low[14,2†]
Daphnia pulex Linnaeus	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40]		No[24]	D-Filtration[13†]	Low[14,2†]
Daphnia pulicaria Forbes	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40,42]	Medium[44]	No[24]	D-Filtration[13†]	Low[14,2†]
Daphnia rosea Sars	Rapid swimming[35†]	Pelagic[38†]	Herbivore[38†]	Low[41,40†]		No[24]	D-Filtration[13†]	Low[14,2†]
Diaphanosoma brachyurum Liéven	Pausing and jumping[35†]	Pelagic[38†]	Herbivore[38†]	High[18]	All[44]	No*	S-Filtration[13†]	
Holopedium gibberum Zaddach		Pelagic[38†]	Herbivore[38†]		Large[44]	No*	S-Filtration[13†]	
Leydigia quadrangularis Schödler		Littoral*	Herbivore*			No*	C-Filtration*	
Sida crystallina Müller		Littoral[15]	Herbivore[15]		Large[44]	No*	S-Filtration[13†]	
Polyphemus pediculus Linnee		Pelagic[46]	Carnivore[46]			No*	Raptorial[46]	

Table 1.2b

Qualitative functional traits of 17 copepod species obtained from a primary literature search including sources in superscript (See Appendix 1). Traits marked with an asterisk (*) are personal observations. Trait attributes given as generalization for a whole genus or family is indicated with a "†"

Species	Habitat	Trophic Level	Optimal Productivity conditions	Feeding Type	Selectivity
Cyclopoida					
Acanthocyclops robustus Sars	Pelagic[63]	Omnivore[63]		Raptorial[25]†	High[28]†
Acanthocyclops vernalis Fischer	Pelagic[25]†	Omnivore[25]†		Raptorial[25]†	High[28]†
Cyclops scutifer Sars	Pelagic[63]	Omnivore[25]†		Raptorial[25]†	High[28]†
Cyclops vicinus Ulianine	Pelagic[64]	Omnivore[25,26]		Raptorial[25]†	High[28]†
Diacyclops bicuspidatus thomasi Forbes	Pelagic[30]	Omnivore carnivore[56,30]		Raptorial[56,30]	High[56,30]
Eucyclops speratus Lilljeborg	Littoral[63]	Omnivore herbivore[65]		Raptorial[25]†	
Mesocyclops edax Forbes	Pelagic[17]	Omnivore carnivore[9]		Raptorial[9]	High [9,47]
Tropocyclops prasinus Fischer	Pelagic [63]	Omnivore herbivore[12]		Raptorial[12]	High[28]†
Thermocyclops crassus Fischer	Pelagic[25]†	Omnivore herbivore[25]†		Raptorial[25]†	High[28]†
Calanoida					
Epischura lacustris Forbes	Pelagic[17]	Omnivore-carnivore[54]	High[41]†	Current-cruiser[12]	High[28]†
Eurytemora affinis Poppe					
Onychodiaptomus birgei	Littoral[62]	Herbivore[63]	High[41]†	Stationary suspension[12]†	High[28]†
Diaptomus gracilis Sars		Herbivore[63]	High[41]†	Stationary suspension[12]†	High[28]†
Leptodiaptomus minutus Lilljeborg	Pelagic[63]	Omnivore[12]	High[41]†	Stationary suspension[12]†	High[28]†
Leptodiaptomus sicilis Forbes	Pelagic[63]	Herbivore[63]	High[41]†	Stationary suspension[12]†	High[28]†
Skistodiaptomus oregonensis Lilljeborg	Pelagic[17]	Omnivore[58]	High[41]†	Stationary suspension[58]†	High[28]†
Skistodiaptomus pallidus Herrick		Omnivore- herbivore[48]	High[41]†	Stationary suspension[48]†	High[28]†
Skistodiaptomus reighardi Marsh	Pelagic[63]	Omnivore[63]		Stationary suspension[12]†	

The last qualitative trait in Table 2(a-b) is selectivity, a relative estimation of how selective an organism is towards its food. Raptorial feeders are generally considered to be more selective than filter feeders, but there are also relative degrees of selectivity exhibited within the filter feeding Cladocera species. These degrees of selectivity can be defined based on how active a species is in seeking out food of a preferable quality, through selective filtering, or particle rejection.

1.3.4 Qualitative Data Results

The qualitative trait matrix contains a number of trait variables available only for some taxonomic groupings (Table 2 a-b). For example, the ability to form helmets does not apply to copepods. Based on our biological knowledge of many of these species, qualitative traits were often assumed to be the same within a genus, or sometimes within a family, or order. The majority of trait information in Table 2 (a-b) is considered to apply to the entire genus, although exceptions mentioned specifically in the literature are cited. The preferred food of most cladocerans is algae, and thus there is no trophic level distinction given between cladoceran species as all are thought to be predominantly herbivorous (Table 2 a), with the exception of *Polyphemus*. Cyclopoids were all classified as raptorial feeders in the five studies where qualitative data was obtained (Table 2 b). Other traits, such as preferred food size and productivity conditions for optimal growth, were found for some cladoceran species but not for cyclopoids. Data is sparse overall for some variables such as the productivity conditions of optimal growth and qualitative food size.

1.3.5 Regression Relationships

The majority of regression equations found in the literature predicted filtering rate or clearance rates (Table 3 a-b). There is a bias in data towards cladocerans, particularly *Daphnia*. There are several regressions predicting feeding rates for *Epischura lacustris*, a common North American calanoid copepod, only one regression for predicting clutch size in *Cyclops spp.* was found. Only five of the regressions predicted functional traits for copepods, while 18 predicted them for cladocerans. Also, while the majority of the regressions (especially for cladocerans) explained a large proportion of the variance ($R^2 > 0.80$), they occasionally varied quantitatively and qualitatively among studies for the same species.

Table 1.3a

A list of 20 regression relationships predicting various cladoceran functional traits including R^2 (when given) and sources (See Appendix 1).

Species	Equation	y	x	R^2	Source
Alona rectangular Sars	$y = 0.246 + 0.143 \log10(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.95	34
Bosmina longirostris Müller	$y = 0.487x^{1.83}$	clearance rate (ml ind^{-1} hr^{-1})	length (mm)	NA	14
Cladocerans	$y = 7.534x^{3.002}$	algal filtering rate (ml ind^{-1} day^{-1})	length (mm)	0.82	27
Cladocerans	$y = 5.105x^{2.176}$	bacterial filtering rate (ml ind^{-1} day^{-1})	length (mm)	0.9	27
Daphnia and *Bosmina spp.*	$y = 22x + 4.87$	diameter of largest particle ingested (μm)	carapace length (mm)	NA	6
Daphnia catawba Coker	$y = 2.04x^{1.74}$	clearance rate (ml ind^{-1} day^{-1})	length (mm)	0.96	23
Ceriodaphnia dubia Richard	$y = 0.251 + 0.161 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.92	34
Daphnia galeata mendotae Sars	$y = 6.31x^{1.58}$	clearance rate (ml ind^{-1} day^{-1})	length (mm)	0.93	23
Daphnia laevis Birge	$y = 0.142 + 0.084 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.91	34
Daphnia pulex Leydig	$y = 10.09x^{1.61}$	clearance rate (ml ind^{-1} day^{-1})	length (mm)	0.97	23
Daphnia rosea Sars	$y = 0.31x^{3.02}$	filtering rate (ml ind^{-1} hr^{-1})	length(mm)	NA	7
Daphnia rosea Sars	$y = 0.22975x^{2.74}$	clearance rate (ml ind^{-1} hr^{-1})	length (mm)	NA	14
Daphnia rosea Sars	$y = 13.80x^{2.24}$	clearance rate (ml ind^{-1} day^{-1})	length (mm)	0.91	23
Diaphanosoma brachyurum Liéven	$y = 0.159 + 0.122 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.93	34
Holopedium gibberum Zaddach	$y = 6.37x^{2.03}$	clearance rate (ml ind^{-1} day^{-1})	length (mm)	0.95	23
Moina macrocopa Straus	$y = 0.194 + 0.133 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.97	34
Scapholeberis kingi Sars	$y = 0.182 + 0.071 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.97	34
Simocephalus vetulus Müller	$y = 0.174 + 0.117 \log_{10}(x)$	rate of population growth day^{-1}	food level (cells ml^{-1})	0.84	34
Zooplankton well fed	$y = 0.157x^{-0.383}$	phosphorus excretion rate at 20°C (μg mg^{-1} h^{-1})	mass (mg)	NA	39
Zooplankton poorly fed	$y = 0.042x^{-0.383}$	phosphorus excretion rate at 10°C (μg mg^{-1} h^{-1})	mass (mg)	NA	39

Table 1.3b

A list of regression equations predicting copepod feeding rates, and clutch size based on length measurements including R^2 and sources (In Appendix 1).

Species	Equation	y	x	R^2	Source
Cyclopoida					
Cyclops spp.	$y = 100.42x^{3.28}$	clutch size	prosome length (mm)	0.39	31
Calanoida					
Epischura lacustris Forbes	$\log_{10}y = -6.76\log_{10}x - 1.15$	grazing rate (ml ind^{-1} day^{-1})	length (mm)	0.658	10
Epischura lacustris Forbes	$y = 1.439x - 1348.2$	clearance rate (ml ind^{-1} day^{-1})	prosome length (µm)	0.433	8
Epischura lacustris Forbes	$y = 0.264 + 0.102x$	*Euchlanis* prey $predator^{-1}$ day^{-1}	prosome length (mm)	0.86	43
Leptodiaptomus minutus Lilljeborg	$y = 0.077x - 13.773$	filtering rate (ml ind^{-1} day^{-1})	prosome length (µm)	0.787	8

For example the three equations for *Daphnia rosea* consisted of different coefficients, and the three regression models for *Epischura lacustris* had different coefficients but also different types of relationships (log-linear and linear) as well. Furthermore, the regressions use slightly different measures (prosome length and total length) to predict different types of feeding rates (clearance rates, and ingestion of a particular prey type), and thus it is difficult to measure one characteristic in order to calculate functional traits for all species.

1.3.6 Functional Community Dendrogram

The dendrogram of 31 species generated using the length, habitat, trophic level and feeding types for zooplankton has a total FD value of 287.14 (Figure 1). The classification method separated initially, a group containing mostly *Daphnia* species (groups 3 and 4 on Figure. 1) from one largely composed of other cladoceran species and copepods (groups 1 and 2 on Figure 1). At a Euclidean distance of 18, four groups were distinguished. The first group contained *D. brachyurum*, *H. gibberum*, *A. affinis*, *O. birgei*, and Bosminidae spp., and can be defined as moderately selective herbivores (including mostly cladocera but also a calanoid species). The second major group was the largest and contained all remaining selective omnivorous and carnivorous copepods, and the cladoceran *Chydorus sphaericus*, which are moderately selective small herbivores. The third group and fourth groups consisted of large and small herbivores respectively, mostly *Daphnia* species, with a generally low selectivity. In each group, however, are groupings of species that would not be considered similar based on taxonomy alone. For example, *O. birgei* (a calanoid copepod) is more similar to bosminids (cladocera) than other calanoids based on the functional traits used. Group 2 is a mixture of calanoid and cyclopoid copepod species and furthermore included *C. sphaericus* which is taxonomically more closely related to *A. affinis* which was clustered further away into group 1.

While the dendrogram generated using body length, habitat, and trophic level showed some patterns of grouping taxa similarly, the dendrogram generated using only body length did not group species of a particular genus or family together (Figure 2). The total measure of FD of the community (sum of all branch lengths) is 178.15. Four different size classes were identified, with Euclidean distances of at least 19.69 from each other.

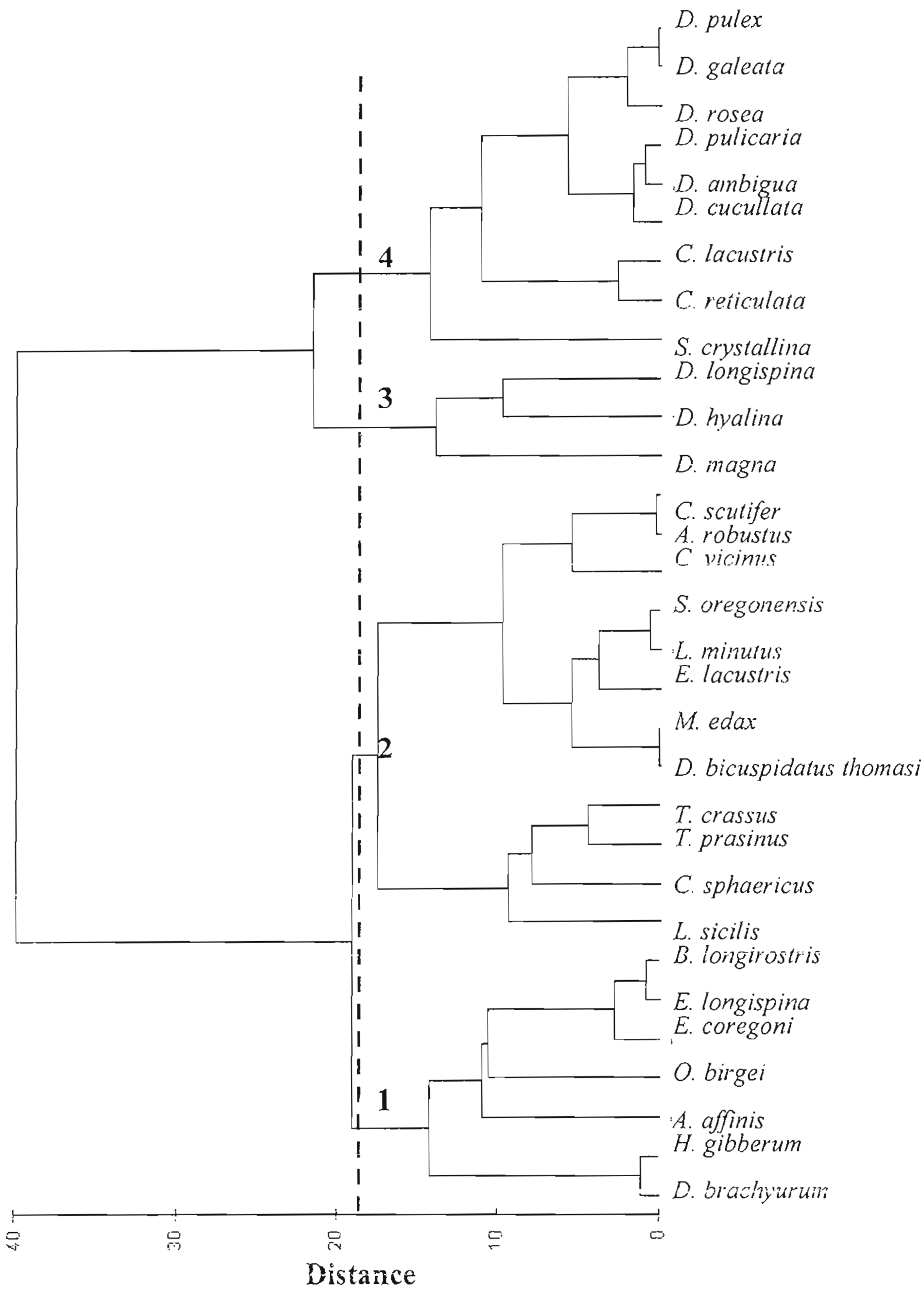

Figure 1.1 A functional dendrogram (FD) generated by hierarchical clustering analysis of the standardized Euclidean distances of each species based on 4 functional traits (body length, habitat, trophic level, and feeding type). A dashed line indicates the split that defines four groupings (numbered) of species as discussed in the text.

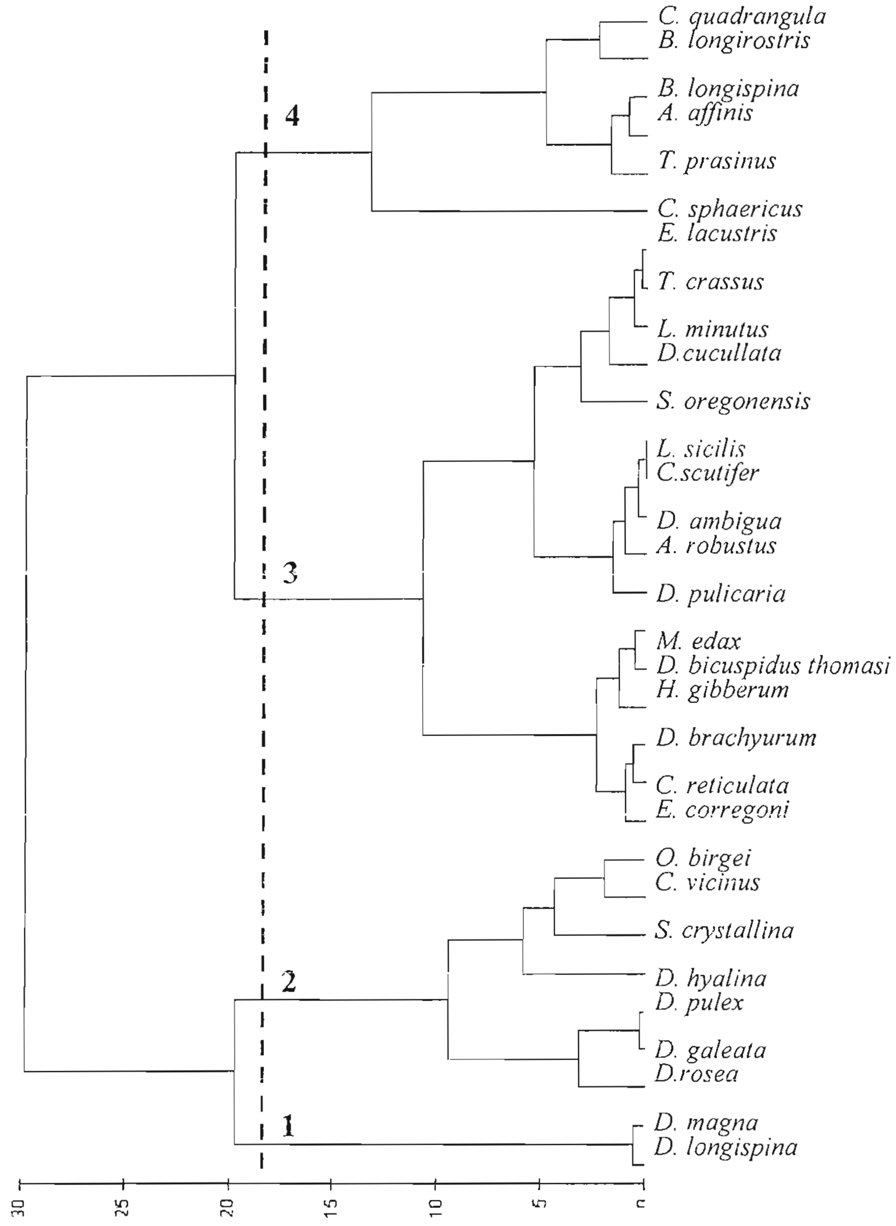

Figure 1.2 A functional dendrogram (FD) generated by hierarchical clustering analysis of the standardized Euclidean distances of each species based solely on body length. A dashed line indicates the split that defines four groupings (numbered) of species as discussed in the text.

1.4 Discussion

In order to apply a functional perspective to zooplankton communities, we must first establish whether function can be adequately estimated for commonly encountered species. Given the large number of studies on zooplankton life history, morphology and physiology in the past several decades, one would expect that a functional classification scheme could be developed. In this review of the literature, we have pieced together the various studies and data therein for common North American species of freshwater cladocerans, calanoid and cyclopoid copepeds. In general, the majority of data was available for cladocerans while there was a relative paucity of qualitative and quantitative data for cyclopoids. This bias reflects the ease of culturing and studying cladoceran, and especially *Daphnia* species, owing to their relatively non-selective filter feeding strategies and nutritional requirements as herbivores (Pennak, 1989). Their feeding strategy differs from that of copepods, which actively capture and ingest individual suspended food particles (Koehl & Strickler, 1981). Also, longer generation times and sexual reproduction lead to culturing difficulties which bias studies away from freshwater copepod species.

While some feeding studies have been conducted on a few species of calanoids, studies of cyclopoid feeding are rare. This has been attributed to a tendency to characterize all cyclopoids as being carnivorous (Sterner, 1989). However, studies on *Tropocyclops prasinus* and *Mesocyclops edax* reveal that while both are omnivorous, the former displays a preference towards herbivory (Peacock & Smyly, 1983), while the latter is more carnivorous (Confer, 1971). The contrast in these studies shows that the uniformity in feeding strategies of cyclopoids should not be assumed. The use of newer food web determination techniques such as stable isotopes may be particularly fruitful for the characterization of trophic levels and food sources of zooplankton within lakes of interest in the near future (Bearhop *et al.*, 2004) and such information could be included in an expanded functional classification scheme.

Zooplankton exhibit a large range of feeding rates within and between species. The differences within and between species in the same genus may reflect differences in laboratory conditions (e.g. food concentrations, container sizes). Therefore, the use of feeding rates measured in the lab as functional traits for zooplankton may translate with some difficulty to natural conditions. Another difficulty with the use of some traits stems from changes in species classification after taxonomic re-evaluation. For example, *Bosmina longirostris* Müller was considered a common North American species until De Melo & Hebert (1994) analyzed allozymic traits and re-analyzed morphology with an electron microscope and showed that this species was only located in California. In the rest of the North American distribution, it has been divided into two species; *Sinobosmina liederi*, and *Sinobosmina freyi*. Functional information on these newly defined species is obviously lacking but likely overlaps significantly with that of *B. longirostris*. Furthermore, the determination of similar parameters for rotifer communities may also be useful for estimates of zooplankton functional diversity as they are an important link to the microbial food web, as well as competitors and prey for some crustacean zooplankton (Nogrady, Wallace & Snell, 1993).

While some functional traits for cladocerans and many of the functional traits for copepods were sparse in qualitative and quantitative functional trait matrices, the regression relationships (Table 3) used to predict zooplankton functions may be most useful for future studies. Additional general multivariate regressions that predict filtering rate and ingestion rate of all zooplankton, cladocerans, and marine calanoids have also been well demonstrated (Peters and Downing, 1984). R^2 values were generally high for regressions using length to predict feeding rates, suggesting it may be appropriate to use length as a soft trait. Since functional measures like Petchey & Gaston's (2002) FD are affected when correlated measures are used, it would be redundant to use correlated measures (Mason *et al.*, 2005) like body size and clearance rate in the same calculation of FD. Still, soft traits can be useful in combination with some hard traits to construct functional niches of species (Diaz *et al.*, 1999; Walker & Langridge, 2002) as we have done here (Figure 1).

The dendrograms in Figure 1 and Figure 2 provides an example of the how a suite of traits can be used to generate a functional dendrogram for regional species pool. The dendrogram based on four functional traits (Figure 1) more closely resembled taxonomic groupings although with some significant exceptions than did the dendrogram constructed based on body size alone (Figure 2). This is not surprising since morphological structure is often related to function in zooplankton and thus although we argue that taxonomic identification (based largely on morphology) is not sufficient, it should still have some relationship with function. The important results are in the differences observed whereby closely related sistergenera for example do not cluster together in the dendrogram. It is obvious from Figure 2, that body size alone does not give a tree that resembles a taxonomic one at all, and probably does not provide an accurate functional descriptor of the community either. It is therefore evident that the functional dendrogram and estimate of FD can depend on which characters we include in the analysis. Petchey and Gaston (2002) demonstrate the importance of choosing a suite of traits that functionally characterizes the community without overemphasizing functional compementarity; too few traits will underestimate the level of complementarity, while too many traits will result in a measure that is effectively the same as species richness. We only show the two extremes in what is possible to calculate for zooplankton FD based on our review of the literature to date. The ultimate test of which characters to use in combination to calculate FD will be determined by the combination that best represents a particular ecosystem function (e.g. total biomass of zooplankton) or most responds to an environmental gradient (such as a gradient of total phosphorus for example; (Chapter II) Blackburn *et al.* (2005) conducted such an analysis for the purposes of determining which functional characteristics of a community of invasive predators were most responsible for driving bird species extinct on islands. They tested all 2^{11} possible combinations of 11 functional traits for predator communities to determine which provided the highest explanatory power for extinctions. Such an analysis could also be conducted for zooplankton communities to determine which functional traits contribute more to their responses or functions in particular lake ecosystems (Chapter II).

To obtain Petchey and Gaston's (2002) FD of a lake community containing only a subset of this regional pool for northeastern North America, one will only need to sum the branch lengths of those species found in the lake in our dendrogram. Not only do these dendrograms provide an example of how these traits can be used, they show how taxonomic relatedness does not relate directly to function, even when we have had to assume in some cases that species within a genus have similar qualitative characteristics. Large taxonomic differences may not necessarily imply large difference in the ecological roles of those species in a community. Therefore, a more functional approach to diversity of lake zooplankton communities may be very useful especially vis-a-vis predicting how community function, in addition to structure, may change under future altered conditions.

A practical approach towards constructing functional classifications would combine hard and soft traits that can be readily measured. For example, multiple sampling through time of a lake undergoing a seasonal succession provides snapshots of the zooplankton community. Measurements of length can be used to infer feeding rates and food niches to a certain degree, while clutch size and age structure can be useful measures of the responses to predation and environmental changes. With the data compiled in this review, such an approach can now begin using some of the characteristics provided here. Again, it will be important to test this classification scheme experimentally, to see which combination of traits most accurately captures changes in community function under varied habitat conditions.

In summary, this study provides a synthesis of available functional traits of zooplankton species based on approximately five decades of laboratory and observational studies. Data was most abundant for cladocerans, particularly *Daphnia* species, while most lacking for cyclopoid species. This information is useful to those who wish to estimate functional diversity for North American freshwater zooplankton communities based on taxonomic information of community composition. It also outlines the limits of our current understanding of niche utilization of zooplankton species, and points to a more integrative functional approach to compiling new data on zooplankton that would be beneficial to the ecological study of lakes. The use of functional measurements of diversity in capturing ecological function of aquatic ecosystems has yet to be explored in detail, but work from terrestrial systems shows that such an approach should provide a greater understanding of the mechanisms which determine community composition and response to major environmental shifts.

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Appendix 1.1

List of references used to compile functional trait matrices

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CHAPITRE II

ZOOPLANKTON BIODIVERSITY AND PRIMARY PRODUCTIVITY: EXPLANATIONS INVOKING RESOURCE ABUNDANCE AND DISTRIBUTION.

by

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Abstract

Empirical and theoretical studies linking zooplankton biodiversity to local environmental gradients have emphasized the importance of productivity, usually measured as total phosphorus (TP). Several mechanisms have been proposed for the observed relationships including the role of phytoplankton resource type and distribution. To test hypothesized mechanisms about these relationships, eighteen lakes in Quebec were sampled for potential productivity (TP), zooplankton community structure, and the vertical distribution of major phytoplankton spectral groups: greens (chlorophytes), blue-greens (cyanophytes), browns (diatoms plus chrysophytes), and cryptophytes. The relationships between zooplankton community richness (S), TP and the spatial distribution and type of resource were assessed. Additionally, estimates of functional diversity (FD), using all combinations of five traits, were calculated to determine how biodiversity relationships change with a measure that incorporates more life history and niche characteristics. While zooplankton S showed the usual tendency to a unimodal relationship with TP, FD linearly declined with increasing eutrophication. This could be attributed to changes in the type and distribution of phytoplankton resources. Zooplankton FD was unimodally related to increasing variation in cyanophyte spatial distribution. A smaller proportion of the variance in zooplankton FD was also explained by the ratio of browns to blue-greens. Redundancy analysis (RDA) revealed an important effect of the presence of planktivorous fish, in addition to blue-green and brown algae concentrations, suggesting both bottom-up and top-down effects for zooplankton community structure. In all observed relationships, a greater variance of FD than S zooplankton measures was explained by physical, chemical, or biotic factors, suggesting that the more mechanistic measure of biodiversity, FD, will benefit ecological research attempting to identify environmental gradients affecting zooplankton diversity. Further focus on heterogeneity of phytoplankton resources, using both comparative and experimental approaches, should prove useful in providing greater understanding of zooplankton diversity.

2.1 Introduction

The mechanisms that drive the abundance and distribution of zooplankton species are of great interest in aquatic ecology. After much theoretical and empirical study, several significant patterns have been identified at the landscape level. Crustacean zooplankton biodiversity (usually measured as species richness) can be influenced by habitat size or lake area (Dodson, 1992; Hoffman & Dodson, 2005; O'Brien *et al.*, 2004), habitat connectivity (Cottenie & De Meester, 2003; Beisner *et al.* submitted manuscript), or potential primary productivity (Dodson, 1992; Hoffman and Dodson, 2005; Waide *et al.* 1999; Tilman & Pacala, 1993). While studies on local diversity drivers (lake area and productivity) suggest mechanistic hypotheses, they are not unequivocally explanatory in themselves. For example, that a region of greater area contains more species may be due to 1) chance (e.g. a sampling effect), 2) a larger presence and diversity of habitats (habitat variability effect), or 3) lower extinction and higher colonization rates (the metapopulation effect) (Connor & McCoy 1979; MacArthur & Wilson, 1967). Similarly, the often observed unimodal relationship between diversity and productivity can result from various mechanisms including: habitat variability, predator-prey dynamics, relative supply of resources, and the outcome of competitive interactions (reviewed in Leibold, 1999). This study focused on two hypotheses used to explain zooplankton diversity across trophic gradients, the resource ratio hypothesis, and the spatial resource heterogeneity hypothesis.

The resource ratio hypothesis assumes that the relative abundance of primary and secondary resources varies with environmental productivity (Leibold 1999). If zooplankton species differ in their minimum requirements of a resource, then more species would be supported by increasing productivity (Schoener, 1976) Accordingly, the change in relative abundance of limiting resources is expected to result in changes in zooplankton species diversity (Leibold 1999). Additionally, it is predicted that species that feed on a primary resource will be replaced by those that specialize on a secondary resource when this second resource is dominant, and thus, that a mix of both types of species would be found at an intermediate level of productivity (Huisman & Weissing, 1995).

In lakes, the quality of phytoplankton food resources may change along a total phosphorus (TP) gradient. A study using previously published data by Watson, McCauley, & Downing (1992) demonstrated a relative increase in "inedible algae" for zooplankton as the concentration of phosphorus increased in lakes. Lakes with increased productivity due to TP loading have increased concentrations of blue-green algae (Smith, 1983; Watson, McCauley, & Downing, 1997), and thus the relative abundance of other groups of phytoplankton decline. These changes in relative abundances of phytoplankton, however, have not been related to zooplankton community dynamics and biodiversity. It is known that blue-green algae is a poor food source for *Daphnia* (Lampert, 1981) and that calanoids such as *Diaptomus* have a competitive advantage when blue-green concentrations are high (Richman & Dodson, 1983). However, the overall effect of blue-green algae dominance on zooplankton biodiversity is unknown. According to the resource ratio hypothesis, the diversity of zooplankton should vary with the relative abundance of primary and secondary resources. While feeding studies have elucidated some zooplankton feeding preferences (e.g. Bogdan & Gilbert, 1982; Richman & Dodson, 1983), it is not known which groups of phytoplankton are the most important determinants of zooplankton diversity. This study will use major phytoplankton spectral groups to determine which groups of phytoplankton play a role in zooplankton diversity *in situ*.

While the relative concentration of different resources may have effects on diversity, the spatial heterogeneity of resources may also play an important role. When total resource abundance fluctuates over time and space, it is hypothesized that species richness will be highest at an intermediate level of this heterogeneity or disturbance (Connell, 1978). This intermediate disturbance hypothesis (IDH) is based on the assumption that species will experience trade-offs, whereby some species have a competitive advantage at high resource abundance and others have a competitive advantage at low resource abundance (Abrams, 1984). Flöder & Burns (2005) observed a quadratic relationship between phytoplankton richness and the interval length of light phases using experimental cultures providing support for IDH. For zooplankton, phytoplankton prey abundance or biomass can represent a variable resource factor because it is known to vary spatially along vertical light and temperature gradients in stratified lakes (Fennel & Boss, 2003). According to the IDH, therefore, lakes with greater intermediate spatial resource heterogeneity should support a more diverse zooplankton community.

Phytoplankton communities display strong vertical spatial heterogeneity (i.e. along the depth profile of a lake) with peaks in total chlorophyll often occurring at the metalimnion (Fee, 1976; Pick, Nalewajko, and Lean, 1984). Although North-Temperate dimictic lakes strongly stratify in the summer, we know little about the influence of different forms of this stratification (e.g. strength, duration, shape) on the development of the communities within. There is evidence that vertical structuring and the associated mixing regimes of lakes are important factors influencing the community structure of at least phytoplankton (Harris, 1999). Changes to mixing regimes are expected owing to various anthropogenic forces, including climate change (Lehman, 2002), eutrophication (Fairchild *et al.,* 2005), and the simplification of watersheds (Northcote *et al.*, 2005). Such effects on lake mixing should lead to altered phytoplankton composition and distribution within lakes (Reynolds, Wiseman & Clarke, 1984). It is an open question as to how these changes to phytoplankton composition and distribution affect zooplankton community structure. According to IDH and other theories of resource heterogeneity on competitive interactions (Leibold, 1999), a unimodal relationship between zooplankton diversity (measured as richness) and the degree of vertical phytoplankton variability may be predicted.

To date, the question of zooplankton biodiversity response to environmental gradients in cross-lake surveys has focused on species richness as a response variable (Dodson *et al.,* 2000, Jeppesen *et al.,* 2000). However, when considering the response of communities to gradients in a more mechanistic way, one might expect that a functional approach that considers *how* species differ ecologically in their responses to resource types will be more informative. For example, the resource heterogeneity hypothesis explains diversity patterns using functional response and life history characteristics of species (Abrams, 1984; Anderies and Beisner 2000), and thus the theory assumes that species differences in a functional, and not simply a taxonomic sense, are the ones that enable coexistence. Along environmental gradients of resource variability, it is the number of different niches that should change with habitat variability, and species numbers will not matter unless additional species are functionally complementary and able to occupy vacant niches (Walker *et al.*, 1999). Therefore, we expect that a measure of the functional diversity in zooplankton communities will be more responsive to gradients of resource variability in space and in time, rather than biodiversity measured as taxonomic richness. Many studies that have focused on the relationship between terrestrial plant biodiversity and ecosystem function have concluded that functional diversity measures explain a greater percentage of variation in ecosystem function (e.g. Tilman *et al.* 1997; Symstad, Siemann, & Haarstad, 2000; Walker *et al.*, 1999). Here, we propose a similar approach to the study of zooplankton communities in terms of their responses to resource heterogeneity.

In this study, the focus will be on the effects of vertical heterogeneity in chlorophyll biomass in four major phytoplankton spectral groups (browns (i.e. diatoms and chrysophytes), blue-greens, greens, and cryptophytes) for zooplankton biodiversity to test the hypothesis that intermediate resource heterogeneity supports a higher diversity of zooplankton. We will also test the resource ratio hypothesis by examining the effect of the relative abundances of the four groups of phytoplankton. The consistency of these hypotheses with observed patterns will be studied using a lake survey approach. The results of this survey will then be useful for identifying directions for future experiments using zooplankton communities. In addition, this study will examine functional species diversity as a potentially superior measure for capturing the functional redundancy or complementarity of a system. We expect that functional diversity will be more strongly related to habitat variability, relative resource abundance, and lake environmental productivity than taxonomic diversity measures.

2.2 Methods

2.2.1 Study Site

Eighteen lakes in the Eastern Townships of Québec, Canada (Figure 1) were chosen along a gradient of productivity and morphological characteristics (summarized in Table 1) to ensure a range of variability in productivity, phytoplankton spectral group abundance, and vertical distribution of phytoplankton. Lakes varied in total phosphorus concentrations from 6.95 to 98.44 μg L^{-1} in Lyster and Tom Cod lakes respectively.

2.2.2 Biotic Data

Lakes were sampled for zooplankton in the summer of 2004 in the deepest zone within a two week period, once in each month of June, July and August. Zooplankton were collected by integrated vertical net hauls (starting at one meter above the bottom of the lake) using a 100 μm mesh net (2 meters long with a 0.5 m opening) and fixed in 75% ethanol. A composite sample from all three sampling times (10% of each original sample) was formed and species therein were identified using taxonomic keys (Thorp & Covich, 2001; Pennak, 1989, De Melo & Hebert, 1994; Amoros, 1984; Smith & Fernando, 1978) and an Olympus dissecting and upright microscopes. In addition to total species composition identification using composite samples, subsamples of 5 mL were removed from samples in July using a pipette and species in subsamples were counted to obtain an estimate of relative abundances until no new species were found after two consecutive sub-samples. A minimum of 400 individuals was counted in all cases. Composite samples were used for calculation of S and FD, while the July samples were used for abundance data for Redundancy analysis. This was done because more confidence can be placed in the abundance data of the singe July sampling event than the mixed samples across the entire summer which were created to estimate species richness levels primarily. Also, using these data provided an estimate of midsummer crustacean zooplankton relative abundance, a community of primary research interest in North Temperate lakes.

Phytoplankton vertical heterogeneity was assessed using the mean coefficient of variation of three profiles each measured in June, July, and September, 2004 at the same time and location as the zooplankton sampling. Phytoplankton concentration profiles were measured using a BBE Fluoroprobe (BBE Moldaenke; Beutler *et al.*, 2002)), an instrument which measures fluorometrically the concentration (in µg/L) of four spectral classes of phytoplankton, representing broadly the taxonomic classes of browns (diatoms plus chrysophytes), greens (chlorophytes), blue-greens (cyanophytes), and cryptophytes, as well as temperature profiles. Total chlorophyll values obtained with the Fluoroprobe were verified with standard chlorophyll *a* estimates from filtered water samples using an ethanol extraction and measurements on a laboratory spectrophotometer (for methods see Winterman and Mots 1965, Wetzel and Likens 1991). The average of three samples was considered representative of the distribution and concentration of phytoplankton spectral groups during the stable, stratified period in these lakes.

Total phosphorus (TP) was used to estimate environmental productivity of each lake. Samples for TP and DOC were drawn from 0.5 m below the surface of each lake using a 2L Van Dorne bottle and were frozen until analysis. In the lab, the samples were digested using 23 alkaline persulfate before passing through an Ultrospec 2100 pro spectrophotometer (Biochrom). Samples taken for DOC analysis were filtered using 0.45 µm surfactant-free membrane filters and measured following sodium persulfate oxidation using a model 1010 TOC analyzer (OI Analytical). Photic zone depth was estimated as 2.79 x secchi depth measured in July for each lake.

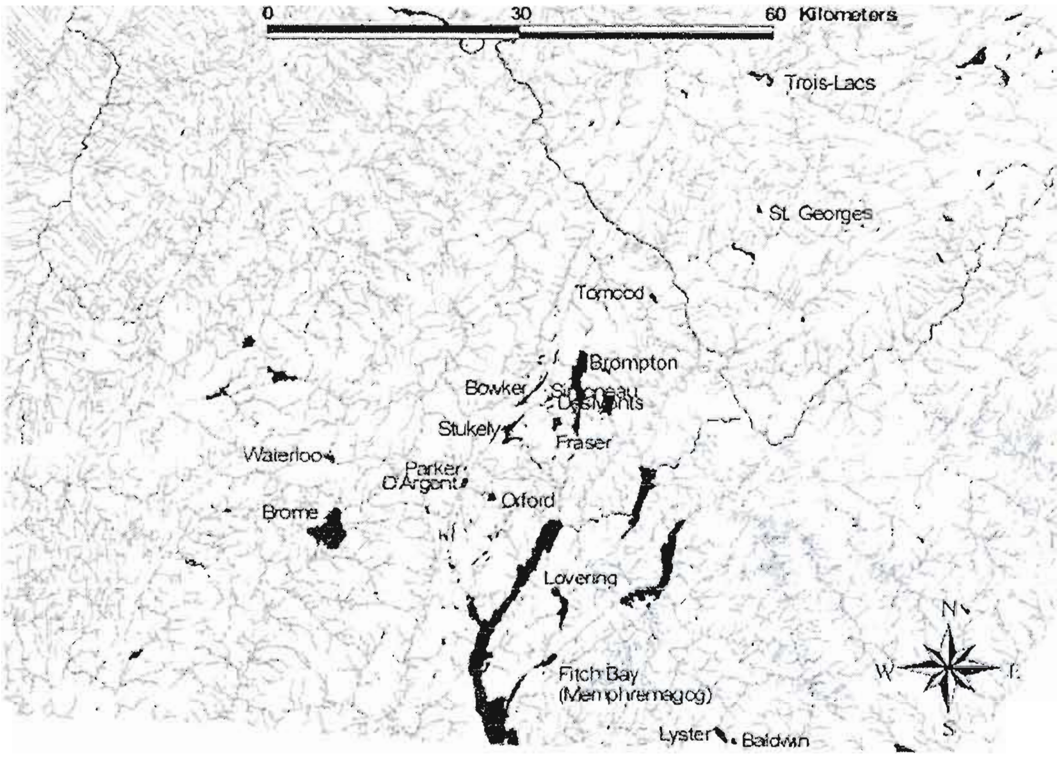

Figure 2.1 Map of 18 lakes sampled for zooplankton diversity in the Eastern Townships region of Québec, Canada

Table 2.1

Characteristics of the 18 sampled lakes in the Eastern Townships

Lakes	Latitude	Longitude	Surface Area (km²)	Maximum Depth (m)	Total Phosphorus (µg L⁻¹)	Secchi Depth (m)	DOC (mg L⁻¹)	pH
Baldwin	N45°01.096'	W071°53.325'	0.27	8.23	11.21	3.25	4.51	7.5
Bowker	N45°25.613'	W072°12.350'	2.50	61.90	7.03	9.50	2.27	7.3
Brome	N45°15.044'	W072°30.498'	14.5	12.60	24.05	3.50	3.78	7.4
Brompton	N45°25.474'	W072°08.661'	11.7	42.40	10.40	4.00	5.89	7.4
D'Argent	N45°18.565'	W072°18.967'	0.96	15.90	16.55	2.75	6.80	7.6
Des Monts	N45°24.319'	W072°11.014'	0.26	6.10	11.70	2.80	5.88	7.7
Fitch	N45°03.875'	W072°13.369'	2.18	16.70	14.76	3.60	4.69	8
Fraser	N45°23.248'	W072°10.614'	1.60	19.80	11.37	3.00	5.72	7.7
Lovering	N45°10.204'	W072°09.035'	4.90	25.00	14.45	3.20	7.09	7.4
Lyster	N45°01.806'	W071°54.775'	1.90	42.00	6.95	5.00	3.84	7.8
Orford	N45°17.591'	W072°16.133'	1.29	39.50	7.90	8.00	3.39	7.7
Parker	N45°19.623'	W072°18.813'	0.23	9.14	23.58	1.75	8.83	7.2
Simoneau	N45°24.634'	W072°11.510'	0.5	24.40	8.97	5.50	4.22	7.3
St. Georges	N45°38.859'	W071°52.952'	0.5	4.30	44.37	1.25	7.76	7.6
Stukely	N45°22.751'	W072°14.794'	4.00	30.50	8.41	5.00	4.93	7.3
Tomcod	N45°32.263'	W072°02.134'	0.80	2.50	98.44	0.75	8.85	8.2
Trois Lacs	N45°48.261'	W071°53.976'	2.40	10.10	37.11	1.75	8.49	8
Waterloo	N45°20.071'	W072°30.919'	1.50	4.50	40.38	1.50	8.27	8.2

2.2.3 Phytoplankton Relative Abundance and Variability

Phytoplankton profiles from the Fluoroprobe included data points at approximately every 1cm of depth over a maximum of 20m. In order to standardize the profiles, data points were averaged for every 10 cm interval to correct for slight differences in sampling efforts in different lakes. To obtain a measure of the variability of the phytoplankton resource, the mean and standard deviation of the concentration of greens, blue-greens, browns, cryptophytes and total chlorophyll along the whole water column was used to calculate the coefficient of variation (CV) of resources in space. The CV measure removed the possibility that variability would be confounded with mean abundance. To obtain a measure of each spectral group's relative abundance, the mean concentration of each group was divided by mean total chlorophyll. Both of these measures were calculated throughout the photic zone (estimated by multiplying the secchi depth by 2.79).

2.2.4 Functional diversity measures

Functional diversity of lake zooplankton communities was calculated using five functional traits: body size, CV of body size, habitat, trophic level, and feeding type. Body size was chosen because it is strongly correlated with ecologically relevant functional attributes such as filter feeding rate and rate of population growth (e.g. Haney, 1985; Nandini & Sarma, 2003). Mean body size for each species was measured using 10-20 individuals per species from each lake (5 or less for extremely rare species). Since our measure of functional diversity (FD; Petchey & Gaston, 2002) could not include different trait values for the same species in different sites, an average length for each species throughout all lakes was calculated. Body length averages for each lake, however, were used to compute the CV of body length between lakes for each species for inclusion in the trait matrix. The CV of body length was included in this study under the assumption that a measure of the variation in body size of zooplankton species along a gradient of environmental forces would be a good estimate of the plasticity and tolerance to environmental gradients of each species. The most common habitat, trophic level, and feeding type traits of each species was obtained from an extensive search of previous literature (Chapter I). Feeding type is the manner in which species or groups obtain their food. Cladocerans have been divided into four classes; 1) daphnid-type (D-type) where filtering is from a stationary position with filtering apparatus on the third and fourth legs, 2) sida-type (S-type) similar to D-type with the exception that the filtering apparatus is located on the first five legs, 3) bosmina-type (B-type) characterized by a horizontal active swimming and less developed filtering apparatus on thoracic appendages, and 4) chydorid-type (C-Filtration) where feeding is predominantly by scraping algal particles from periphyton. Raptorial predators like cyclopoids actively capture and kill prey, while stationary suspension feeders are more passive with less frequent swimming. Finally *Epischura lacustris* is differentiated from both raptorial and stationary suspension feeding as it swims continuously while creating feeding currents thus being characterized as a "current cruiser". Habitat preference (preference for littoral or pelagic habitats), trophic level (herbivore, carnivore, omnivore, omnivore- with a proclivity towards carnivory, and omnivore with a proclivity towards herbivory) and feeding type (*Daphnia*-type, *Sida*-type etc.) reflected a gradient of categorical numbers (Appendix 1 and also see Chapter I). The gradients for trophic level and feeding type were that of increasing carnivory and food selectivity respectively (see Appendix 1 for a list of functional traits of each species).

Using the five standardized (mean of zera and a standard deviation of one) functional traits listed above a community dendrogram based on Euclidean distances between each pair of species was estimated for all of the species found in the region. Dendrograms were created using the unweighted pair group clustering method using arithmetic averages (UGMA) (see Krebs , 1999). The functional diversity (FD) of each lake was then calculated as the sum of branch lengths of those species found therein. FD was calculated using all combinations of two or more traits, resulting in a total of 26 initial FD estimates. For a more detailed review of FD see Petchey & Gaston (2002). All FD measures were calculated using R 2.20 and code obtained from O. Petchey's website, which included a refinement to the means by which total branch lengths were computed (Petchey and Gaston 2006): that the branch lengths required to connect all species are summed, but branch lengths connecting species to the root of the dendrogram is not included. FD can be considered as a quantitative measure of the richness of functional traits, or the degree of complementarity within a community (Petchey & Gaston, 2002).

2.2.5 Statistical Analysis

FD can be calculated based on any combination of observed traits (Petchey & Gaston 2002) with a tendency to regain a value comparable to S when too many traits are included (Mason *et al.*, 2006). To determine which combination of traits should be used, regression relationships with an ecosystem variable is usually performed (Blackburn *et al.* 2005). Species richness and each functional diversity measure using all possible combinations (26) of five traits (Appendix 2) were related to environmental productivity (TP). This was done to determine which combination of functional traits are best explained by productivity, and to eliminate other functional trait combinations that were most poorly explained from future analyses. In this initial step, a false discovery rate correction was used to correct for multiple comparisons ($\alpha=0.05$).

To test the suitability of the resource ratio hypothesis in crustacean zooplankton communities, mean biomass of each spectral group of phytoplankton was related to TP concentration. Initially, the prediction that mean resource biomass increased along the productivity gradient was verified. Then zooplankton species richness and FD were related to relative biomass of each spectral group (expressed as proportion of total) of phytoplankton. These regressions were used to determine which groups of phytoplankton were most important for zooplankton diversity. Finally, the ratio of biomass of the two phytoplankton groups identified as most important were related to zooplankton diversity using linear or quadratic regressions. In the case where both linear and quadratic relationships were significant, the fit line with a higher Akaike weight was chosen (see Johnson & Omland, 2004).

In order to test the suitability of the resource heterogeneity hypothesis, the relationship between the CV of each spectral group of phytoplankton and TP was determined, again to be sure that phytoplankton heterogeneity varied along a productivity gradient. Then, species richness and FD were related to the CV of phytoplankton groups using regressions testing for a quadratic or linear relationship.

2.2.6 Biotic influences of zooplankton species composition and abundance

To determine more mechanistically how particular zooplankton species respond to phytoplankton concentrations, and to contrast responses to resource availability with top down effects of fish predation, a redundancy analysis (RDA) was used to relate zooplankton species abundances to phytoplankton concentrations and the presence of fish predators using CANOCO (ter Braak, 1994). The zooplankton species dataset was Hellinger-transformed (Legendre & Gallagher 2001) after rare species (found in fewer than 3 lakes) were removed. The environmental matrix consisted of the mean photic zone concentrations of green, blue-green, brown, and cryptophyte algae, and the presence or absence of common species (found in greater than 3 lakes) of planktivorous and piscivorous fish. Fish information spans several decades and comes from the MRNF (Ministère des Ressources Naturelles et de la Faune; previously Société de la Faunes et des Parcs du Québec) database (Pierre Lévesque pers. comm.). Forward selection using a Monte-Carlo permutation test (1000 permutations) was used to determine significant environmental influences for inclusion in the final model. Species in the model were labeled according to the species groupings identified by the functional dendrogram of the FD measure that was most strongly related to environmental productivity.

To determine ecologically relevant groups of zooplankton for use in the above analysis, the dendrogram of the FD measure most strongly related to environmental productivity was generated, and functional groups were identified. Species belonging to these groups were then plotted to determine whether individual species belonging to these groups of species respond to environmental gradients in the same manner.

2.3 Results

Zooplankton diversity measures along with the coefficients of variation of phytoplankton groups and total chlorophyll are summarized in table 2.

2.3.1 Effect of Environmental Productivity (TP) on Diversity

Regressions with species richness generally exhibited a large degree of scatter, and while no significant effect of TP on species richness was observed (R^2=0.20, P = 0.18), a curvilinear trend was present (Figure 2 A). When functional diversity, using traits 1 and 4 (body length and trophic level respectively), was used, a significant negative linear relationship was observed (Figure 2 B; R^2_{adj}=0.50, P = 0.0006). Since traits 1 (body length) and 4 (trophic level) were the most significantly related to TP, the remaining 25 combinations of functional traits were not included in further analysis (See Appendix 2 for results). The diversity of these traits are most affected by TP, and this should occur because TP alters phytoplankton abundance and distribution, Therefore in order to fit the predictions of the resource heterogeneity and resource ratio hypothesis, the diversity of traits 1 and 4 should be most strongly related to resource heterogeneity or relative resource abundance.

2.3.2 Resource Ratio Hypothesis

The biomass of green, brown, cryptophyte and especially blue-green algae (P <0.025; Figure 3 A-D) all increased with increasing TP concentrations. While the proportion of green algae had no significant effect on FD (Figure 4 A), lakes with a higher proportion of blue-greens were less functionally diverse in zooplankton (Figure 4 B), though this relationship was not highly significant (P = 0.065). FD increased significantly with an increased proportion of browns (*P* = 0.002; Figure 4 C), and a similar increasing trend in FD with cryptophytes (Figure 4 D) was observed. No trends were significant, nor visible in regressions between log species richness and logged proportions of greens, blue-greens, browns, and cryptophyte algae (all *P* > 0.3; Figure 5 A-D).

Since the strongest relationships were found between FD and browns and blue-greens (Figures 4 B and C), the relationship between FD and the ratio of brown algae to blue-green algae was used to test the resource ratio hypothesis. A significant curvilinear relationship was found between FD and the ratio of brown algae to blue-green algae concentrations (Figure 6 A). This curvilinear model was slightly better than a linear model with AIC values of -40.18 and -39.38 respectively (Akaike weight of 60% for a curvilinear model). Species richness was not significantly related to the ratio of brown to blue-green algae concentration (Figure 6 B).

Table 2.2

Table of zooplankton FD in each lake along with the biomass and coefficient of variation of total greens, blue-greens, diatoms, cryptophytes, and total chlorophyll.

	Functional Diversity	CV Green	CV Blue-green	CV Diatoms	CV Cryptophytes	CV Total	Mean Total Chl (µg L⁻¹)	Green Biomass (µg L⁻¹)	Blue-green Biomass (µg L⁻¹)	Diatom Biomass (µg L⁻¹)	Cryptophyte Biomass (µg L⁻¹)
Baldwin	25.46	0.75	1.32	0.81	1.06	0.61	3.78	0.34	0.33	2.45	0.66
Bowker	23.91	0.66	10.91	0.51	1.88	0.46	1.39	0.04	0.00	0.86	0.47
Brome	20.45	2.70	0.91	0.66	1.05	0.24	4.78	0.48	1.62	1.80	0.87
Brompton	26.34	0.52	1.67	0.29	2.73	0.19	1.74	0.16	0.30	0.92	0.37
Dargent	21.11	0.36	0.86	0.36	0.55	0.35	2.52	0.51	0.35	1.28	0.37
Des Monts	21.85	0.36	1.05	0.39	1.14	0.26	2.71	0.63	0.29	1.58	0.21
Fitch	27.54	0.93	1.41	0.40	0.40	0.20	3.74	0.18	1.01	1.44	1.11
Fraser	23.18	0.44	0.94	0.34	0.35	0.21	2.70	0.29	0.36	1.46	0.59
Lovering	16.17	0.62	0.43	0.46	0.31	0.29	1.98	0.15	0.28	1.04	0.52
Lyster	24.42	1.37	3.26	0.45	0.81	0.24	0.95	0.03	0.03	0.62	0.27
Orford	26.36	2.08	6.37	0.90	1.34	0.69	1.86	0.13	0.06	1.19	0.49
Parker	21.89	0.38	1.62	0.51	0.87	0.37	6.55	1.10	2.17	2.70	0.59
Saint georges	15.40	0.29	0.71	0.30	0.64	0.30	8.82	5.01	4.35	2.94	0.88
Simoneau	25.25	1.73	2.25	0.80	0.59	0.50	6.94	0.05	0.26	1.66	0.59
Stukely	18.66	2.51	0.91	0.49	0.95	0.27	1.24	0.04	0.19	0.52	0.50
Tomcod	14.21	0.19	0.18	0.16	0.26	0.18	23.09	1.51	16.93	1.97	2.68
Troislacs	21.40	0.30	3.16	0.37	0.34	0.34	4.86	0.81	0.09	2.54	1.41
Waterloo	17.30	1.01	0.26	1.26	0.40	0.22	20.30	0.81	15.76	0.96	2.76

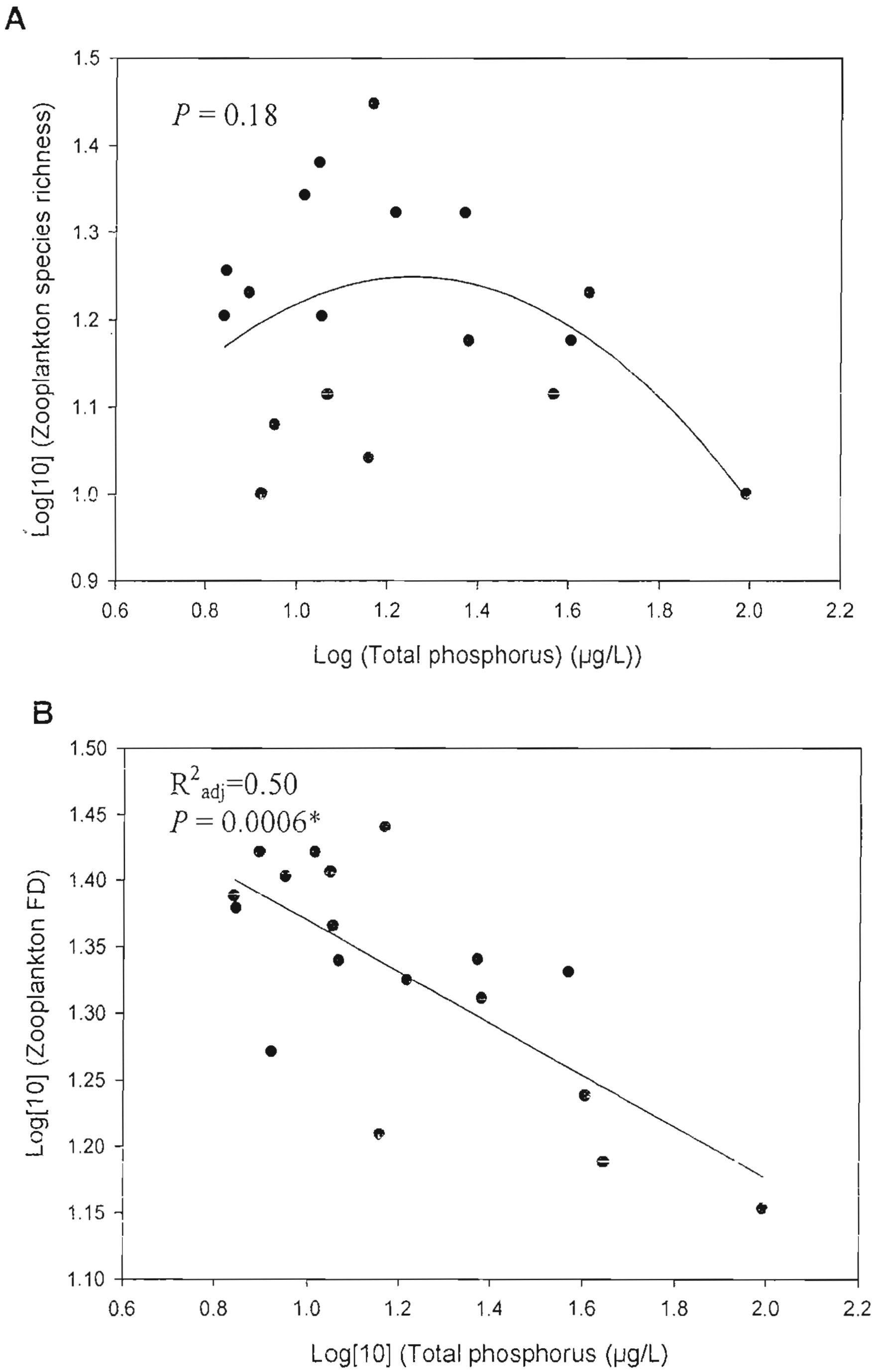

Figure 2.2 Log-transformed regressions of (A) functional diversity using traits 1 and 4 (body length and trophic level respectively) and (B) species richness against concentration of total phosphorus

2.3.3 Resource Heterogeneity Hypothesis

Lakes with a higher concentration of TP had significantly lower vertical variability in the concentration of each phytoplankton group in the photic zone (Figure 7 A-D), with the exception of browns ($P > 0.10$) which also had the smallest CVs. When the CV of total chlorophyll was related to the concentration of TP, no significant relationship was found (Figure 7 E). FD increased significantly with the CV of green (Figure 8 A), blue-green (Figure 8 B), and cryptophyte (Figure 8 D) algae throughout the photic zone. The strongest of these relationships was found between FD and the CV of blue-green algae ($R^2_{adj}=0.63$, $P < 0.0001$). A curvilinear model was slightly better than a linear one with AIC values of -45.36 and -44.27 respectively (Akaike weight of 63% for curvilinear model). A curvilinear model and a linear model significantly explained FD using CV of greens and cryptophytes respectively. No effect of the CV of brown algae, and total chlorophyll was found on functional diversity (Figures 8 C and E). The unusual pattern in the relationship between FD and the CV of total chlorophyll seemed to be due to a high zooplankton diversity and range in variability of total chlorophyll in oligotrophic lakes (<10 μg TP/L), but high zooplankton diversity and lower variability of total chlorophyll in several mesotrophic lakes (10-20 μg TP/L). No significant relationships between species richness and the CV of greens, blue-greens, browns, cryptophytes, and total chlorophyll were observed in the photic zone (Figure 9 A-E), though there was a weak trend for a curvilinear relationship between species richness and the CV of greens.

2.3.4 Biotic influences of zooplankton species composition and abundance

Since FD using body length and trophic level was most strongly related to environmental productivity, a functional dendrogram using these two traits was constructed (Figure 10). This dendrogram allowed for the identification of three distinct zooplankton groups; 1) copepods (calanoids and cyclopoids) with the exceptional inclusion of the predatory cladoceran *Polyphemus pediculus*, 2) Small cladocerans including bosminids, *Chydorus*, and *Diaphanosoma*, with the inclusion of one small *Daphnia* species (*Daphnia parvula*), and 3) *Daphnia* species with the addition the herbivorous calanoid of *Leptodiaptomus sicilis*, and the littoral cladoceran *Sida crystallina*.

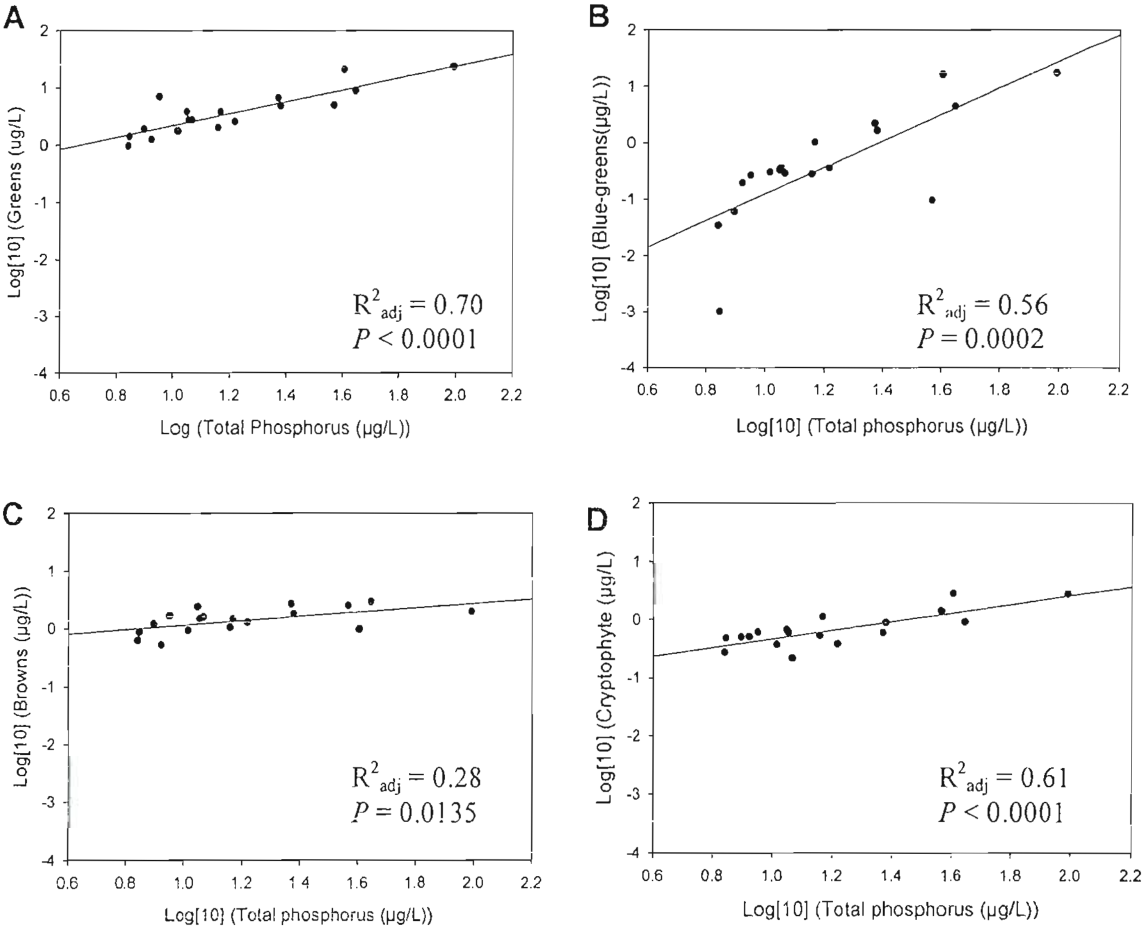

Figure 2.3 Log-transformed regressions of the concentration of (A) green, (B) blue-green, (C) brown, and (D) cryptophyte algae, with environmental productivity (total phosphorus)

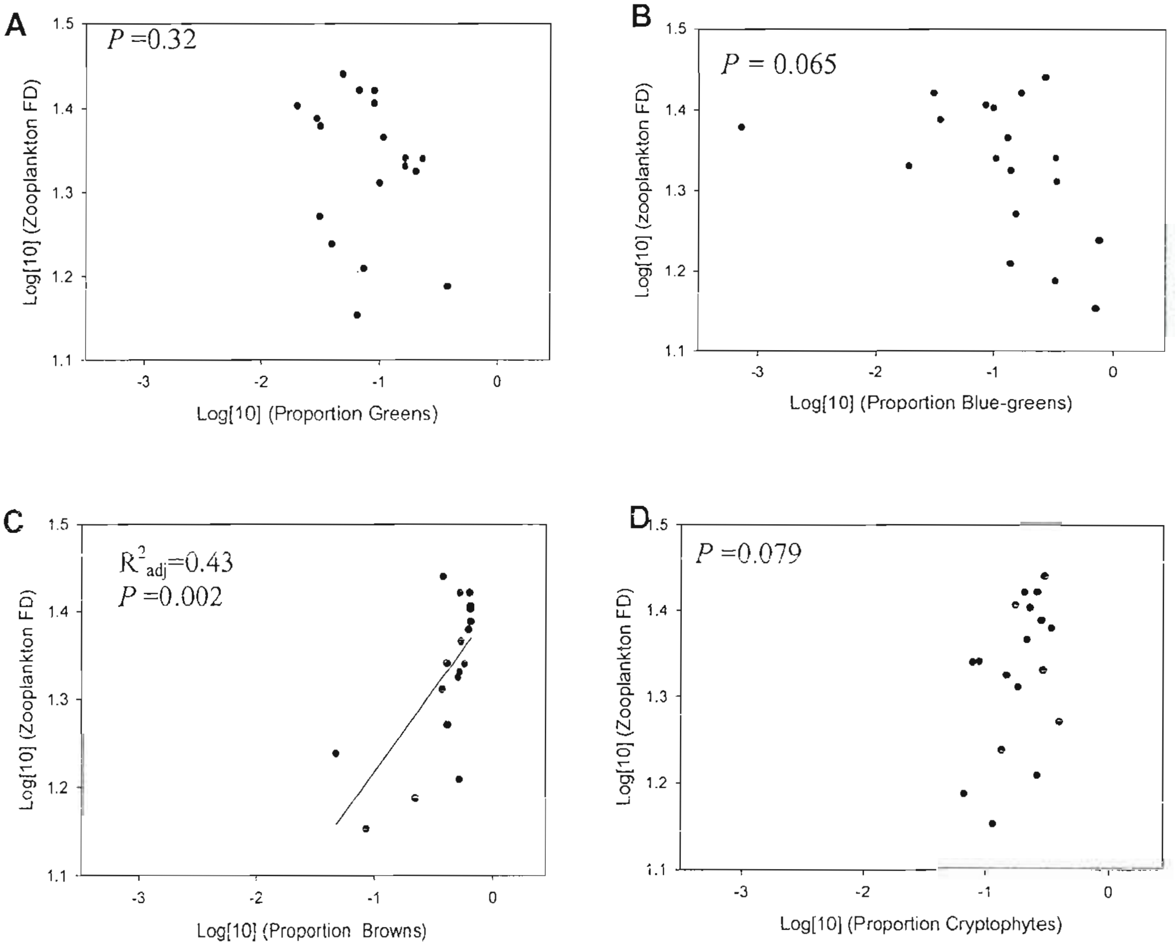

Figure 2.4 Log-transformed regressions of zooplankton functional diversity using traits 1 and 4 (body size and trophic level respectively) with the proportion of (A) green algae, (B) blue-green algae, (C) brown, and (D) cryptophyte concentration throughout the photic zone

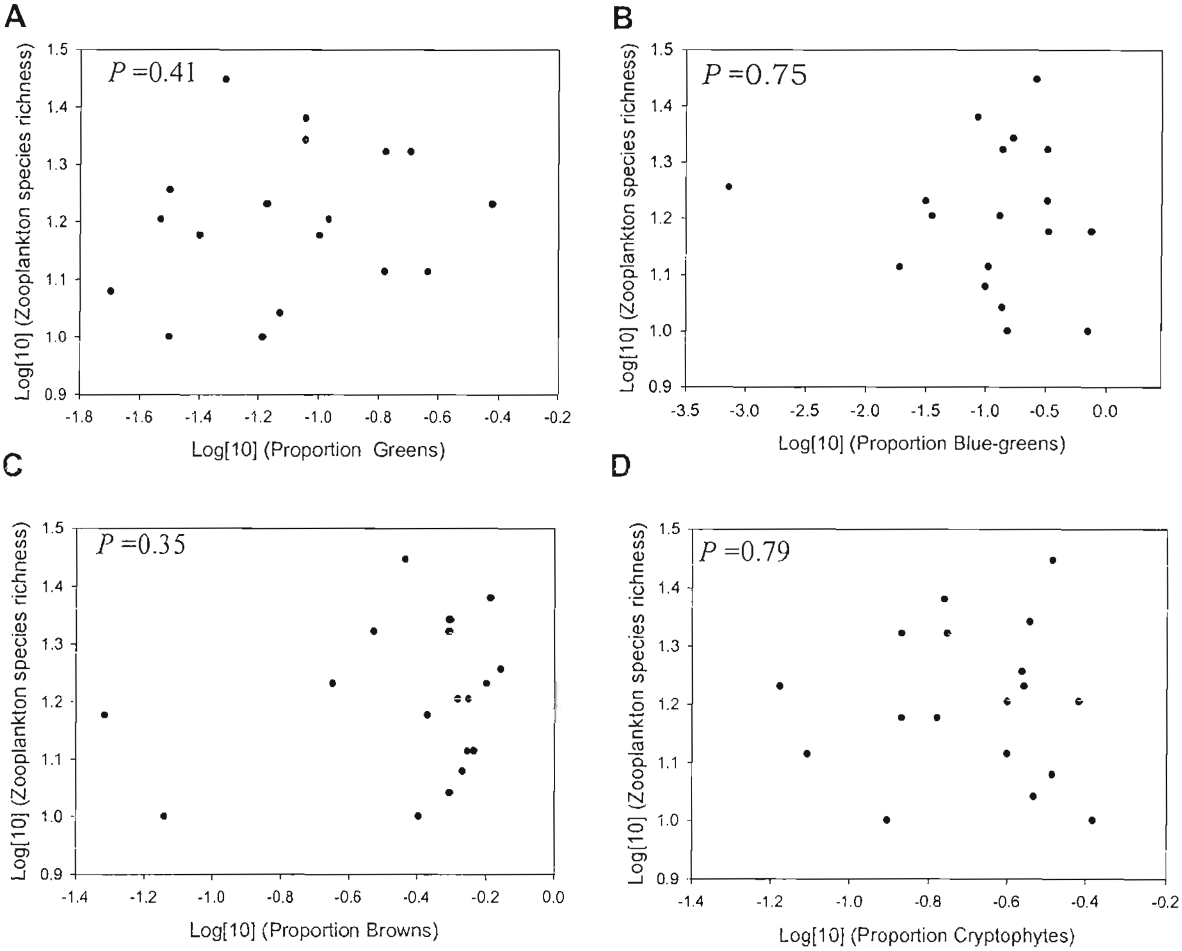

Figure 2.5 Log-transformed regressions of species richness with the proportion of (A) green algae, (B) blue-green algae, (C) brown algae, and (D) cryptophyte concentration throughout the photic zone

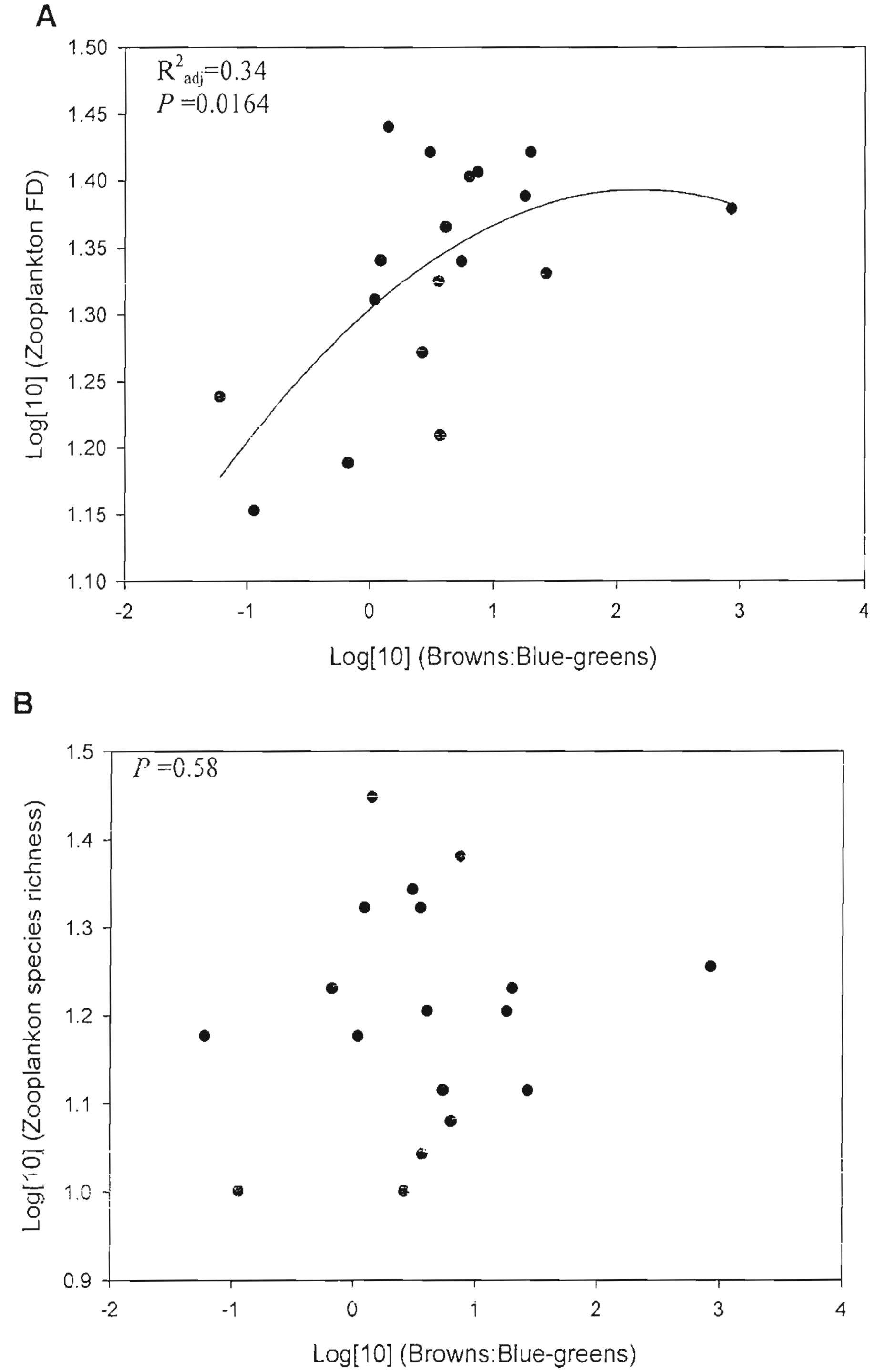

Figure 2.6 Log-transformed regression of (A) functional diversity using traits 1,4 (body length and trophic level respectively) and (B) species richness with the ratio of brown to blue-green algae concentrations measured in the photic zone

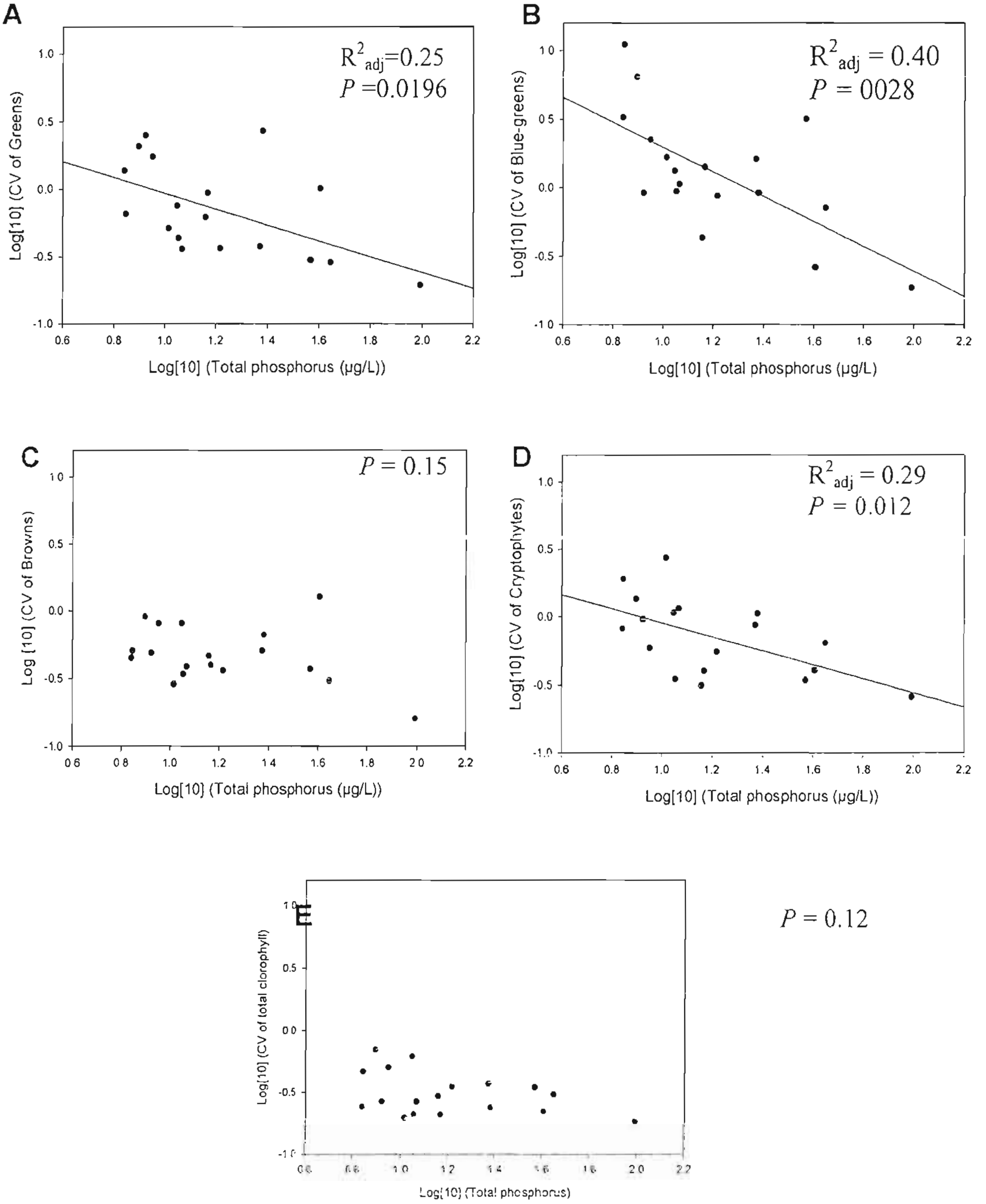

Figure 2.7 Log-transformed regressions of photic zone CV in (A) green algae, (B) blue-green algae, (C) brown algae, (D) cryptophyte algae, (E) total chlorophyll, with environmental productivity (total phosphorus)

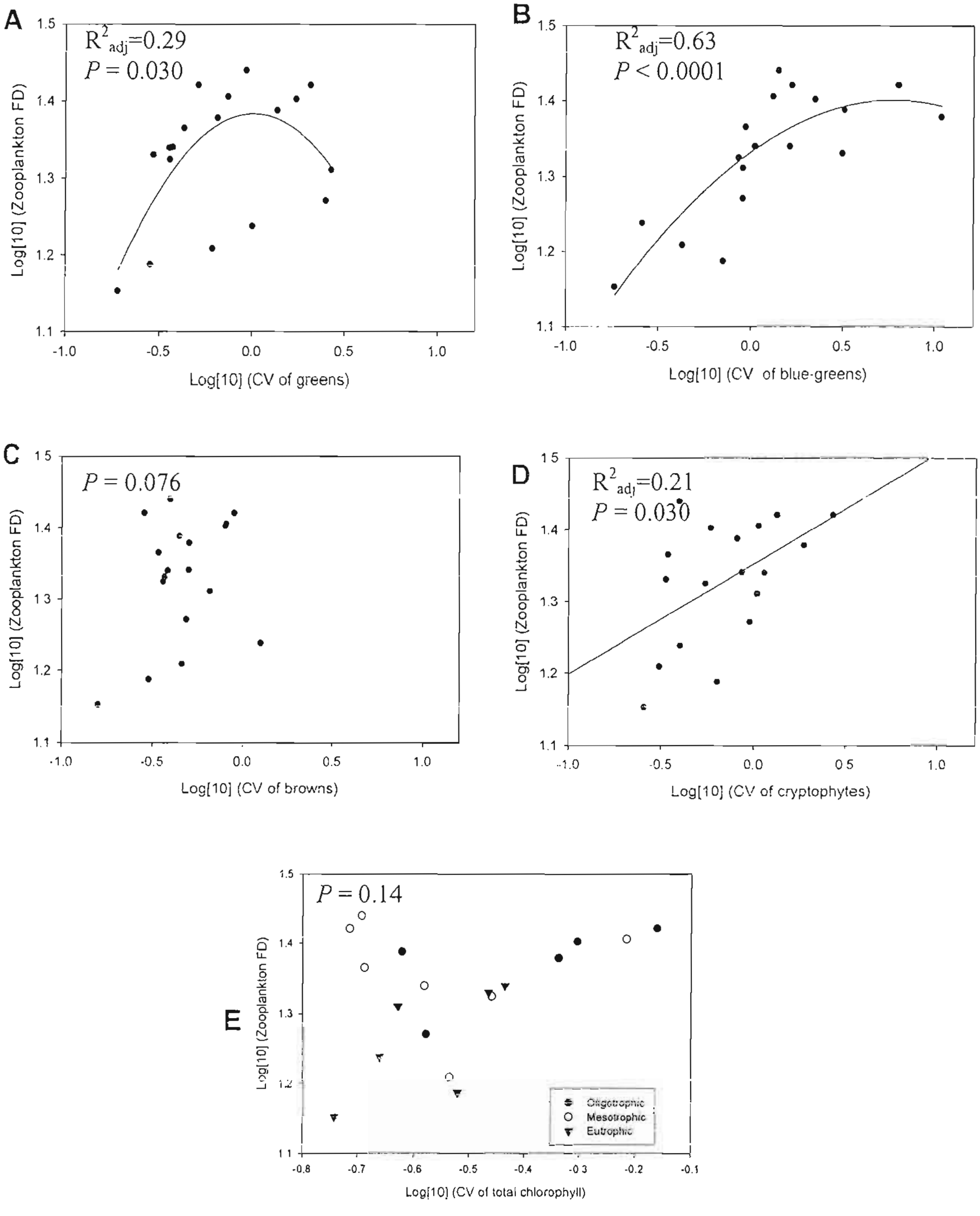

Figure 2.8 Log-transformed regressions of zooplankton functional diversity using traits 1 and 4 (body size and trophic level respectively) with the photic CV in (A) greens, B) blue-greens, (C) browns, (D) cryptophytes, and (E) total chlorophyll concentration

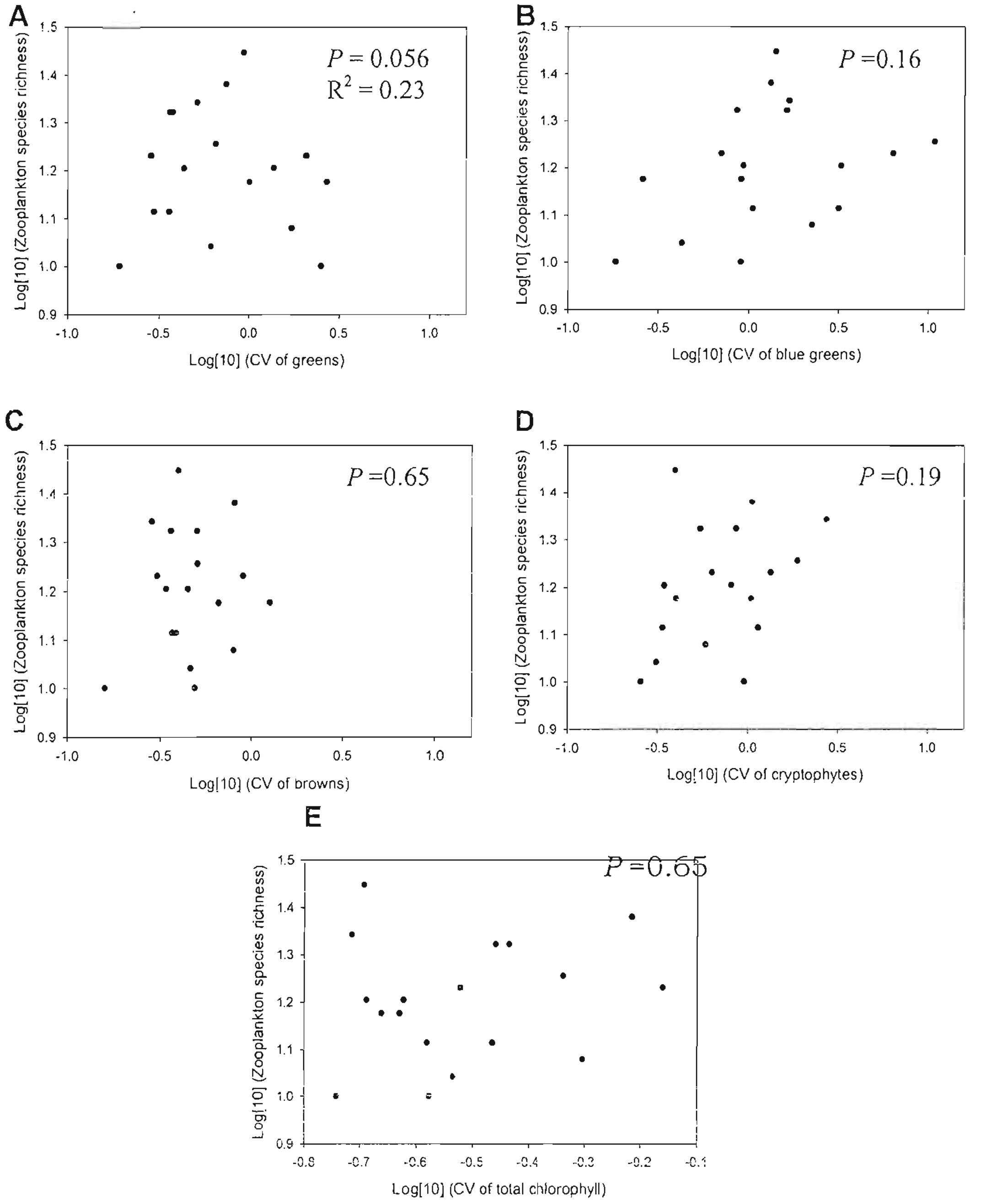

Figure 2.9 Log-transformed regressions of zooplankton species richness with the photic CV in (A) greens, (B) blue-greens, (C) browns, (D) cryptophytes, and (E) total chlorophyll concentration

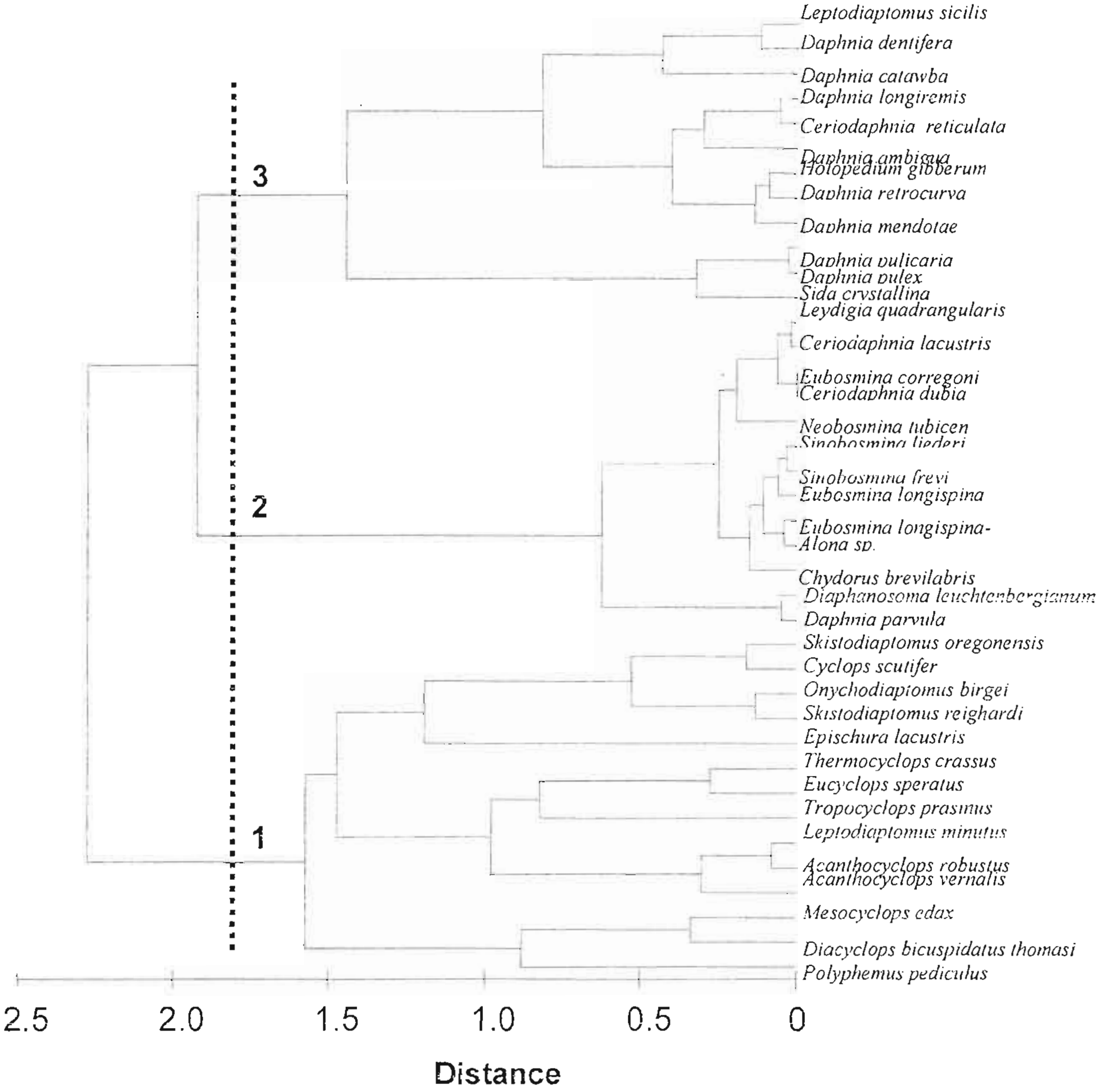

Figure 2.10 Functional dendrogram based on the Euclidean distances between all zooplankton species found in 18 Eastern Township lakes. The dendrograms was created using the unweighted pair group clustering method using arithmetic averages (UGMA). The division of the tree into three functional branches is indicated by the dashed line, and each resulting functional grouping is numbered

The responses of each species belonging to the three broad functional groupings above are shown in the biplot of species and environmental variables in Figure 11. Four environmental variables significantly explained 50% of zooplankton species composition and abundance (P = 0.0010 for all axes); the concentrations of blue-green and brown algae, and the presence of the planktivorous fish species *Coregonus clupeaformis*, and *Osmerus mordax*. The biplot shows that different species are more strongly affected by different environmental variables. Blue-green algae had a strong positive effect on *Chydorus brevilabris*, *Eubosmina corregoni*, and *Tropocyclops prasinus*, and a negative effect on *Daphnia longiremis*, *Sinobosmina liederi*, *Holopedium gibberum*, and *Epischura lacustris*. Brown algae concentration had a positive effect on *Acanthocyclops vernalis*, and *Ceriodaphnia lacustris*, and a negative effect on *Eubosmina longispina-oriens*, and *Daphnia mendotae*. *Osmerus mordax* presence had a positive effect on *Cyclops scutifer*, *Daphnia catawba*, and *Daphnia pulicaria*, and *Coregonus clupeaformis* presence had a positive effect on *Sinobosmina freyi*, and *Diaphanosoma leuchtenbergianum*. It is also clear from Figure 11 that particular functional groups defined using the functional dendrogram (Figure 10) are not reacting similarly to the joint effects of planktivore presence, and blue-green and brown algae abundance. Groups 1, 2, and 3 are found scattered in all directions in the biplot.

Table 2.3

Relative abundances of crustacean zooplankton species in each lake.

Lake	Baldwin	Bowker	Brome	Brompton	d'Argent	Des Monts	Fitch	Fraser	Lovering
C. affinis	0.14	0	0	0	0.11	0	0	0	0
C. lacustris	1.11	0	0.47	0	0.19	0.39	0.83	0	0.08
C. reticulata	2.25	0	0	0	0	0	1.65	0.32	0
C. brevilabris	0.10	0	0	0	0	0	0.11	0	0
D. ambigua	0	0	0	0.15	1.15	0	0.21	0	0
D. catawba	0	0.43	0	0.30	0	2.96	0	0.04	0
D. longiremis	0	0	0	0.07	9.37	0	0.78	0.73	5.89
D. mendotae	0.25	0.20	0.07	0.05	0.06	2.70	0.46	1.30	2.78
D. parvula	0	0	0	0	0	0	0.42	0	0
D. pulex	0	0	0	0	0	0	0	0	0
D. pulicaria	0	0.47	0	0.25	0	0	0	0	0
D. retrocurva	0.68	0	0	0	5.35	0	2.12	0.08	0
D. leuchtenbergianum	0.24	0	0	0.07	3.64	0	0.12	0	0
H. gibberum	0.49	0.09	0	0.05	0.34	7.14	0.24	0.32	0.43
L. quadrangularis	0	0	0	0	0.03	0	0	0	0
E. coregoni	0.06	0	0.94	0	0	0	0	0	0
E longispina	0.07	0.16	0	0.04	0.02	0	0	0	0.23
E. longispina-oriens	0.00	0	0	0	0	0	0.74	0.01	0
N. tubicen	0.03	0	0	0.05	0	0	0	0	0
S. freyi	0.41	0.06	8.89	0.20	2.29	35.77	2.62	0.74	0.05
S. liederi	0.05	0.06	0	0.35	0.67	0	0.62	0.05	0
P. pediculus	0	0	0	0	0	0	0	0	0
A. robustus	1.45	0	0.09	0	0	0	4.57	0	0
A. vernalis female	8.28	0	0	0	0	0.89	0	0	0
C. scutifer	0	0.80	0	2.63	1.96	0	1.15	0.43	0
D. bicuspifatus thomas	0	0.50	0	41.29	5.88	28.51	8.47	60.03	10.17
E. speratus	0	0	0	0	1.96	0	0	0	0
M edax	1.45	0.19	1.46	3.38	7.84	16.93	0.13	5.30	0.19
T. prasinus	0.29	0	0	0	0.98	7.13	1.39	1.28	0
E. lacustris	0.03	0	0	0	0.13	0	0.11	0	0.24
L. minutus	1.71	0.45	0.82	3.96	1.92	2.66	1.57	2.71	4.01
L. sicilis	0	0	0	0	0	0	2.23	0	0
S. oregonensis	0.71	0	0.06	0	1.28	0.44	0	0	0
S. reighardi	0	0	5.84	0	0	0	0	0	0

Table 2.3 (continued)

Relative abundances of crustacean zooplankton species in each lake.

Lake	Lyster	Orford	Parker	Simoneau	St. Georges	Stukely	Tom Cod	Trois Lacs	Waterloo
C. affinis	0	0	0	0	0	0	0	0	0
C. lacustris	0	0	1.43	0	53.34	0	0	0	0.20
C. reticulata	0	0	0	0	0	0	0	0	0
C. brevilabris	0.02	0	0.22	0.02	0.53	0	88.52	0	10.60
D. ambigua	0	0	2.51	0.05	14.55	0	0	0	0
D. catawba	0.02	0.06	0	0.12	0	0	0	0	0
D. longiremis	0	3.99	0	0	10.92	0	0	0	0
D. mendotae	0.22	0.12	0	2.21	0	0.37	3.71	0	4.22
D. parvula	0	0	0	0	0	0	0	0	0
D. pulex	0	0	0	0.02	0	0	0	0	0
D. pulicaria	0.18	0.03	0	0	0	0.91	0	0	0
D. retrocurva	0	0	7.25	0	34.80	0.20	0.18	2.26	1.49
D. leuchtenbergianum	0	0	0.22	0.02	0	0	0	0.75	1.43
H. gibberum	0.06	0.33	0	0	7.20	0.15	0	0	0
L. quadrangularis	0	0	0	0	0.27	0	0	0	1.63
E. corregoni	0	0	0	0.02	0	0	22.26	0	10.80
E longispina	0	0	3.03	0	0	0	0	0.15	0
E. longispina-oriens	0	0.47	0	0	0	1.41	2.65	0	0
N. tubicen	0	0	0	0	0	0	0	0	0
S. freyi	0.17	1.16	3.99	0	5.87	0	0	1.26	0
S. liederi	0	0	0	0	0	0	0	0	0
P. pediculus	0	0	0	0.04	0	0	0	0	0
A. robustus	0	0	0	0	0	0	0	0.25	14.08
A. vernalis female	0	0	0.32	0	9.66	0	17.89	0	0
C. scutifer	3.03	6.72	0	0.61	0.00	0	0	0	0
D. bicuspifatus thomas	0	0	0.32	16.29	0	7.35	0	0	0
E. speratus	0	1.01	0	0	0	0	0	0	0
M edax	0.12	1.13	13.48	3.45	26.49	2.54	0	11.82	6.96
T. prasinus	0	0.87	0	0	8.39	0	125.23	0	0
E. lacustris	0.08	0.07	0	0.05	0	0.02	0	0.94	0
L. minutus	0.37	1.98	2.32	1.79	4.00	3.49	0	0	23.62
L. sicilis	0	1.49	0	0	0	0	0	0	0
S. oregonensis	1.64	0	1.16	0	0	0	0	4.28	0
S. reighardi	0	0	0	0	0	0	4.77	0	0

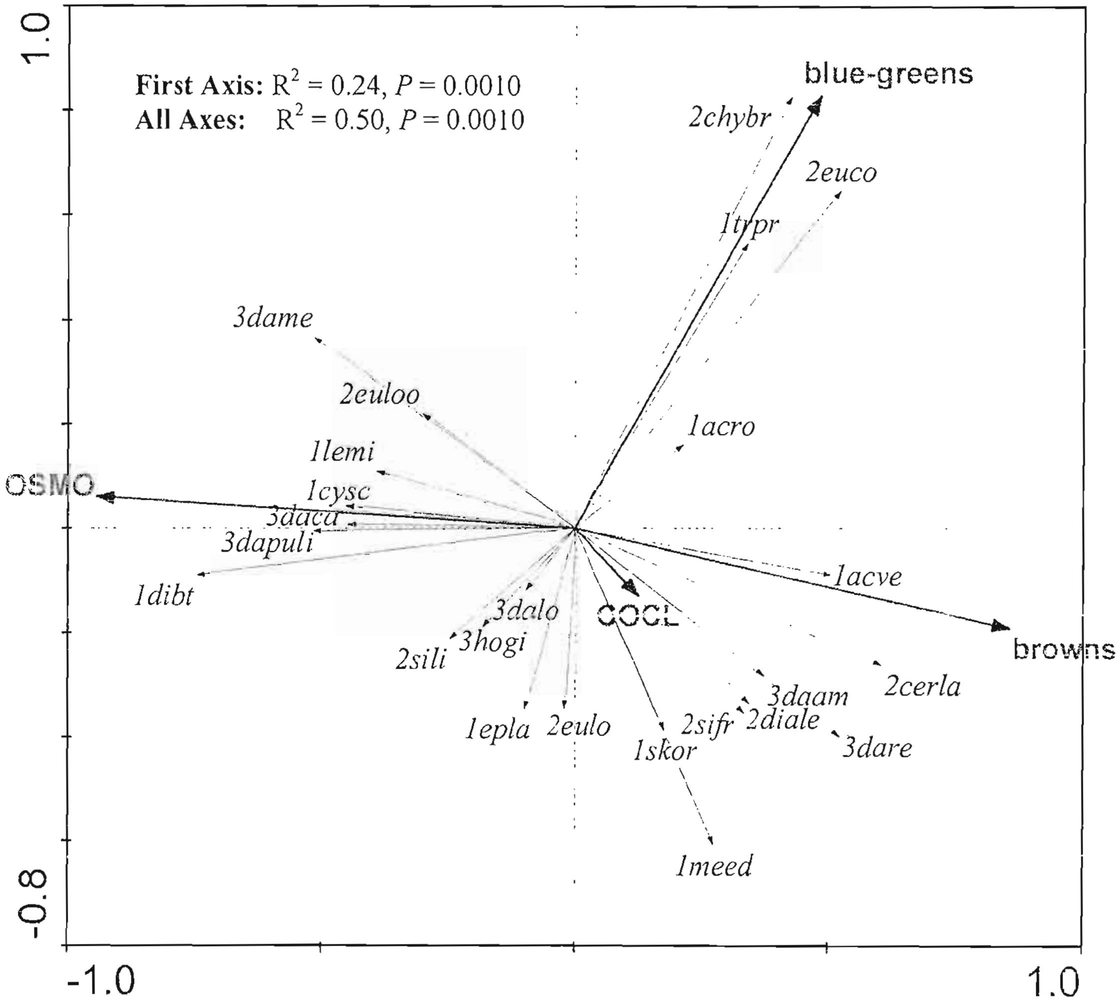

Figure 2.11 Results of Redundancy Analysis (RDA) of the response of Hellinger-transformed zooplankton abundance (number per liter) to fish presence (COCL = *Coregonus clupeaformis*, OSMO = *Osmerus mordax*) and blue-green and brown algae concentration. Species names are abbreviated with the first two letters of the genus and the specific epithet (See Appendix 1). Numbers before abbreviated species names indicate the functional group defined from the functional dendrogram (see Figure 10) to which each species belongs.

2.4 Discussion

The often observed curvilinear relationship between species richness and environmental productivity (Dodson, 1992; Dodson *et al.*, 2000; Waide *et al.*, 1999) was not found in this study despite a wide range of phosphorus concentrations in studied lakes. A trend towards a quadratic relationship, however, suggests that the lack of a significant relationship is due to low statistical power with 18 lakes. Further, taxonomic species richness was not significantly related to any of the environmental drivers (phytoplankton abundance, resource ratios, heterogeneity, TP) examined in this study.

Despite low power for the species richness responses, a strong negative relationship was found between FD and environmental productivity when traits of body size and trophic level were used. Regression plots between functional diversity and TP, resource concentrations, ratios, and heterogeneity have less scatter than those using species richness (as observed in the R^2_{adj} values of regressions) suggesting that functional diversity can be a more responsive biodiversity measure for crustacean zooplankton. However, in addition to being more responsive, functional measures also appear to show different relationships than those usually observed with S. Rather than the more common quadratic relationship expected when using species richness, a negative linear relationship was observed here between FD and TP. Since FD is a measure that characterizes zooplankton niches(Diaz & Cabido, 2001), the different pattern may be due to a tighter relationship between FD and niche complexity, than for richness. The heterogeneity hypothesis, predicts a curvilinear relationship between resource heterogeneity and productivity (Rosenzweig & Abramsky, 1992), but we found a negative linear relationship between spatial vertical heterogeneity (CV of phytoplankton concentrations) and TP. Since there was considerable variation in productivity (TP), it is unlikely that this observed linear relationship reflects insufficient sampling of low productivity lakes. Thus, the hypothesized curvilinear relationship between heterogeneity and productivity may not be applicable to these Eastern Township lakes. This negative relationship between resource heterogeneity and productivity likely then drove the negative linear relationship between zooplankton FD and TP (confirmed by a positive linear relationship between FD and resource heterogeneity (CV)). Whether the relationship between FD and heterogeneity in this study is linear or curvilinear remains uncertain since the Akaike weight of the curvilinear relationships was only slightly better than that of the linear ones.

To date, literature supporting the resource ratio hypothesis in lakes has been limited to theoretical and empirical studies on phytoplankton (e.g. Huisman & Weissing, 1995; Makulla & Sommer, 1993). These studies have shown that the ratios of silica to phosphorus (Makulla & Sommer, 1993) and nutrients to light (Huisman & Weissing, 1995) can influence the dominance by and coexistence of phytoplankton species. In this current study, we noted an increase in dominance of blue-green algae even as the biomass of all spectral groups of phytoplankton resources increased with phosphorus concentrations. This increasing dominance by blue-green algae with increasing productivity is supported by previous work (e.g. Watson *et al.* 1997; Smith 1983).

Despite the increases in all phytoplankton groups with productivity, it was mainly an increase in the proportion of browns that was associated with an increase in functional diversity of the herbivore community. Zooplankton FD was maximized when the ratio of brown to blue-green algae was high, which would generally be thought to reflect a situation where a greater proportion of phytoplankton biomass is edible to most zooplankton (Temte and Vanni, 1990). Still, since the curvilinear relationship fit to the data here was only marginally better than a linear fit, only weak evidence exists to support the resource ratio hypothesis where a maximum diversity of consumers is found at intermediate ratios of food types. The slope of the relationship between brown algae and productivity is not as steep as that of the relationship between blue-greens and productivity, and thus, lakes with a high ratio of browns to blue-greens have lower total phytoplankton biomass in addition to a difference in composition.

While it may be possible that lakes with intermediate to high phytoplankton biomasses dominated by browns would have lower zooplankton diversity than lakes with a mix of blue-greens and browns, this observation would be difficult to observe in natural settings due to the biological requirements of brown algae. This is especially the case for diatoms that are also limited by silica concentrations in the water column (Kalff & Watson, 1986). Thus, owing to the biological limitations of brown and blue-green algae, it may not be possible to observe a ratio of browns to blue-greens beyond the point at which zooplankton diversity is maximized in this dataset and that would be sufficiently high to observe a corresponding decline in zooplankton diversity. Based on the observed effect of the ratio of browns to blue-green algae, the two limiting resources for the zooplankton community in this study were identified as diatoms plus chrysophytes, and blue-green algae. Given the strong response of zooplankton FD to resource spatial heterogeneity, it is also likely that the limitation of FD by *both* resource type and spatial heterogeneity lead to the observed response. That is, at low TP concentration, spatial heterogeneity in phytoplankton resources promoted zooplankton functional diversity while at higher TP, the combined reduction in spatial and compositional heterogeneity lead to a decline in FD.

This is the first study to our knowledge relating spatial heterogeneity of phytoplankton to the diversity of zooplankton in the field. Previous studies have utilized experimental approaches or have focused on temporal heterogeneity. An experimental study by Weider (1992) showed that highest genetic diversity of *Daphnia* clones are supported by an intermediate frequency of disturbance (dilution of food concentration). A field study by Eckert & Walz (1998) found no effect of the frequency of strong wind events on zooplankton species diversity. In our study, a significant quadratic relationship between zooplankton functional diversity and the vertical spatial variation (CV) of blue-green and green algae in the water column of lakes was observed as well as a linear increase with spatial variation in cryptophytes. The spatial variability of blue-green algae, explained over 30% more of the variation in FD than any other spectral group variability, and thus variability in this group of phytoplankton may be the most important for zooplankton diversity. While the curvilinear relationship between zooplankton FD and the CV of blue-greens lends supporting evidence to the spatial resource heterogeneity hypothesis and IDH in zooplankton communities, there was lack of the decline, and only a levelling off in FD at extreme levels of heterogeneity as predicted by this hypothesis. While an abundance of blue-green algae can favour small-bodied *Daphnia* species (Gliwicz & Lampert 1990) bosminids, and copepods (Fulton & Paerl 1987), the spatial variation in abundance of blue-green algae would segregate suitable niches for a variety of zooplankton species. Although CV provides only a crude measure of spatial variability, other more complex and disaggregated measures (e.g. complexity from spectral analysis, covariance of phytoplankton groups, and size of peak in concentration) did not correlate well with zooplankton functional diversity. It is possible that a higher dimensional view that examines how resources vary horizontally as well as vertically and through time would provide greater insight into the importance of heterogeneity on zooplankton functional diversity. Furthermore, examination of the biomass profiles of phytoplankton may help us determine certain characteristics that are highly important for crustacean zooplankton diversity. For, example the strange relationship observed between FD and the CV of total chlorophyll may be explained by the presence of metalimnetic peaks of total chlorophyll in mesotrophic lakes.

Further support for the resource ratio hypothesis and the effect of spatial heterogeneity on zooplankton diversity is evident from the traits comprising functional diversity that were most strongly related to TP: body size and trophic level. The diversity of body sizes and trophic levels was highest in those lakes that had increased variation in abundance of blue-green algae, and in those lakes with an intermediate ratio of browns to blue-greens. This suggests that both large-bodied and small-bodied *Daphnia*, and varying trophic levels of copepods and cladocerans are more likely to coexist in lakes with higher spatial resource heterogeneity and at a high ratio of browns to blue-greens. Under conditions of blue-green dominance, zooplankton community structure has been observed to shift towards a composition of small cladoceran and cyclopoid species (Jeppesen *et al.*, 2000).

Using redundancy analysis, the concentration of blue-green and brown algae, and the presence or absence of the planktivorous fishes *Osmerus mordax*, and *Coregonus clupeaformis* were revealed as the most important determinants of zooplankton species composition and abundance. The responses of the three broad functional groups were scattered in the biplot, indicating that these functional groupings were not sufficient to predict how these species will respond to their environments when fish were included as drivers. The functional groupings in this study were identified based on fits with TP, a bottom up effect, and thus did not use traits related to the response of zooplankton to predation. Thus it is not surprising to observe a segregation of functional groups based on the most dominant environmental factor (TP) but not based on top down effects of fish predation. Although, a general observation has been that in the presence of planktivorous fish, average zooplankton community body size declines (Mills & Schiavone 1982, Jeppesen *et al.*, 2000, Beisner, Dent & Carpenter 2003), ultimately, other functional traits such as helmet formation, predator aversion strategies, migration, may also be important for predicting species responses to all habitat factors.

As with the test of the resource ratio discussed above, the most important resources for zooplankton species identified in the RDA were brown algae (diatom plus chrysophytes) and blue-green algae. Further support for the resource ratio hypothesis thus emerges in the different responses species have to brown and blue-green algae as seen in the biplot. The addition of planktivorous fish to the best model demonstrates the presence of both top-down and bottom-up effects on zooplankton species occurring simultaneously, an observation also found by Pinel-Alloul, Niyonsenga, & Legendre (1995). We thus found supporting evidence for a top-down predator effect, in addition to the effects of resource heterogeneity. The RDA shows a diversity of responses of zooplankton communities to their predators and resources at the species level, and provides a similar narrative to the analyses revolving around the response of functional groups to environmental gradients in these lakes.

Mechanistic hypotheses that are used to explain diversity patterns invoke concepts of trade-offs in functional responses, differences in feeding preferences, and predator aversion strategies (Abrams, 1984; Leibold 1999; Vance, 1978). We would thus expect that a measure of diversity that takes into account the mechanisms inherent in that hypothesis would be more useful to test it. For example, functional diversity using traits that relate to feeding strategies, and feeding rates, could be used to study the functional attributes of zooplankton communities leading to catastrophic shifts in lakes from clear to turbid states as suggested in Weithoff (2003) for phytoplankton. Based on the observation that functional diversity was much more strongly related to important environmental forces, we believe that this measure can enhance our ability to discover important patterns of species composition, diversity, and abundance in zooplankton as well.

One problem with lake surveys is the correlation of variables (e.g. here for resource concentration, resource heterogeneity and environmental productivity). Here, spatial resource heterogeneity of blue-green algae explained 29% and 13% more of the variance in FD than the ratio of diatom to blue-green algae, and TP respectively. Conversely, Stevens and Carson (2002) invoked an experimental approach to separate these often correlated variables, and concluded that it was resource supply rate, not heterogeneity that most affected terrestrial plant richness. Our results suggest for zooplankton community functional diversity that it is spatial heterogeneity of resources that matter – at least of blue-green algae. While observational surveys using regressions to explain patterns in diversity cannot conclusively provide evidence for causal mechanisms driving diversity, they are useful in providing direction to further mechanistic studies. Mesocosm experiments that vary the relative abundance and spatial segregation of different algal groups could be used to further verify the causal forces influencing zooplankton diversity as suggested in this study.

In summary, a relatively strong relationship between the spatial heterogeneity of blue-green algae and functional diversity of zooplankton was observed. While support was found for the resource ratio hypothesis, the ratio of diatoms and chrysophytes to blue-green algae concentration explained less of the variance in FD than overall heterogeneity of blue-green algae concentration. The inclusion of top-down effects of planktivore presence with the bottom-up effects of blue-green and brown algae concentration increased the explained variance in species abundance and composition. The functional traits most related to lake productivity were body size and trophic level, suggesting it is the diversity of these zooplankton traits that are most affected by productivity and its consequent changes in phytoplankton resource ratios and resource spatial availability.

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Appendix 2.1

List of species and their functional traits. Body length and CV of body length were measured, while habitat, trophic level and feeding type were obtained by a literature search. Filtration types C, D, S, and B represent filtration typical of chydorids, daphnids,sidids, and bosminids respectively. Superscripted numbers and letters indicate the categorical trait value for FD calculation, and additional to those given in Chapter I respectively

Species	Abbreviations in RDA	Body Length (mm)	CV of Body Length	Habitat	Trophic Level	Feeding Type
Cladocerans (trait #)		(1)	(2)	(3)	(4)	(5)
Alona sp.		0.41^{A}	0.54^{A}	Littoral^{2}	Herbivore^{1}	C-Filtration^{4}
Ceriodaphnia dubia		0.44	0.22	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Ceriodaphnia lacustris	cerla	0.46	0.15	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Ceriodaphnia reticulata		0.93	0.75	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Chydorus brevilabris	chybr	0.31	0.26	Littoral^{2}	Herbivore^{1}	C-Filtration^{4}
Daphnia ambigua	daam	0.80	0.12	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia catawba	daca	1.41	0.22	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia dentifera		1.26	0.04	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia longiremis	dalo	0.91	0.18	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia mendotae	dame	1.08	0.19	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia parvula		0.67	0.17	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia pulex		1.60	0.071	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia pulicaria	dapuli	1.61	0.15	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Daphnia retrocurva	dare	1.01	0.23	Pelagic^{1}	Herbivore^{1}	D-Filtration^{1}
Diaphanosoma leuchtenbergianum	dialc	0.65	0.23	Pelagic^{1}	Herbivore^{1}	S-Filtration^{2}
Holopedium gibberum	hogi	1.04	0.26	Pelagic^{1}	Herbivore^{1}	S-Filtration^{2}
Leydigia quadrangularis		0.46	0.33	Littoral^{2}	Herbivore^{1}	S-Filtration^{2}
Eubosmina corregoni	euco	0.44	0.23	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Eubosmina longispina	eulo	0.37	0.20	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Eubosmina longispina-oriens	euloo	0.39	0.13	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Neobosmina tubicen		0.53	0.073	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Sinobosmina freyi	sifr	0.35	0.33	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Sinobosmina liederi	sili	0.34	0.074	Pelagic^{1}	Herbivore^{1}	B-Filtration^{3}
Polyphemus pediculus		0.89	0.10	Littoral^{2}	Carnivore^{5}	Raptorial^{7}
Sida crystalina		1.74	0.23	Littoral^{2}	Herbivore^{1}	S-Filtration^{2}

Appendix 2.1 (continued)

Species	Abbreviations in RDA	Body Length (mm)	CV of Body Length	Habitat	Trophic Level	Feeding Type
Cyclopoids						
Acanthocyclops robustus	acro	0.87	0.30	Pelagic[1]	Omnivore[3]	Raptorial[7]
Acanthocyclops vernalis	acve	0.74	0.094	Pelagic[1]	Omnivore[3]	Raptorial[7]
Cyclops scutifer	cysc	1.08	0.12	Pelagic[1]	Omnivore[3]	Raptorial[7]
Diacyclops bicuspidatus thomasi	dibt	0.83	0.095	Pelagic[1]	C-Omnivore[4]	Raptorial[7]
Eucyclops speratus		0.90	0.16	Littoral[2]	H-omnivore[2]	Raptorial[7]
Mesocyclops edax	meed	0.97	0.13	Pelagic[1]	C-Omnivore[4]	Raptorial[7]
Tropocyclops prasinus	trpr	0.51	0.15	Pelagic[1]	H-omnivore[2]	Raptorial[7]
Thermocyclops crassus		0.78[B]	0.032[B]	Pelagic[1]	H-omnivore[2]	Raptorial[7]
Epischura lacustris	epla	1.53	0.078	Pelagic[1]	C-Omnivore[4]	Current cruiser[6]
Leptodiaptomus minutus	lemi	0.84	0.11	Pelagic[1]	Omnivore[3]	Stationary suspension[5]
Leptodiaptomus sicilis		1.21	0.16	Pelagic[1]	Herbivore[1]	Stationary suspension[5]
Skistodiaptomus oregonensis	skor	1.14	0.11	Pelagic[1]	Omnivore[3]	Stationary suspension[5]
Skistodiaptomus reighardi		1.30	0.24	Pelagic[1]	Omnivore[3]	Stationary suspension[5]
Onychodiaptomus birgei		1.35	0.15	Littoral[2]	Omnivore[3]	Stationary suspension[5]

A. Downing J.A. 1981. In situ foraging responses of three species of littoral cladocerans. *Ecological Monographs*, **51**, 85-104.

B. Hopp U., Maier G., & Bleher R. 1997. Reproduction and adult longevity of five species of planktonic cyclopoid copepods reared on different diets: a comparative study. *Freshwater Biology*, **38**, 289-300.

Appendix 2.2

Results of regressions between functional diversity and environmental productivity (total phosphorus concentration). Functional diversity was calculated using combinations of 5 traits: 1) body size, 2) CV of body size, 3) habitat, 4) trophic level, and 5) feeding type. P-values significant before the application of the false discovery rate correction are indicated with a “*”

Trait Combination	R^2	*P*-Value
1,2	0.079	0.26
1,3	0.074	0.28
1,4	0.53	0.0006*
1,5	0.38	0.0066*
2,3	0.011	0.68
2,4	0.0044	0.79
2,5	0.0013	0.89
3,4	0.0096	0.70
3,5	0.043	0.41
4,5	0.265	0.017*
1,2,3	0.043	0.41
1,2,4	0.20	0.065
1,2,5	0.066	0.30
1,3,4	0.16	0.098
1,3,5	0.031	0.48
1,4,5	0.37	0.0075*
2,3,4	0.0070	0.74
2,3,5	0.0090	0.71
2,4,5	0.0057	0.76
3,4,5	0.012	0.67
1,2,3,4	0.040	0.43
1,2,3,5	0.026	0.52
1,2,3,5	0.11	0.18
1,3,4,5	0.12	0.17
2,3,4,5	0.00071	0.92
1,2,3,4,5	0.098	0.21

CONCLUSIONS GÉNÉRALES

L'objectif principal de cette étude était d'examiner comment la biodiversité du zooplancton est affectée par le phosphore total ainsi que par les changements subséquents sur l'hétérogénéité des ressources de phytoplancton et sur leur abondance relative. Un objectif additionnel était d'observer comment les patrons de la richesse spécifique et de la diversité fonctionnelle répondent à des gradients de productivité, aux ratios et à l'hétérogénéité des ressources.

Au chapitre I, j'ai effectué une revue de la littérature portant sur le zooplancton d'Amérique du Nord depuis les 50 dernières années et j'ai examiné la possibilité d'utiliser la diversité fonctionnelle dans les études de zooplancton. Le chapitre I presente les tableaux des traits qualitatifs et quantitatifs, en plus des équations de régression qui pourraient être utilisées pour calculer les traits « hard » en utilisant des traits « soft » facilement mesurables (par exemple taille de l'organisme). La majorité des donnés trouvée concernaient les cladocères alors que les données ont manqués pour les cyclopoides. Il y avait aussi une pénurie de donnés spécifique à chaque espèce. Un dendrogramme des communautés régionales des espèces communes de zooplancton en Amérique du Nord a été généré pour démontrer la différence entre les regroupements taxonomiques des espèces et ceux obtenus par traits fonctionnels. J'en ai conclu que les données fonctionnelles de la littérature ne sont pas suffisantes, mais ils peuvent être utilisé en combinaison avec les traits « soft » pour générer les niches fonctionnelles des espèces de zooplancton.

Au chapitre II, j'ai testé les hypothèses de ratios et d'hétérogénéité spatiale des ressources comme les explications de la relation entre le phosphore total et la diversité du zooplancton avec une approche comparative de lacs. En plus, les traits mesurés dans le labo et obtenus par la revue de littérature du chapitre I ont été utilisés pour mesurer la diversité fonctionnelle de 18 lacs en Estrie. J'ai trouvé une relation curvilinéaire entre la diversité fonctionnelle et la distribution spatiale des algues bleues-vertes, un résultat qui supporte l'hypothèse « spatial resource heterogeneity ». De plus, une relation curvilinéaire a aussi été retrouvée entre la diversité fonctionnelle et le ratio des algues brunes à bleues-vertes, mais la proportion de la variation de la diversité fonctionnelle liée au ratio des algues brunes à bleues-vertes est plus petite que celle expliquée par la distribution spatiale des algues bleues-vertes. L'analyse de redondance a démontré un effet de la présence de deux espèces de poisson (*Osmerus mordax* et *Coregonis clupeaformis*) et de la concentration de les algues bleues-vertes et brunes sur la composition et l'abondance du zooplancton. Ce résultat suggère que les effets « bottom-up » et « top-down » altèrent la composition et l'abondance des communautés du zooplancton. Les mesures de la diversité fonctionnelle ont été reliées plus fortement à des variables explicatives environnementales (TP, hétérogénéité et abondance relative du phytoplancton). Donc, j'en conclus que l'utilisation de la diversité fonctionnelle peut être profitable aux études cherchant à comprendre les patrons d'abondance et de distribution des espèces de zooplancton.

Deux conclusions découlent des études menées dans les chapitres I et II. Premièrement, tandis que l'hétérogénéité spatiale et le ratio des ressources peuvent être importants pour les communautés de zooplancton, ils suivent les effets « top-down ». Des études expérimentales seront nécessaires afin de déterminer l'importance relative des effets spécifiques « bottom-up » et « top-down ». Deuxièmement, quand on utilise les hypothèses qui sont basée sur la supposition de la fonctionnalité des espèces, la mesure de la diversité fonctionnelle peut être plus appropriée.