INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Université d'Ottawa · University of Ottawa

Plankton Development and Trophic Interactions in Rivers

Développement et Interactions Trophiques du Plancton dans des Rivières

Ben Kumar Basu

Thesis submitted to the School of Graduate Studies and Research
University of Ottawa
in partial fulfillment of the requirements for the
Doctor of Philosophy (Ph.D.) degree in the
Department of Biology, University of Ottawa, Ottawa, Ontario, Canada
K1N 6N5

Thèse soumise à l'École des études supérieures et de la recherche
Université d'Ottawa
en vue de l'obtention du doctorat dans
le Département de Biologie, Université d'Ottawa, Ottawa, Ontario, Canada
K1N 6N5

This work is dedicated to my mother and father who have

supported me from the beginning.

Abstract

The factors regulating the development and trophic interactions of planktonic communities were determined in 31 medium to large size temperate rivers. In addition, the Rideau River, Ontario, was studied in detail over three field seasons. Variables measured included: phytoplankton biomass as measured by chlorophyll *a* concentration; zooplankton biomass (rotifers and crustaceans); heterotrophic bacterial abundance; heterotrophic flagellate abundance; nutrient concentrations (phosphorus and nitrogen); dissolved organic carbon concentration; river discharge; water residence time; depth; temperature; and light attenuation.

Phytoplankton was abundant in eutrophic rivers (> 15 $\mu g\ L^{-1}$ of chlorophyll *a*) and was most strongly related to nutrient concentrations, primarily total phosphorus, which explained up to 76% of the variation in chlorophyll *a*. Phytoplankton biomass in the rivers was not related to the hydrological parameters of water residence time or discharge, possibly due to the short generation time of phytoplankton (hours to days). Light did not appear to limit phytoplankton biomass due to shallow depths and extensive vertical mixing. In the Rideau River phytoplankton biomass exhibited longitudinal heterogeneity, but in general increased in a downstream direction, concomitant with increases in nutrient concentrations. Phytoplankton biomass did not appear to be affected by zooplankton grazing in the rivers. However, phytoplankton biomass may have been negatively impacted by benthic filter feeders, in particular the invasive zebra mussel (*Dreissena polymorpha*), in the downstream reaches of the Rideau River.

Zooplankton biomass in the rivers was low (usually < 20 μg L^{-1} dry mass) and small taxa dominated the zooplankton communities (e.g. rotifers, bosminids). Large zooplankton taxa, such as *Daphnia* sp., were much less abundant. Due to longer generation times (days to weeks), zooplankton biomass was primarily related to water residence time which explained 33% of the variation. Zooplankton appeared susceptible to advective loss in the rivers. A positive resource effect of either nutrients or phytoplankton on zooplankton biomass, typically observed in lakes, was weaker in the rivers. In comparison to lakes, zooplankton appeared less tightly coupled to phytoplankton. As with phytoplankton, zooplankton biomass in the Rideau River increased with downstream travel and appeared to be negatively affected by benthic filter feeders.

Heterotrophic bacteria were abundant in the rivers (4.5 X 10^6 cells ml^{-1}) and, as in lakes, bacteria were most strongly related to nutrient concentrations (total phosphorus) and phytoplankton biomass (chlorophyll *a*). In contrast to lakes, no relationship between bacterial abundance and dissolved organic carbon was observed, possibly due to the more allochthonous, refractory nature of river dissolved organic carbon.

Heterotrophic flagellates were also abundant in the rivers (4.0 X 10^3 cells ml^{-1}) and were most strongly related to bacterial abundance and nutrient concentrations (total phosphorus). Neither bacterial nor flagellate abundance was related to water residence time. A negative relationship between zooplankton biomass and bacterial or flagellate abundance was not observed, possibly because of the low biomass (hence low grazing pressure) of zooplankton in the rivers. Due to the scarcity of zooplankton in rivers, there

may be little transfer of energy from the planktonic microbial food web to planktonic metazoans.

Résumé

Les facteurs qui règlent le développement et les interactions trophiques de la communauté planctonique ont été déterminés dans 31 rivières tempérées. De plus, la rivière Rideau, en Ontario, a été examinée d'une manière exhaustive pendant trois saisons d'échantillonage. Les variables qui ont été mesurées comprennent: la biomasse du phytoplancton, mesurée par la concentration en chlorophylle *a*, la biomasse du zooplancton. l'abondance des bactéries et flagellés hétérotrophes, la concentration en nutriments (phosphore et azote), la concentration en carbone organique dissout, le débit, le temps de rétention de l'eau, la profondeur, la température, et l'atténuation de la lumière.

Le phytoplancton était abondant dans les rivières eutrophes (> 15 $\mu g\ L^{-1}$ chlorophylle *a*) et la concentration en chlorophylle *a* était directement proportionnelle à la concentration en phosphore total. Le phosphore total a expliqué 76% de la variation en chlorophylle *a*. La biomasse du phytoplancton n'était pas reliée aux paramètres hydrologiques (le débit ou le temps de rétention), sans doute parce que le phytoplancton possède un temps de génération plus court (de l'ordre d'heures ou de quelques jours). La lumière ne limitait pas la biomasse du phytoplancton parce qu'il y avait assez de mélange vertical et les rivières étaient peu profondes. Dans la rivière Rideau, il y avait beaucoup de variation longitudinale, mais en général, la biomasse du phytoplancton augmentait en aval, en parallèle avec une augmentation en nutriments. La biomasse du phytoplancton n'était pas affectée par le broutage de la communauté zooplanctonique dans les rivières. Cependant, dans la rivière Rideau, la biomasse du phytoplancton semblait être réduite en aval par les organismes

benthiques, notamment la moule zébrée (*Dreissena polymorpha*), espèce exotique qui filtre de grands volumes d'eau.

La biomasse du zooplancton dans les rivières était très basse (ordinairement < 20 µg L^{-1} biomasse sèche) et les plus petits taxons dominaient la communauté zooplanctonique (e.g. rotifera, *Bosmina* sp.). Les taxons plus gros, comme *Daphnia* sp., étaient plus rares. La biomasse du zooplancton était reliée principalement au temps de rétention, ce qui a expliqué 33% de la variation. Dans les rivières, le zooplancton est susceptible à la perte advective parce que le zooplancton possède un temps de génération plus long (jours ou semaines). La relation positive, observée dans les lacs, entre les nutriments ou le phytoplancton et la biomasse du zooplancton était faible dans les rivières. Comme la biomasse du phytoplancton, la biomasse du zooplancton semblait augmenter en aval mais être réduite par la moule zébrée.

Les bactéries hétérotrophiques étaient abondantes dans les rivières (moyenne de 4.5 X 10^6 cellules ml^{-1}) et comme dans les lacs, l'abondance des bactéries était directement proportionnelle à la concentration en nutriments (phosphore total) et à la biomasse du phytoplancton (chlorophylle *a*). Par opposition aux lacs, dans les rivières, aucune corrélation significative n'a pu être établie entre les bactéries et la concentration en carbone organique dissout. Il est possible que la plupart du carbone organique dissout dans les rivières provienne du bassin versant et soit réfractaire.

De plus, les flagellés hétérotrophiques étaient abondants dans les rivières (moyenne de 4.0 X 10^3 cellules ml^{-1}). Les flagellés ont été reliés principalement aux bactéries et à la concentration en nutriments (phosphore total). Aucune corrélation n'a pu être établie entre

les bactéries ou les flagellés et le temps de rétention de l'eau. Une relation négative entre la biomasse du zooplancton et les bactéries ou les flagellés n'a pas été observée sans doute parce que la biomasse du zooplancton était basse. Il est possible que le transfert énergétique de la boucle microbienne aux métazoaires planctoniques soit peu important dans les rivières.

Acknowledgments

I wish to thank Frances Pick for her invaluable and inexhaustible enthusiasm, support and insight- marks of a good supervisor. I also wish to thank my committee members Dr.'s Antoine Morin, Scott Findlay, and Cam Wyndham for their guidance and constructive suggestions since the beginning of my research. Special thanks go to all past and present members of the Pick/ Currie labs. Thanks to Jason, Cass. and John for help in the field. Thanks to Andrew, Mike, Paul D., Lizzy, Robin, Rowena, Monique, Tony, Michelle, Théo and Richard for matters both academic and social.

Nutrient analysis was performed at the Regional Municipality of Ottawa-Carleton, Surface Water Quality Branch courtesy of Stuart Dean and Dale Lynch. Discharge values were provided by the Water Survey of Canada. Thanks to David Lean (N.W.R.I.) for field facilities and dissolved organic carbon data. H. Rollins and G. Marinoni provided stress therapy.

This research was supported by a Natural Sciences and Engineering Research Council (NSERC) and an Ontario Ministry of the Environment and Energy, Environmental Youth Corps (EYC) grant to F.R.P. and NSERC and EcoResearch fellowships to B.K.B.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction to River Plankton

1.1 General Introduction

Rivers are a vital component of the biosphere. Although they contain less than one percent of the world's freshwater (Wetzel 1983), their ecological and social significance is enormous. Rivers transport nutrients, suspended solids, organic matter and biota from upstream terrestrial sources to downstream lakes and oceans. In doing so, rivers act as a link between the land and the sea and between upstream and downstream regions within a drainage basin. Although rivers may share certain similarities with headwater streams and with lakes, they represent a flowing water habitat that is distinct from either smaller streams or lakes. In effect, as well as being conduits of transport, rivers can be viewed as distinct aquatic ecosystems (Hynes 1972, Ryder and Pesendorfer 1989).

The social importance of rivers stems from the use of river water for transportation, irrigation, potable supply, hydroelectric power, industry, recreation, and fisheries (Oglesby *et al.* 1972, Hynes 1972, Jones 1984). Humans have historically settled in close proximity to rivers due to the multiple uses (and abuses) for which river waters are required. From the socio-economic perspective, rivers are a valuable natural resource and the maintenance of a high level of river "water quality" and integrity is desirable.

Despite the obvious importance of rivers both ecologically and socially, the biota of large rivers has been studied to a lesser extent than the biota of lakes and streams. This imbalance in research has left a significant gap in our knowledge concerning the biology of river ecosystems. As Thorp *et al.* (1994) stated, from a functional perspective large rivers represent "ecological black boxes". Indeed, of all studies conducted on flowing

water, only about four percent have dealt with large (greater than fifth order) rivers (Hynes 1989). Furthermore, among these few studies conducted on large rivers, the majority have focused on the distribution and abundance of fish or benthic macroinvertebrates (Randall *et al.* 1995, Thorp *et al.* 1994). Research conducted on the planktonic or open water component of river ecosystems is particularly rare. Landmark papers in river ecology such as the Vannote *et al.*(1980) River Continuum Concept scarcely mention the potential for planktonic processes in river ecosystems. In fact, classical and even recent text books of river ecology can only speculate about river plankton due to a lack of concrete information (Hynes 1972, Allen 1995).
This lack of research should be of concern because abundances and interactions which occur among planktonic primary producers and primary consumers (i.e. phytoplankton, zooplankton and microbes) can affect basic parameters of water quality as well as higher trophic levels (e.g. benthic invertebrate and fish production).

Disciplinary boundaries, historically established among freshwater scientists, may be the cause for this lack of research concerning river plankton. These boundaries (perhaps artificial) have resulted in limnologists working almost exclusively in lentic freshwater and stream ecologists rarely working on organisms other than vertebrates or benthos when examining rivers (Thorp *et al.* 1994). Only recently have these two groups of scientists been converging to study neglected components of large river ecosystems (Reynolds 1988, de Ruyter van Steveninck *et al.* 1992, Thorp *et al.* 1994).

Early researchers recognized the existence of a true planktonic community in running waters (Zacharius 1898, Margalef 1960, Greenberg 1964) and it is now widely

accepted that genuine plankton development can occur in large rivers with relatively long water residence times (Lack 1971, Jones and Barrington 1985, de Ruyter van Steveninck *et al.* 1990a, 1990b, 1992, Pace *et al.* 1992, Kohler 1993). Despite this recognition, however, the study of planktonic riverine food webs lags at least two decades behind that of lake food webs. The factors regulating planktonic development in rivers and the interactions amongst riverine planktonic communities remain virtually unknown.

The limited biological information concerning large rivers in general, and river plankton in particular, makes it difficult to address complex ecological questions (Thorp *et al.* 1994). Before applied issues such as contaminant dynamics or fisheries management can be examined, basic research aimed at better elucidating the factors that regulate, and the processes that occur, within planktonic river food webs is required.

In order to address this topic, the present research concerns the development, regulation, and trophic interactions of planktonic communities within large, temperate, lowland rivers. Riverine phytoplankton, zooplankton, bacterioplankton and protozoan communities are examined. A review of the limited research previously conducted on river plankton is provided below.

1.2 River Phytoplankton

The work which has been conducted on rivers clearly shows a regular development of extensive phytoplankton biomass in medium-sized to large rivers. A medium to large river is considered fifth order or larger according to Strahler's (1957) stream classification method. Many European lowland rivers develop chlorophyll *a*

concentrations (Chl *a*) over 100 μg L^{-1} (Lack *et al.* 1978, Jones 1984, Moss *et al.* 1984, Jones and Barrington 1985, Descy 1987, de Ruyter van Steveninck *et al.* 1992, Kohler 1993). Chl *a* concentrations over 100 μg L^{-1} have also been observed in a few large North American rivers (Baker and Baker 1979, Soballe and Bachman 1984). In lake terms, these rivers would certainly be categorized as hypereutrophic and would be regarded as having "poor water quality" (Wetzel 1983). However, algal biomass concentrations in rivers can also exhibit extensive longitudinal heterogeneity (Soballe and Bachman 1984, Chessman 1985, Cole *et al.* 1992). Some rivers can progress from eutrophy to oligotrophy (and vice versa) over short distances (< 10 km) (Soballe and Bachman 1984, Basu and Pick 1995, Chapters 2 and 3 of the present thesis). This heterogeneity and water flow, make rivers inherently more difficult, and perhaps more interesting to study than lakes.

The suspended phytoplankton of larger rivers is thought to consist primarily of phytoplankton originating from two sources (Hynes 1972): i) lentic algae, derived from standing waters in which there is an export of planktonic species into the draining tributaries (Talling and Rzoska 1967, Reynolds 1988, Uehlinger 1993), and ii) algae which originate within flowing water and are capable of *in situ* reproduction (often termed "potamoplankton") (Reynolds 1988, Murakami *et al.* 1992). In large rivers, algae of benthic origin, although present, represent a small fraction of total suspended phytoplankton (Lack 1971, Basu and Pick 1995, Yang *et al.* accepted). River phytoplankton attains significant biomass only in larger rivers where long water residence times and low flow rates allow plankton to grow and reproduce (Margalef 1960, Lack

1971, Kohler 1993). Planktonic processes in low order streams are likely less significant (Vannote *et al.* 1980).

The growth and attrition of phytoplankton populations in rivers are thought to be subject to the same general environmental factors as those in lakes- chemical factors (inorganic nutrient concentrations, primarily phosphorus and nitrogen), physical factors (light, temperature), and biotic factors (competition, grazing) (Wetzel 1983, Reynolds 1988). In contrast to lakes, however, phytoplankton in rivers may also be affected by hydrological factors such as river discharge and water residence time.

An inverse correlation between phytoplankton biomass and river discharge has been observed (Jones 1984, Jones and Barrington 1985, Reynolds 1988). Increases in river discharge are believed to decrease phytoplankton biomass by shortening residence time and, consequently, the time available for potamoplankton to develop (Baker and Baker 1979, Reynolds 1988).

Other researchers have concluded that river phytoplankton is less sensitive to the effect of discharge or water residence time and more strongly regulated by nutrient concentrations. A significant positive relationship between river phytoplankton abundance or biomass and total phosphorus concentration has been observed in several studies (Soballe and Kimmel 1987, Moss *et al.* 1989, Van Nieuwenhuyse and Jones 1996, Basu and Pick 1995, 1996, Chapters 2, 3 and 4 of the present thesis).

Due to the turbulent and often turbid conditions found in many large rivers, it has also been suggested that light conditions may regulate river phytoplankton development (Krogstad and Lovstad 1989, Cole *et al.* 1992). In deep sections of rivers, when the depth

of mixing is much greater than the depth of the photic zone, it is possible that the average irradiance to which algal cells are exposed is near or below the threshold for net growth (Lewis 1988, Cole *et al.* 1992).

Clearly, many factors may regulate the development of phytoplankton in rivers. However, a general consensus as to the most important of these factors has yet to be achieved.

1.3 River Zooplankton and Relationships Between Phytoplankton and Zooplankton in Rivers

In comparison to the algal component, there has been much less attention devoted to the zooplankton component of river plankton. Thorp *et al.* (1994) described the biological knowledge concerning riverine zooplankton as being "abysmal". From the few published studies, it appears that zooplankton biomass and abundance in rivers is much lower than in lakes of comparable nutrient and chlorophyll concentrations (Bothar and Kiss 1990, Pace *et al.* 1992, Thorp *et al.* 1994, Basu and Pick 1996, Chapter 4 of the present thesis). Pace *et al.* (1992) suggested that this difference may be due to the shorter residence times of water in rivers, but they did not have direct estimates of these times. The major factors regulating zooplankton biomass in rivers remain unknown.

In addition, the relationships between zooplankton and phytoplankton in rivers and how these relationships compare with those observed in lakes remain unexplored. In lakes, zooplankton biomass has either been positively related to phytoplankton biomass (or total phosphorus concentration)- a resource effect (McCauley and Kalff 1981, Hanson and Peters 1984, Canfield and Watkins 1984) or negatively related to phytoplankton

biomass- a grazing effect (McQueen *et al.* 1986, Quiros 1990). De Ruyter van Steveninck *et al.* (1990a) observed an inverse correlation between zooplankton biomass and phytoplankton biomass in the lower reaches of the River Rhine. They suggested that this was due to a strong grazing effect of zooplankton on phytoplankton. However, the extent of trophic coupling between phytoplankton and zooplankton in rivers and its generality remains an open question despite its fundamental ecological importance (i.e. energy flow, food web structure).

1.4 The Microbial Component of River Plankton

In the aquatic microbial food web, heterotrophic bacteria consume dissolved organic matter of autochthonous or allochthonous origin and, in turn, are consumed by heterotrophic flagellates and small ciliates (Azam *et al.* 1983, Berninger *et al.* 1991). The aquatic microbial food web can contribute energy to the classical aquatic food web (i.e. phytoplankton ---> zooplankton ---> fish) by packaging dissolved organic matter into larger particles (heterotrophic bacteria, flagellates and ciliates) which are directly available for consumption by metazoan zooplankton (Azam *et al.* 1983, Vaqué *et al.* 1992, Gasol and Vaqué 1993). The overwhelming majority of studies concerning microbial food webs have been conducted in marine and lentic freshwater environments. It has been suggested that the microbial food web is an important component of overall food web structure and function (Azam *et al.* 1983, Fenchel 1986, Cole *et al.* 1988).

In contrast, comparatively little research has focused on heterotrophic bacteria and protozoa in river habitats (Edwards and Meyer 1986, Carlough and Meyer 1990, Meyer

1990, Dolan and Gallegos 1991, Findlay *et al.* 1991). The microbial food web could be particularly important to carbon and nutrient dynamics in river systems due to the often high loadings of allochthonous organic matter (Edwards and Meyer 1986, Findlay *et al.* 1991, Sabater *et al.* 1993), and low zooplankton abundances (Pace *et al.* 1992, Basu and Pick 1996, Chapter 4 of the present thesis). Under such conditions, significant carbon flow and/or nutrient regeneration may occur via the microbial food web. Previous research has demonstrated that the abundance of heterotrophic bacteria and their primary consumers, the heterotrophic flagellates, can be high in rivers (Edwards and Meyer 1986, Carlough and Meyer 1990, Sabater *et al.* 1993). Determining the factors related to the abundance of heterotrophic bacteria and flagellates in lotic waters represents the first step in examining microbial food webs in rivers.

1.5 Research Approach

Two approaches were used during this research of river plankton. The first approach (Chapter 2 and Chapter 3) involved studying plankton development and interactions in substantial detail within a single river. The river chosen for these studies was the Rideau River, Ontario. The advantage of this approach was that seasonal and spatial (longitudinal) variation in plankton development could be closely examined. The disadvantage of this approach was that it was "case specific": results could not necessarily be generalized and extrapolated to other rivers.

Therefore, in order to obtain results which could be generalized, the second approach (Chapter 4 and Chapter 5) involved examining the factors regulating planktonic

communities and trophic interactions within 31 temperate rivers. This comparative approach was of coarser spatial and temporal resolution, but allowed for the development of general relationships and for a comparison of results with similar lake surveys.

1.6 Summary of Chapter Contents

The remainder of this introduction will serve to outline the contents and summarize major results of each chapter that follows. Chapters 2, 3, 4, and 5, as outlined below, were written as individual papers, published or accepted for publication. Each chapter is capable of "standing on its own". As a result of this format, some repetition is inherent, especially in the "Introduction" and "Methods" sections. The decision was made to maintain the integrity of the chapters so that each could be read independently.

1.6.1 Outline of Chapter 2

Chapter 2 is an examination of the longitudinal and seasonal patterns of phytoplankton development within the Rideau River and of the environmental factors regulating this development. The prediction that phytoplankton biomass, as measured by chlorophyll *a* (Chl *a*), would gradually increase with downstream travel was explored. The significance of factors that potentially regulate algal biomass in the Rideau was also evaluated. These factors included nutrient concentrations, temperature, discharge and water residence time.

Results indicated that planktonic Chl *a* concentration in the Rideau exhibited extensive longitudinal and seasonal variation. Chl *a* concentrations in the Rideau were

not simply a reflection of concentrations in the headwaters, as there was usually a significant decrease in Chl *a* upon movement from the lentic waters of Lower Rideau Lake into the lotic Rideau River proper. Within the river itself, reaches of net increase in Chl *a* (planktonic sources) were identified as were reaches of net decrease (planktonic sinks). Chl *a* concentration was positively related to total phosphorus (TP) concentration, though only 16% of the variation in Chl *a* could be explained by TP alone. Chl *a* was not significantly related to river discharge and light limitation of phytoplankton development was unlikely. These results led to the proposition that zooplankton grazing may be affecting phytoplankton biomass in the Rideau.

The preliminary study on the Rideau provided necessary background information and raised new questions concerning plankton development within the river. Therefore, in order to address unexplained variation and downstream declines in phytoplankton biomass, and to further explore interesting longitudinal patterns in planktonic development, studies on the Rideau were greatly expanded to include riverine zooplankton (crustaceans and rotifers) and to sample at more sites on the river (described in Chapter 3).

1.6.2 Outline of Chapter 3

Chapter 3 provides a detailed examination of the longitudinal and seasonal development of both phytoplankton and zooplankton within the Rideau River over two field seasons. Factors regulating planktonic development and interactions between

phytoplankton, zooplankton and the recently introduced zebra mussel (*Dreissena polymorpha*) are addressed.

The objectives of this chapter were: i) to describe the longitudinal and seasonal pattern of both phytoplankton and zooplankton development within the Rideau River, ii) to determine the factors most strongly related to phytoplankton biomass, iii) to determine the factors most strongly related to zooplankton biomass and iv) to examine potential interactions between phytoplankton and zooplankton in terms of either resource control of zooplankton by phytoplankton or grazing control of phytoplankton by zooplankton.

As observed in the preliminary Rideau study (Chapter 2), there was an initial decrease in phytoplankton biomass as water flowed from the headwaters into the river proper. The same was true for zooplankton biomass. Following these decreases, the biomass of both phytoplankton and zooplankton increased with downstream travel, peaked and subsequently decreased. This pattern was consistent from month to month and year to year and could be modeled using a second order polynomial equation. The downstream declines in biomass were attributed to the feeding activity of the exotic zebra mussel, as nutrient or light limitation were not likely in these downstream reaches.

Overall, Chl *a* was again positively related to total phosphorus and zooplankton was positively related to Chl *a* (indicative of a resource effect of phytoplankton on zooplankton). A negative relationship between zooplankton and phytoplankton biomass or longitudinal "phasing" of planktonic communities (*sensu* de Ruyter van Steveninck *et al.* 1990a) were not observed. Increases and decreases in the biomass of both planktonic

communities coincided. Neither Chl *a* nor zooplankton biomass were significantly related to river discharge.

1.6.3 Outline of Chapter 4

Results and conclusions drawn from Chapters 2 and 3 concern only one individual river. In order to obtain results which are applicable to temperate rivers in general, research in Chapter 4 adopted a comparative approach.

By measuring chlorophyll *a* concentration, zooplankton biomass, nutrient concentrations (total nitrogen (TN) and total phosphorus (TP)), water residence time, depth, and attenuation coefficients within 31 large rivers in Ontario and Quebec, the following hypotheses were tested: i) Chl *a* concentration is positively related to nutrient concentrations and water residence time, ii) zooplankton biomass is positively related to Chl *a* (and/or TP) concentration and water residence time, and iii) relationships between phytoplankton biomass and zooplankton biomass are weak, due to overriding physical limitation imposed on one or both of these communities (i.e. the effect of water residence time).

There was a highly significant and positive relationship between Chl *a* and TP. There was no significant relationship between Chl *a* and water residence time. In contrast, crustacean biomass, rotifer biomass and total zooplankton biomass were significantly and positively related to water residence time. Mean total zooplankton biomass in the rivers was lower than levels typically observed in lakes. The zooplankton community was dominated by rotifers and small crustaceans indicating that smaller

zooplankton taxa may have an advantage in short residence systems. After controlling for the effect of water residence time on zooplankton biomass, there was a weak positive relationship between phytoplankton biomass and zooplankton biomass. A negative relationship between zooplankton and phytoplankton biomass was not observed.

These results indicate an important similarity between rivers and lakes at the phytoplankton level (i.e. TP-Chl *a* relationship) and an important difference at the zooplankton level (i.e. residence time-zooplankton relationship). In addition, there is a much weaker relationship between phytoplankton and zooplankton within rivers in comparison to lakes, indicating that in rivers these trophic levels may be less tightly coupled.

1.6.4 Outline of Chapter 5

The microbial food web is an important component of overall food web structure and energy flow in lentic freshwaters (Azam *et al.* 1983). This may also apply to rivers. In Chapter 5 the research effort is shifted toward the microbial component of river food webs. The objective was to determine factors related to heterotrophic bacterial and flagellate abundance in rivers. Data was collected from the 31 river survey introduced in Chapter 4.

There was a highly significant, positive relationship between bacterial abundance and both total phosphorus and chlorophyll *a*. Bacterial abundance was not related to dissolved organic carbon concentration as has been observed in lakes. A significant positive relationship was observed between flagellate abundance and both bacterial

abundance and total phosphorus. Neither bacterial nor flagellate abundance was significantly related to water residence time. No relationship between zooplankton biomass and bacterial or flagellate abundance was observed. Zooplankton, whether rotifers or crustaceans, appeared to be too limited to significantly affect flagellate or bacterial abundance. The scarcity of metazoan zooplankton indicates that in rivers there may be little transfer of energy from the microbial food web to planktonic metazoans in comparison to lakes.

1.6.5 Outline of Chapter 6

As will be described in the subsequent chapters of this thesis, in some instances the factors regulating planktonic development and interactions in rivers are similar to those observed in lakes. In other instances, however, the advective movement of water (and its attendant effect on water residence time) can significantly affect river plankton and create conditions which differ from lakes. Chapter 6 summarizes the major conclusions from the previous chapters. The information gained concerning plankton development in rivers is highlighted. This is done through a comparison of planktonic development and interactions in rivers with those in lakes. As well, suggestions for the direction of future research are offered.

Chapter 2

Longitudinal and Seasonal Development of Planktonic Chlorophyll *a* in the Rideau River, Ontario

Modified from Basu, B.K. and F.R. Pick. 1995. Canadian Journal of Fisheries and Aquatic Sciences. 52: 804-815. (with permission)

2.1 Abstract

Planktonic chlorophyll *a* concentrations in the Rideau River, Ontario, showed longitudinal and seasonal variation and ranged from 2 to 19 μg L^{-1}. Chl *a* concentrations in the river were not simply a reflection of the concentrations in the headwaters of Lower Rideau Lake. Upon movement from the lentic headwaters into the lotic river waters there was usually a significant decrease in Chl *a* concentration. Downstream there were reaches of net increase in Chl *a* (sources), reaches of no change in concentration, and reaches of net decrease (sinks). Increases in concentration only occurred over reaches with retention times of 72 hours or longer. No increases in Chl *a* concentration occurred over a reach with a retention time less than 50 hours. Chl *a* concentration was not significantly correlated to discharge. Chl *a* concentration was positively related to total phosphorus concentration ($R^2 = 0.16$, $p = 0.02$). About 50% of the variation in Chl *a* concentration could be accounted for by a combination of total phosphorus, nitrate, and soluble reactive phosphorus concentrations.

2.2 Introduction

Phytoplankton dynamics have been studied extensively in lentic freshwaters (lakes and reservoirs), yet comparatively little research has focused on lotic waters (rivers) (Reynolds 1988, Murakami *et al.* 1992). As a result, the factors which regulate the spatial and seasonal development of suspended algae in rivers are poorly known. Previous work on rivers has demonstrated the regular development of extensive algal biomass in medium to large rivers. Many European lowland rivers can develop chlorophyll *a* (Chl *a*) concentrations over 100 $\mu g\ L^{-1}$ (Lack *et al.* 1978, Jones 1984, Moss *et al.* 1984, Jones and Barrington 1985, Descy 1987, de Ruyter van Steveninck *et al.* 1992, Kohler 1993). Chl *a* levels over 100 $\mu g\ L^{-1}$ have also been observed in large North American rivers (Baker and Baker 1979, Soballe and Bachman 1984). In contrast, some large rivers have low concentrations of Chl *a*. Lewis (1988) observed Chl *a* concentrations below 0.5 $\mu g\ L^{-1}$ in the Orinoco river. Furthermore, algal biomass levels in rivers exhibit extensive longitudinal heterogeneity (Soballe and Bachman 1984, Chessman 1985, Cole *et al.* 1992).

The suspended algae of large rivers consists primarily of algae originating from two sources (Hynes 1972): i) lentic algae, derived from standing waters in which there is an export of planktonic species into the draining tributaries (Talling and Rzoska 1967, Reynolds 1988, Moss *et al.* 1989a) and ii) potamoplankton: algae capable of in situ reproduction within flowing water (Reynolds 1988, Murakami *et al.* 1992). In large rivers, algae of benthic origin, although present, represent a small fraction of total

suspended algae (Lack 1971). "True river phytoplankton" or potamoplankton attains significant biomass only in large rivers where residence times and low flow rates allow planktonic organisms sufficient time for growth and reproduction (Margalef 1960, Lack 1971, Jones and Barrington 1985, de Ruyter van Steveninck *et al.* 1990a, Kohler 1993).

Large rivers in which potamoplankton develops are characterized by: i) water residence times ranging from days to weeks which vary with discharge, ii) continuous turbulent mixing, and iii) an abundant nutrient supply due to an extensive association with their watersheds (Moss *et al.* 1989a). These characteristics may affect potamoplankton development as follows.

Downstream advection in rivers may limit planktonic development by removing organisms faster than they can reproduce (Reynolds 1988, Pace *et al.* 1992). Within individual rivers potamoplankton biomass has been inversely correlated with the river's discharge (Jones 1984, Jones and Barrington 1985, Descy 1987, Reynolds 1988). Within a river, discharge itself is negatively correlated with water residence time. As Reynolds (1988) outlines, if potamoplankton biomass is to be maintained or increase within a large river, there must be reaches within the river which have long enough residence times so that *in situ* reproduction counteracts advective loss.

Turbulent mixing is beneficial to algal development because it can eliminate nutrient depleted water pockets adjacent to algal cells (Reynolds 1988) and maintain diatoms in suspension (Soballe and Kimmel 1987). Turbulent mixing also may be detrimental to algal development by carrying phytoplankton below the photic zone (Cole

et al. 1992). In deep sections of rivers, when the depth of mixing is greater than the depth of the photic zone, it is possible that the average irradiance to which algal cells are exposed is near or below the threshold for net growth (Cole *et al.* 1992, Lewis 1988). In shallower sections, with reduced mixing depths, the average irradiance may be sufficient to allow for net positive growth (Cole *et al.* 1992).

Increased nutrient concentrations should benefit potamoplankton development. However, Soballe and Bachman (1984) studying the Des Moines River and Sabater and Munoz (1990) working on the River Ebro have shown potamoplankton biomass to be less dependent on nutrient concentration than lentic phytoplankton biomass. Soballe and Kimmel (1987) using the NES (National Eutrophication Survey) and NASQUAN (National Stream Water Quality Accounting Network) data bases concluded that algal abundance in U.S. rivers was less predictable (lower R^2) on the basis of nutrient supply than in natural lakes.

The present study examined the longitudinal and seasonal development of suspended algae within a large Ontario river (Rideau River) of relatively high nutrient status (approximately 30 $\mu g\ L^{-1}$ of total phosphorus). Within the Rideau River, algae of benthic origin contribute less than 10% to total suspended algal biomass (Yang *et al.* in press). By sampling seven sites on the river we examined the longitudinal differences in algal biomass over a six month period from May to October, 1993. In addition, three reaches of varying water retention times were defined between sites in the river and the inflow algal biomass and outflow algal biomass of each reach measured to identify

reaches of net algal development. First, we predicted that potamoplankton biomass as measured by chlorophyll *a* (Chl *a*) concentration gradually increases downstream. As the water moves downstream, the "time for development" increases and it is expected that algal biomass will increase. This gradual increase has been previously observed by Greenberg (1964), Capblancq and Descamps (1978), Holmes and Whitton (1981), and Moss *et al.* (1984). Secondly, the significance of factors which potentially regulate algal biomass in rivers was evaluated. These factors included temperature, nutrient concentration, discharge and retention time. In short residence systems, abiotic factors such as river discharge or temperature may control algal biomass more than nutrient concentrations (Soballe and Kimmel 1987). Finally, we predicted that algal biomass will increase through a river reach only when the retention time of the reach is sufficiently long that growth and reproduction exceed advective loss (Reynolds 1988). We anticipated changes in biomass over the reaches with longer retention times and no change over the reaches with shorter retention times.

2.3 Methods

2.3.1 Study Area

The Rideau River is located in south-eastern Ontario. From its headwaters in Lower Rideau Lake, it flows in a north-easterly direction for 110 km before joining the Ottawa River at Ottawa (45° 27' N, 75° 42' W) (Figure 2.1). The watershed area of the Rideau at Ottawa is 3830 km^2. The mean annual discharge of the Rideau River is 38.9 m^3

s^{-1}, and the mean discharge from May to October is 19.4 m^3 s^{-1}. (Water Survey of Canada. Historical Streamflow Summary, Ontario 1990).

Most of the Rideau is wide and slow flowing. Width varies from 60 m to 700 m with a mean width of approximately 150 m. Depth varies from < 1 m to 10 m with a mean depth of approximately 4 m. Only six reaches of shallow, fast flow occur along the Rideau (Andrewsville Rapids, Burritt's Rapids, Manotick Rapids, Black Rapids, Carleton Rapids, and Strathcona Park Rapids). The discharge and water levels of the Rideau River are highly regulated by Parks Canada in order to maintain navigational channels in the summer and fall, and to prevent flooding in the spring. A series of 13 lock stations and weirs are used to regulate river flow and allow for navigation. Being lake-fed and regulated, discharge does not change appreciably along the Rideau's length and there are no major tributaries within the section studied. The two main tributaries are Kemptville Creek and the Jock River with mean annual discharges of 5.1 and 6.5 m^3 s^{-1}, respectively. The mean discharge for Kemptville Creek from May to October is 1.9 m^3 s^{-1} and for the Jock River, 2.7 m^3 s^{-1} (Water Survey of Canada, Historical Streamflow Summary, Ontario 1990).

The geology of the region consists of a mixture of sedimentary and Precambrian bedrock with large areas of silty clay and sandy loam (Davidson 1990). Approximately 70% of the watershed area is agricultural land, the remainder either urban or forested (Davidson 1990).

Seven sites (numbered 1 to 7) were sampled along the Rideau River. Site 1 was located in the headwaters, Lower Rideau Lake, while sites 2 to 7 were located within the river proper (Figure 2.1). In addition, three reaches of varying water retention time were defined between sampling sites. The reaches were termed "long", "medium" and "short" retention. The long retention reach was located between site 2 and site 3. The medium retention reach was located between site 6 and site 7. The short retention reach was located between site 4 and site 5 (Figure 2.1). Each of these three reaches was eight kilometres in length.

The volumes of the reaches were determined by multiplying the surface area of each reach (determined by planimetry) by its average depth. Average depth was determined using a depth sounder (LCR 400ID, Marine Information Systems) and available bathymetric maps. The average depths of the reaches with long retention, medium retention and short retention were 2 metres, 5 metres and 3 metres, respectively. Discharge values were obtained from the Water Survey of Canada which maintains a continuous gauging site at Ottawa. Mean discharge was calculated as the average of the daily discharge for the period seven days prior to and including the sampling dates in a manner similar to that of Pace *et al.* (1992). Theoretical retention times of the reaches were determined by dividing reach volume by mean discharge (Soballe and Threlkeld 1985).

2.3.2 Field Sampling

At each site water samples were taken using a four meter vertically integrated tube across a bank to bank transect. Samples were taken at the one third, one half and two thirds distances across (Shaw 1987). It was assumed that the water column was vertically homogenous as has been shown for other rivers of similar size and discharge (Capblancq and Descamps 1978, Baker and Baker 1979, Pace *et al.* 1992, but cf: Pieterse *et al.* 1986). Furthermore, depth profiles of temperature obtained in early August indicated no strong vertical stratification. At each site, six 2-L samples (two at each distance across) were taken for algal Chl *a* and three 300-ml samples (one at each distance across) were taken for total phosphorus (TP), soluble reactive phosphorus (SRP), and nitrate+nitrite concentration determinations. Surface water temperature was measured with a mercury thermometer. Samples were stored in Nalgene plastic bottles and kept cool and dark during transport to Ottawa. Sampling was conducted once a month from May to October 1993.

2.3.3 Laboratory Analysis

Water samples were filtered through Whatman GF/F filters for Chl *a* analysis. Chl *a* was extracted using DMSO and acetone (Burnison 1980) and concentrations (uncorrected for phaeopigments) were calculated using the equations of Jeffrey and Humphrey (1975).

Chemical analysis was performed at the Regional Municipality of Ottawa-Carleton Surface Water Quality Laboratories using a Skalar auto-analyzer. TP concentration was determined by acid digestion to orthophosphorous followed by reaction with ammonium molybdate and ascorbic acid (RMOC 1993). SRP concentration was determined by reacting orthophosphorous with ammonium molybdate and potassium antimony tartrate followed by reduction with ascorbic acid (RMOC 1993). Nitrate + nitrite concentration was determined by reducing nitrate to nitrite, diazotizing the nitrite with sulfanilimide and coupling with ethylenediamine dihydrochloride (RMOC 1993). The detection limit for TP and nitrate + nitrite was 5.0 $\mu g\ L^{-1}$, for SRP 2.0 $\mu g\ L^{-1}$ (RMOC 1993).

2.3.4 Statistical Analysis

Statistical Analysis was performed using either SAS (SAS Institute Inc. Cary N.C.) or Sigmastat (Jandel Scientific, San Rafael CA.) statistical software. Parametric tests performed included 2-Way Model I ANOVA, linear regression, multiple linear regression, and Tukey multiple comparisons. All parametric tests satisfied the assumptions of normality (Wilkes-Shapiro test) and homoscedasticity (Levene's test) following any necessary data transformation. Non-parametric 2-Way ANOVA and Tukey-type multiple comparisons (Zar 1984) were used when data could not be transformed to satisfy normality and homoscedasticity assumptions. The significance value for all statistical tests was 5% ($p = 0.05$).

2.4 Results

2.4.1 Chlorophyll *a* Concentration: Seasonal and Spatial Trends

There was considerable variation in Chl *a* concentrations both spatially and seasonally within the 90 km section of the Rideau River examined. Following data transformation parametric two-way ANOVA revealed significant differences in Chl *a* concentration among sites and among months (overall ANOVA, $p < 0.0001$, $F = 114.4$, for site, $p < 0.0001$, $F = 257.6$, for month, $p < 0.0001$, $F = 159.1$). *A posteriori* Tukey multiple comparisons revealed several trends with respect to Chl *a* among sites. Chl *a* concentrations decreased significantly from the headwater site (site 1) to the first river site (site 2) in the months of May, August, September, and October (Figure 2.2). The largest decrease occurred in September (from 19 $\mu g\ L^{-1}$ to 3 $\mu g\ L^{-1}$). Following this initial decrease, Chl *a* concentration significantly increased from site 2 to site 3 in these months. From site 3 to site 4 a significant increase in Chl *a* concentration occurred in all months (Figure 2.2). At site 4 at least 10 $\mu g\ L^{-1}$ of Chl *a* was always observed. There was never an increase in Chl *a* concentration from site 4 to site 5 (Figure 2.2). From site 5 to site 6 a significant decrease in Chl *a* concentration occurred in all months except May and October. From site 6 to site 7 significant increases in Chl *a* concentration occurred in all months except May and October (Figure 2.2).

To summarize, the longitudinal trends which predominated over most months were: a decrease in Chl *a* concentration from site 1 to site 2, an increase from site 2 to site 3, an increase from site 3 to site 4, no change from site 4 to site 5, a decrease from site 5 to site 6 and an increase from site 6 to site 7.

Tukey multiple comparisons revealed two seasonal trends in Chl *a* concentration among the river sites. Sites 1 and 3 exhibited a high concentration in May (between 9 and 11 $\mu g\ L^{-1}$ of Chl *a*) followed by a significant decrease in June and July (between 4 and 6 $\mu g\ L^{-1}$ of Chl *a*). This was followed by a significant increase from July to August and September. From September to October there was a significant decrease in Chl *a* concentration. (Figure 2.2, 2.3a). Site 2 exhibited no seasonal trend and Chl *a* biomass was always low (range from 2.05 to 5.43 $\mu g\ L^{-1}$, mean for all months ± SE = 4.26 ± 0.31 $\mu g\ L^{-1}$, n = 34). At the downstream sites (sites 4, 5, 6 and 7) a high concentration was observed from May until July (mean ± SE for all sites = 14.1 ± 0.03 $\mu g\ L^{-1}$, n = 71). This was followed by a significant decrease in August (mean ± SE for all sites = 6.3 ± 0.41 $\mu g\ L^{-1}$, n = 24) after which the concentration did not change significantly (Figure 2.3b).

2.4.2 Discharge and Water Temperature

The discharge hydrograph for the Rideau River is typical of that for other temperate Ontario rivers (Water Survey of Canada 1990). A high spring discharge of approximately 90 $m^3\ s^{-1}$ in May was followed by lower discharges in the summer months. The lowest discharge occurred in August (10.0 $m^3\ s^{-1}$) (Figure 2.4). River water

temperature also exhibited a distinct seasonal pattern with a low of 10 °C in October and a high of 25 °C in July (Figure 2.4). In any one month, there were no significant longitudinal differences in temperature along the river.

2.4.3 Nutrient Concentrations: Seasonal and Spatial Trends

The mean TP concentration over the entire sampling period for all seven sites combined was 34.8 ± 0.88 μg L^{-1} (mean ± SE, n = 125). Non-parametric two-way ANOVA followed by Tukey-type multiple comparisons, indicated that sites in the Rideau River proper (sites 2 through 7) had significantly higher TP concentrations than the Rideau headwater site (site 1) (overall ANOVA: $p < 0.0001$, $F = 34.3$, for site: $p < 0.0001$, $F = 99.28$, for month: $p < 0.0001$, $F = 67.62$). There were generally no significant differences in TP concentration among any of the river sites (Figure 2.5a, 2.6a for May and July, all other months exhibited a similar pattern). Seasonally, there was a significant increase in TP concentration from June to July and a significant decrease in TP concentration from August to September within the river sites (Figure 2.7a for site 6, all other river sites exhibited a similar pattern). There were no significant differences in TP concentration in Lower Rideau Lake (site 1) over the sampling period with a mean concentration of 22.2 ± 3.2 μg L^{-1} (mean ± SE, n = 18).

The overall mean soluble reactive phosphorus (SRP) concentration in the sampled portion of the Rideau River was 8.2 ± 0.58 μg L^{-1} (mean ± SE, n = 126). There were significant differences in SRP concentration among sites and among months

(non-parametric two-way ANOVA, $p < 0.0001$, $F = 84.69$, for site, $p < 0.0001$, $F = 255.61$, for month, $p < 0.0001$, $F = 116.69$). Both spatially and seasonally SRP tended to vary as TP varied (Figure 2.5a, 2.6a, 2.7a).

The mean $NO_2 + NO_3$ concentration of all sample sites and months combined was 42.5 ± 4.3 $\mu g\ L^{-1}$ (mean ± SE, $n = 123$). Non-parametric two-way ANOVA indicated significant differences in $NO_2 + NO_3$ concentration among sites and among months (overall ANOVA, $p < 0.0001$, $F = 90.46$, for site, $p < 0.0001$, $F = 419.6$, for month, $p < 0.0001$, $F = 131.8$). $NO_2 + NO_3$ concentrations were significantly higher at the downstream sites 6 and 7 than in the remainder of the river (Figure 2.5b, 2.6b). Seasonally, $NO_2 + NO_3$ concentrations were higher in May than in the other months. There were no significant differences from June to October (Figure 2.7b).

2.4.4 Determinants of Algal Biomass

Multiple regression analysis was used to identify which (if any) combination of the independent variables could best be used to predict Chl *a* concentration within the Rideau River. The dependent variable, Chl *a* concentration, and the independent variables TP concentration, SRP concentration, and $NO_2 + NO_3$ concentration were log transformed to achieve normality (Wilkes-Shapiro, $p = 0.201$, $n = 107$), homoscedasticity ($p = 0.259$, $n = 107$) and linearity prior to multiple regression analysis. For the multiple regression, log Chl *a* concentration was the dependent variable and log TP concentration, log $NO_2 + NO_3$ concentration, log SRP concentration, temperature and discharge were the

independent variables. A correlation matrix (Pearson product moment correlation) revealed that among the independent variables, log TP concentration was significantly and highly positively correlated with temperature, the correlation coefficient equal to 0.62 (Table 2.1). Discharge was significantly negatively correlated with temperature and positively with log $NO_2 + NO_3$ concentration. log SRP concentration was significantly positively correlated with log TP concentration, temperature and log $NO_2 + NO_3$ concentration. These latter correlations, though significant, were not high because the correlation coefficients were all below 0.60 (Table 2.1). The most suitable multiple regression equation (i.e. with the highest coefficient of determination, all regressors significant, and limited multicollinearity) was:

log Chl *a* = -0.95 + 1.41 log TP + 0.09 log $NO_2 + NO_3$ - 0.56 log SRP

($p < 0.001$, $R^2 = 0.51$, RMS = 0.03)

Neither discharge nor temperature were significant regressors. Of the variance in log Chl *a* concentration accounted for by this multiple regression, 71% was contributed by the log TP concentration term. Therefore, in order to obtain a more simple equation, a linear regression was performed between the logarithms of the Chl *a* and TP concentrations.

Average Chl *a* and TP concentrations for river sites were log transformed to achieve normality (Wilkes Shapiro, $p = 0.18$, $n = 36$) and homoscedasticity ($p = 0.19$, $n = 36$) prior to linear regression of Chl *a* with TP. Results of the linear regression analysis indicated that log Chl *a* concentration tended to increase as log TP concentration increased ($p = 0.02$, $R^2 = 0.16$, residual mean square = 0.05) (Figure 2.8). However, this

regression was significant only with the inclusion of a single point with low TP concentration and low Chl *a* concentration (indicated in Figure 2.8). Removal of this point resulted in no detectable relationship between log Chl *a* concentration and log TP concentration ($p = 0.16$, $R^2 = 0.06$, RMS = 0.046).

2.4.5 Algal Biomass Change Through the Defined Reaches

Retention times of the river reaches designated as long, medium and short retention time varied as discharge varied seasonally (Table 2.2). Through the reach with a long retention time (between site 2 and site 3) Chl *a* concentration increased in May, August, September and October and remained unchanged in June and July (Figure 2.2). Through the reach with a medium retention time (between site 6 and site 7) Chl *a* concentration increased significantly in all months except May and October (Figure 2.2). Through the reach with a short retention time (between site 4 and site 5) there was never an increase in Chl *a* concentration and significant decreases in concentration occurred in May and October (Figure 2.2).

Rates of biomass change calculated from the change in Chl *a* concentration from inflow site to outflow site of each river reach (Kohler 1993) indicated that net increases only occurred through the reaches with long and medium retention times (Table 2.3). In the reach with short retention time no increases occurred and net loss occurred during May and October (Table 2.3). In the reach with medium retention rate of biomass change

was low in May, increased to a maximum in August and decreased in September and October (Table 2.3).

2.5 Discussion

Considerable longitudinal variation in Chl *a* concentration was observed in the Rideau River. Results clearly showed large increases and decreases in Chl *a* concentration between river sites. Longitudinal heterogeneity appears to be a characteristic feature of Chl *a* concentrations within riverine environments (Capblancq and Descamps 1978, Baker and Baker 1979, Moss *et al.* 1984, Soballe and Bachman 1984, Soballe and Threlkeld 1985, Chessman 1985, Dauta 1986, de Ruyter van Steveninck *et al.* 1990a, Pace *et al.* 1992, Kohler 1993). In the Rideau River, Chl *a* concentrations did not simply increase gradually downstream as has been observed in other rivers (Greenberg 1964, Capblancq and Descamps 1978, Holmes and Whitton 1981). In the Rideau, there were distinct stretches of river over which net increases and net decreases occurred. Dauta (1986) observed that in the River Lot, overall longitudinal development of phytoplankton was marked by phases of increase and phases of decline. Jones (1984), Kohler (1993) and Cole *et al.* (1992) also observed localized river reaches over which algae increased or declined. In the Hudson River, Pace *et al.* (1992) isolated reaches of net population growth and net population loss when examining zooplankton communities. From the results of the present study and those cited above, it appears that planktonic populations do not simply increase gradually with downstream flow. As

Reynolds (1988) suggests, downstream changes in algal biomass may occur in a "stepwise" manner in which there are reaches of net growth ("sources"), reaches of net loss ("sinks") and reaches of no change. The ability to detect such reaches may depend upon the scale at which observations are taken. In studies in which reach length has been a few kilometres or tens of kilometres, localized increases or decreases in planktonic populations have been observed (Jones 1984, Dauta 1986, Pace *et al.* 1992, Cole *et al.* 1992, Kohler 1993, and the present study). Other studies covering hundreds or thousands of river kilometres tend to indicate more gradual changes in planktonic populations (e.g. Greenberg 1964, Talling and Rzoska 1967).

The initial decrease in Chl *a* concentration upon movement from site 1 to site 2 has been similarly observed in other lake-river transitions. Talling and Rzoska (1967) suggest interception of plankton by submerged vegetation and loss due to benthic filtration as possible mechanisms to account for the decreases in plankton concentration upon movement from a lake into a river. The outflow of Lower Rideau Lake has an extensive development of aquatic macrophytes which may contribute to the decrease in Chl *a* concentration by intercepting outflowing phytoplankton. Kohler (1993) suggests that algae which develop in lentic waters are "ill-suited" to lotic conditions. Uehlinger (1993) concluded that physiological damage occurred to fragile lake phytoplankton upon movement into the more turbulent River Glatt. In the Rideau, the initial decrease in Chl *a* concentration after 14 kilometers of river travel resulted in low Chl *a* concentrations at

site 2 for all months. This low Chl *a* concentration occurred despite high nutrient concentrations.

From site 2 to site 3 (the reach with long retention), a significant increase in Chl *a* concentration occurred in four of the six months sampled. The retention time of this reach was a minimum of 72 hours during the high discharge of May and during other months it was from one to two weeks. As the retention time of a body of water increases, the effects of advection on the planktonic community decrease (Soballe and Kimmel 1987, Pace *et al.* 1992). Soballe and Threlkeld (1985) observed significant increases in Chl *a* concentration between the inflow and the outflow of a river impoundment with a mean retention time of 2.4 days. Retention times within the long retention reach of the Rideau were always sufficiently long for increases in Chl *a* concentration to occur. In addition, the average depth of this reach was approximately two meters. This shallow depth likely meant that as algal cells circulated through the water column, they received sufficient light for positive growth. Attenuation coefficients in the Rideau are typically less than 1.5 m^{-1} (see Chapter 3). This would allow for a euphotic depth (1% light level) of approximately 3 metres. Cole *et al.* (1992) hypothesized that algal blooms in the Hudson River could only occur where the depth was less than four meters. At greater depths phytoplankton was carried below the photic zone (by turbulent mixing) and remained below the 1% light level for a period of time long enough to make net positive algal growth impossible (Cole *et al.* 1992). In the Rideau, this type of light limitation is not likely. Shallow depths result in the majority of the water column (sometimes the

entire water column) being in the euphotic zone. Sufficient retention time and sufficient light availability (due to a shallow depth) resulted in net increases in Chl *a* generally occurring through the reach with long retention time. This initial development of algae may act to inoculate the river with potamoplankton. Kohler (1993) observed that the main flow of the River Spree was inoculated with algae originating from slower flowing reaches. The lack of increase in Chl *a* concentration in June and July from site 2 to site 3 parallels the clear water phase which occurred in Lower Rideau Lake (site 1) at this time. Clear water phases have been observed for other rivers following a spring bloom (Chessman 1985, Bothar and Kiss 1990, Cole *et al.* 1992, Kohler 1993).

In all months there was a significant increase in Chl *a* concentration from site 3 to site 4 (approx. 40 km). There was clearly positive net growth over this section of the river. Chessman (1985) observed similar results in the La Trobe River, in which an inoculum of algae originating from a mid-river impoundment continued to increase downstream. From the decrease in Chl *a* concentration observed from site 1 to site 2 and the subsequent increases from site 2 to site 3 and site 3 to site 4, we conclude that a "true" potamoplankton developed within the Rideau River. The algae in the river were not simply a reflection of the algae in the headwaters. Similarly, Lewis (1988) concluded that most of the phytoplankton biomass in the Orinoco river originated from within channel sources, not from floodplain or headwater lakes. Once a significant Chl *a* concentration was established in the Rideau by site 4 (km 62) there was never an increase from site 4 to site 5 (the reach with a short retention time). The retention time of this reach was at most

58 hours and was often under 40 hours. Therefore, time was not sufficient for an increase in Chl *a* concentration over this reach. The average depth of this reach was approximately three meters. Once again, this shallow depth meant that phytoplankton were likely not circulated below the photic zone and not light limited.

The decrease in Chl *a* concentration which occurred from site 5 to site 6 remains the most puzzling longitudinal trend in the Rideau River. There are no obvious sedimentation areas within this section of river. The river deepens from approximately three metres average depth to five metres average depth between these sites. However, the possibility of light limitation again seems unlikely with a euphotic depth of 3 metres. In a turbid river (the Hudson), with attenuation coefficients from 2 m^{-1} to 4 m^{-1} Cole *et al.* (1992) determined that algal respiration would be greater than photosynthesis (i.e. net loss) when the depth became greater than approximately seven meters. In the Rideau, the depth at which photosynthesis equalled respiration would likely be greater than seven metres because of less non-biogenic turbidity.

Another cause of the decrease in Chl *a* concentration from site 5 to site 6 may have been herbivore grazing upon algae, as de Ruyter van Steveninck *et al.* (1992) observed in the River Rhine. This would be possible had a large zooplankton community developed over this stretch of the Rideau. Lacking data concerning zooplankton biomass, however, we could not determine the effect of zooplankton grazing on algal biomass.

Planktonic development within the Rideau may also be influenced by the presence of shallow, fast flowing reaches (rapids) and numerous weirs (water falls about 1 to 2 m

over each weir). These "physical disturbances" along the river may expose plankton to damaging turbulence and subsequently lead to decreases in concentrations (*sensu*: planktonic "sink"). From site 5 to site 6 there is one section of rapids at Manotick about 500 m in length and one weir. In contrast, the long, slow flowing reaches behind each weir may be conducive to planktonic development and act as planktonic "sources".

From site 6 to site 7 (the reach with medium retention) significant increases in Chl *a* concentration were consistently observed. It appeared that the retention time through the reach with medium retention was always sufficient (except in May) for an increase in algal biomass to be observed. The average depth of this reach was approximately five meters, so light limitation is again unlikely.

Although Chl *a* concentration in the Rideau River was significantly related to TP concentration, the low coefficient of determination for this regression ($R^2 = 0.16$) indicated that much variability remained unexplained and removal of a single point eliminated any significant relationship between Chl *a* concentration and TP concentration. It was clear that when nutrient concentrations (TP, SRP, and nitrate + nitrite) did not vary significantly from site to site, Chl *a* concentration did vary from site to site. Soballe and Kimmel (1987) studying the large NES and NASQUAN data sets concluded that algal abundance in rivers was significantly less predictable than in natural lakes. In our study, R^2 was much lower for the river data ($R^2 = 0.16$) than for published TP-Chl *a* regressions based on lake data (e.g. Dillon and Rigler 1974). Soballe and Kimmel (1987) showed algal abundance per unit phosphorus increasing in the sequence:

rivers < impoundments < natural lakes. When we included the SRP and nitrate + nitrite terms into the equation predicting Chl *a* concentration the coefficient of determination was still relatively low ($R^2 = 0.51$). The positive relationship between Chl *a* and both TP and nitrate + nitrite seem reasonable. The negative relationship between Chl *a* and SRP may result from algal utilization of dissolved phosphorus. As there is less algal biomass (Chl *a*), not as much dissolved phosphorus is taken up and SRP concentration increases. Nonetheless, other factors in addition to nutrient concentrations may determine Chl *a* concentration in the Rideau River.

We observed no significant relationship between Chl *a* concentration and discharge in the Rideau River. This runs counter to most other river studies in which algal biomass is negatively correlated with discharge (summarized by Reynolds 1988). The absence of a relationship between Chl *a* and discharge may be due to the limited range of discharges over which sampling was conducted. In the Rideau, the maximum discharge occurs in April and high discharge occurs in November. By sampling from May to October we failed to sample during these high discharge periods. Bothar and Kiss (1990), working on the Danube, concluded that from May until October water discharge conditions were always favourable for potamoplankton development. They also may have sampled over too limited a range of discharges to observe any discharge effects.

In this study, the rates of biomass increase through the reaches with long and medium retention time were low (usually under 0.15 d^{-1}). Positive biomass change only occurred through the long and medium retention reaches. In the reach with short retention

time no increases were observed. It would appear that within the reaches with long and medium retention, sufficient time was available for potamoplankton to increase in concentration. The shallow depth of these reaches (two meters and five meters) likely prevented circulation of algal cells below the photic zone and associated light limitation. The reach with a short retention time, although also shallow (three meters), did not act as a potamoplankton "source". The water in this reach may have been retained for too short a time period for any detectable increase in Chl *a* concentration to occur.

2.6 Summary

Chl *a* concentrations within the Rideau River displayed considerable longitudinal variation. There appeared to be reaches of net increase in algae (sources), reaches of no change, and reaches of net decrease (sinks). Chl *a* did not simply increase gradually downstream and may develop in a "stepwise" manner within the Rideau. Chl *a* concentration only increased over the reaches with long and medium retentions, never over the reach with short retention times. The shallow depths of all three reaches makes it unlikely that algal cells were circulated below the photic zone for a period of time sufficient to limit growth. At best, there exists a weak positive relationship between Chl *a* concentration and TP concentration in the Rideau River. A limited range of discharges may be responsible for the lack of a significant relationship between Chl *a* and discharge. This suggests that additional abiotic or biotic factors may also regulate algal biomass in the Rideau River. Continued research including the parameters of light availability,

zooplankton biomass, and grazing is required to more fully account for the variation in Chl *a*. As well, the interesting longitudinal patterns in planktonic development require further investigation. These will be addressed in the following chapter.

Table 2.1. Correlations between log TP concentration, discharge, temperature, log SRP concentration, and log nitrate + nitrite concentration for the Rideau River. Pearson product moment correlation coefficients with probabilities in parentheses. n = 107.

	discharge	log [SRP]	log [NO_2+NO_3]	temperature
log [TP]	-0.038 (0.699)	0.414 (<0.001)	0.109 (0.262)	0.615 (<0.001)
discharge		-0.044 (0.653)	0.452 (<0.001)	-0.257 (0.008)
log [SRP]			0.415 (<0.001)	0.369 (<0.001)
log [nitrate+ nitrite]				-0.105 (0.284)

Table 2.2. Calculated retention times of Rideau River reaches. Retention times calculated as reach volume divided by mean river discharge for period seven days prior to and including sampling date.

	Retention Time (hours)					
River Reach	May	June	July	Aug	Sept	Oct
long retention (site 2 to site 3)	72	198	218	395	367	271
medium retention (site 6 to site 7)	19	67	74	154	120	103
short retention (site 4 to site 5)	8	26	29	58	45	39

Table 2.3. Changes in Chl *a* concentration (Δ Chl *a*) in μg L^{-1} from inflow site to outflow site and calculated rates of change of biomass in log units per day (k) for Rideau River reaches of varying retention time. n.s. signifies a non-significant change in Chl *a* concentration and a net growth rate of zero.

	River Reach		
	long retention (site 2 to site 3)	medium retention (site 6 to site 7)	short retention (site 4 to site 5)
Month	Δ Chl *a* k	Δ Chl *a* k	Δ Chl *a* k
May	+6.03 0.25	n.s 0	-3.21 -0.66
June	n.s. 0	+2.41 0.07	n.s. 0
July	n.s. 0	+4.26 0.10	n.s. 0
August	+3.77 0.04	+5.26 0.14	n.s. 0
September	+4.03 0.05	+3.68 0.13	n.s. 0
October	+3.38 0.09	n.s. 0	-5.53 -0.45

Figure 2.1. Locations of sampling sites and defined river reaches of varying retention time along the Rideau River, Ontario. Distances refer to the number of kilometres downstream from the sampling site in Lower Rideau Lake (site 1).

Figure 2.1

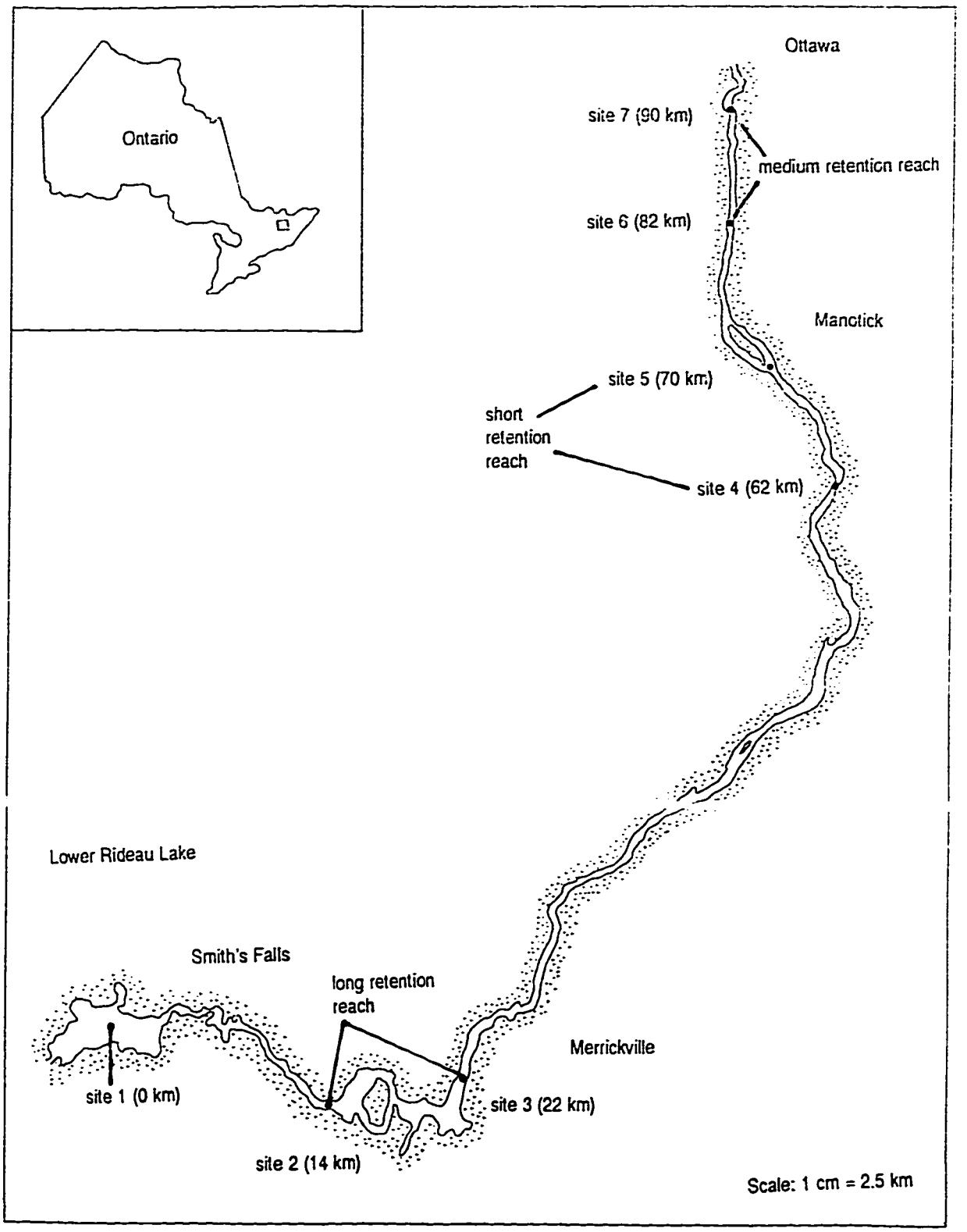

Ontario
Ottawa
site 7 (90 km)
medium retention reach
site 6 (82 km)
Manotick
site 5 (70 km)
short
retention
reach
site 4 (62 km)
Lower Rideau Lake
Smith's Falls
long retention
reach
Merrickville
site 1 (0 km)
site 3 (22 km)
site 2 (14 km)
Scale: 1 cm = 2.5 km

Figure 2.2. Concentrations of chlorophyll *a* in the Rideau River during (A) May, (B) June, (C) July, (D) August, (E) September, and (F) October 1993. Sites are those identified in Figure 2.1. Plotted are means ± standard deviations, n = 6. Means with the same letter are not significantly different at 5%.

Figure 2.2

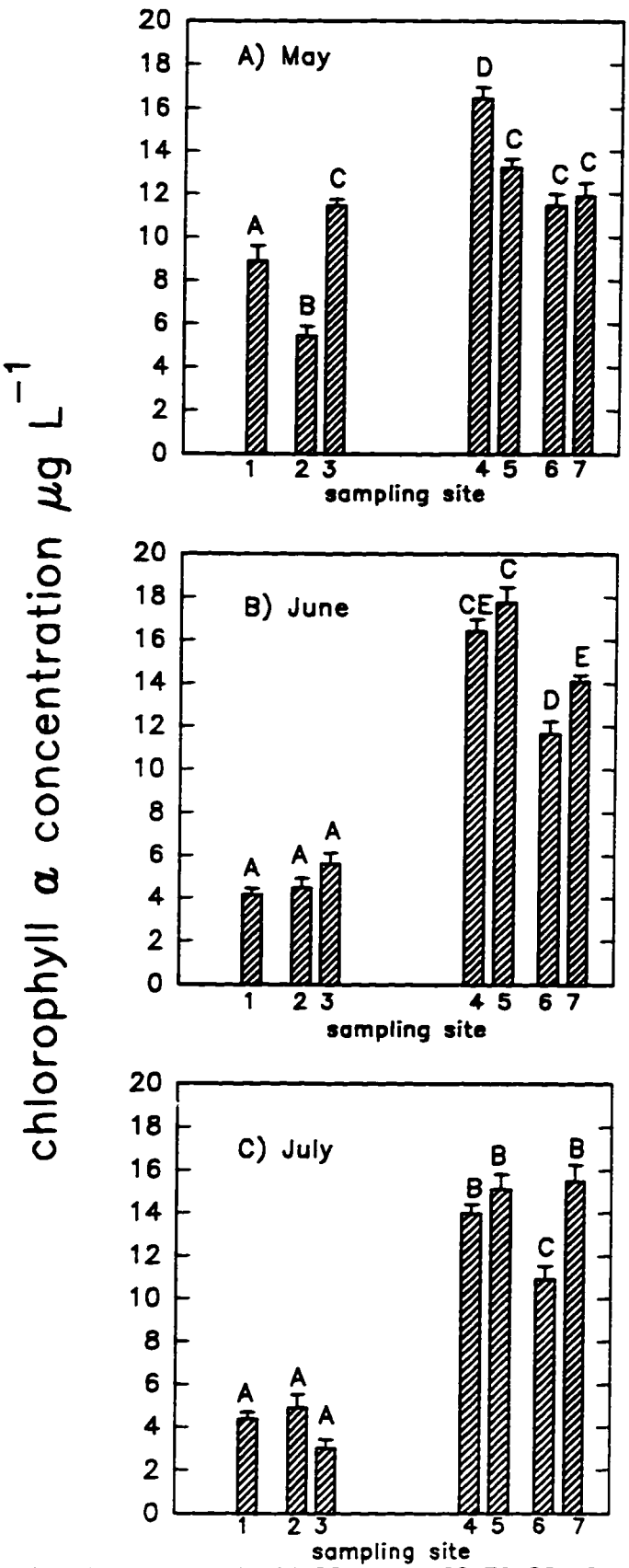

A) May
B) June
C) July
chlorophyll a concentration μg L⁻¹
sampling site
River km downstream of headwaters: 0 14 22 62 70 82 90

Figure 2.2 cont.

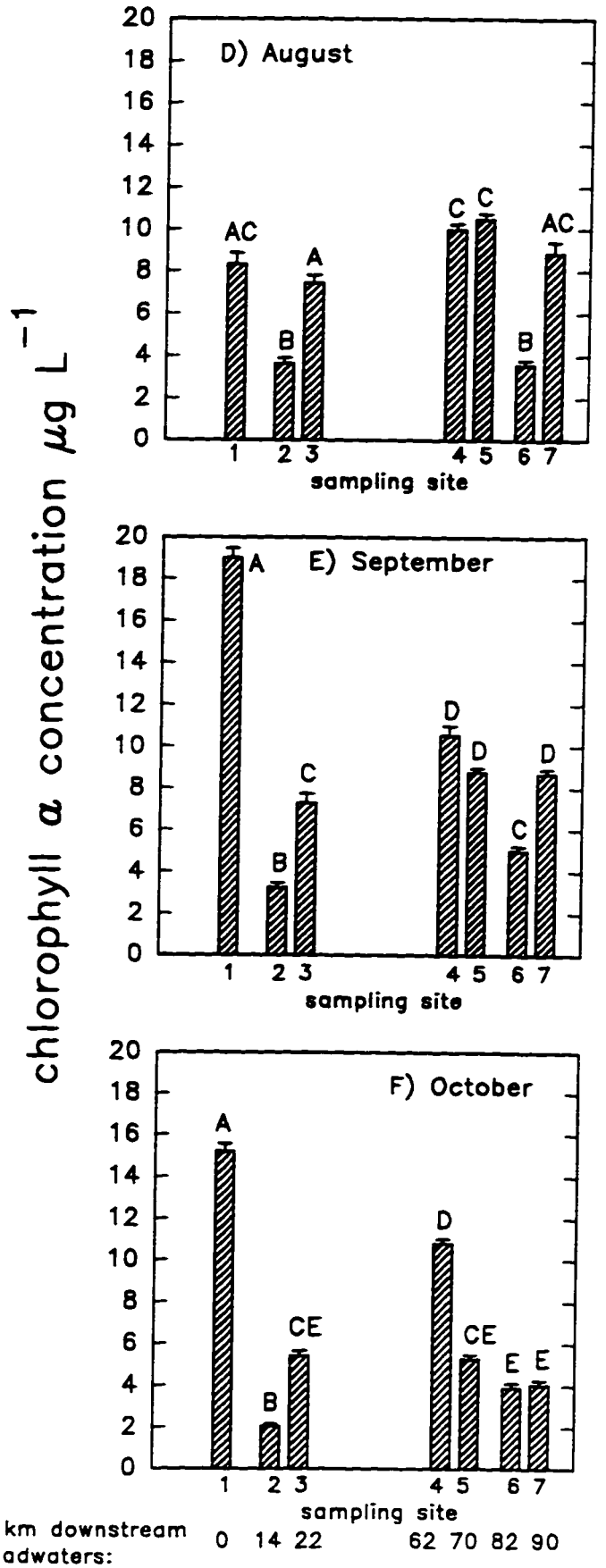


Figure 2.3. Seasonal variation in chlorophyll *a* at site 1 (A) and site 6 (B) on the Rideau River in 1993. Plotted are means ± standard deviations, n = 6. Means with the same letter are not significantly different at 5%.

Figure 2.3

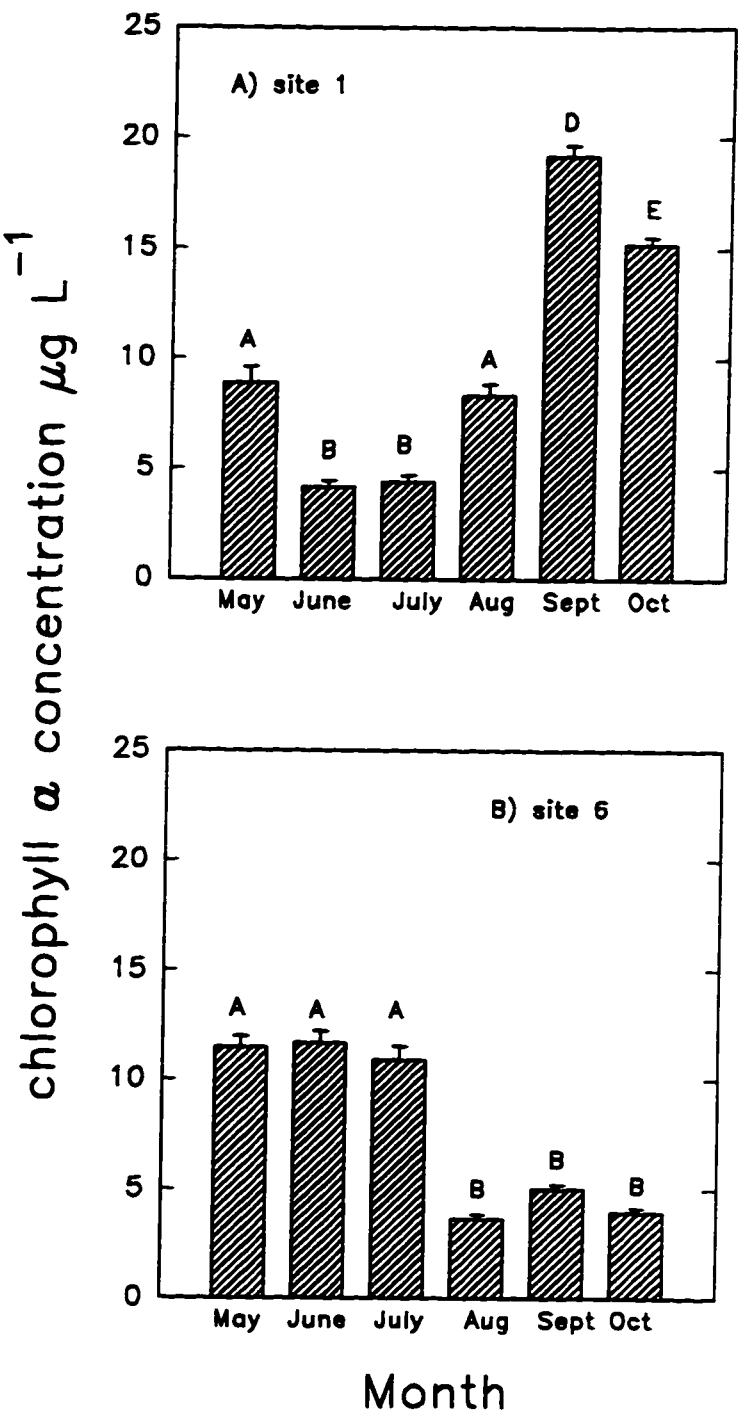

A) site 1
B) site 6
chlorophyll a concentration μg L⁻¹
25
20
15
10
5
0
A
B
B
A
D
E
A
A
A
B
B
B
May
June
July
Aug
Sept
Oct
Month

Figure 2.4. Seasonal pattern of discharge (bars) and temperature (line) for the Rideau River during the sampling period of 1993. Discharge for each month is the mean discharge for the period 7 d prior to and including sampling dates.

Figure 2.4

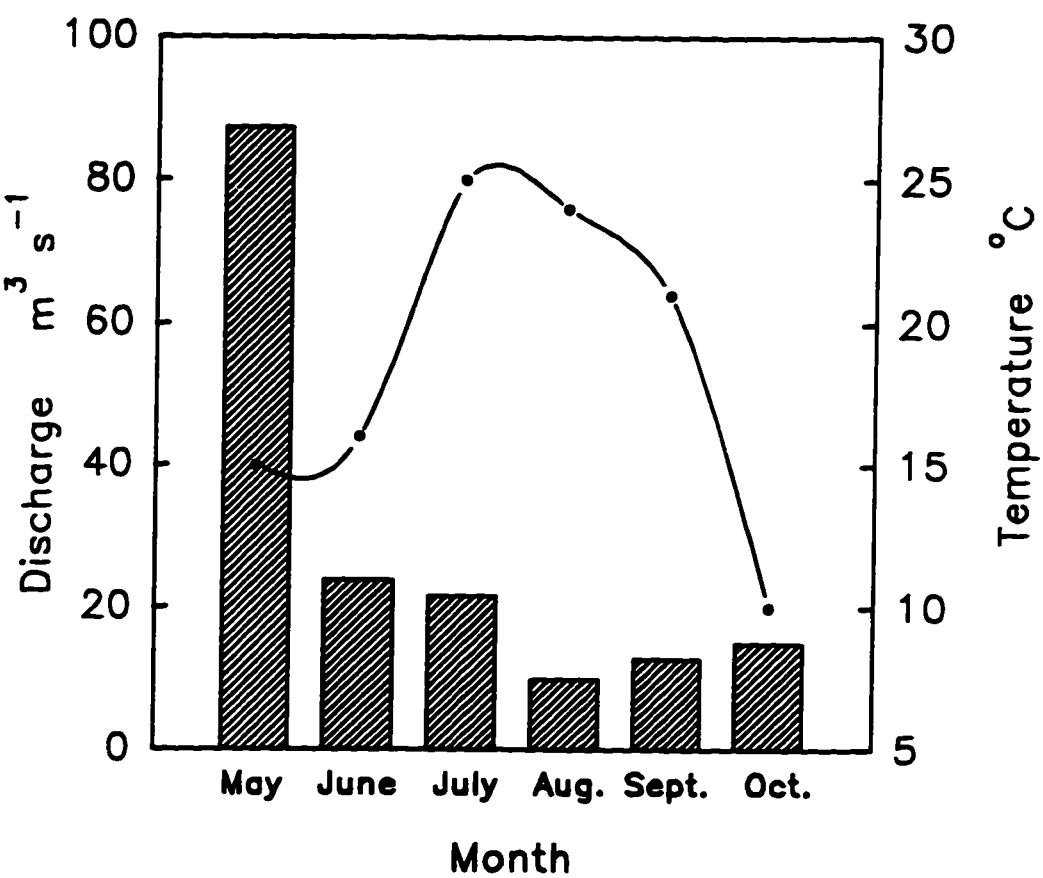

100
80
60
40
20
0
Discharge $m^3 s^{-1}$
30
25
20
15
10
5
Temperature °C
May
June
July
Aug.
Sept.
Oct.
Month

Figure 2.5. Longitudinal variation in (A) total phosphorus (TP) and soluble reactive phosphorus (SRP) concentrations and (B) nitrate and nitrite concentration in the Rideau River during May 1993. Sites are those identified in Figure 2.1. Plotted are means ± standard deviations, n = 3. Means with the same letter are not significantly different at 5%.

Figure 2.5

Ben Kumar Basu

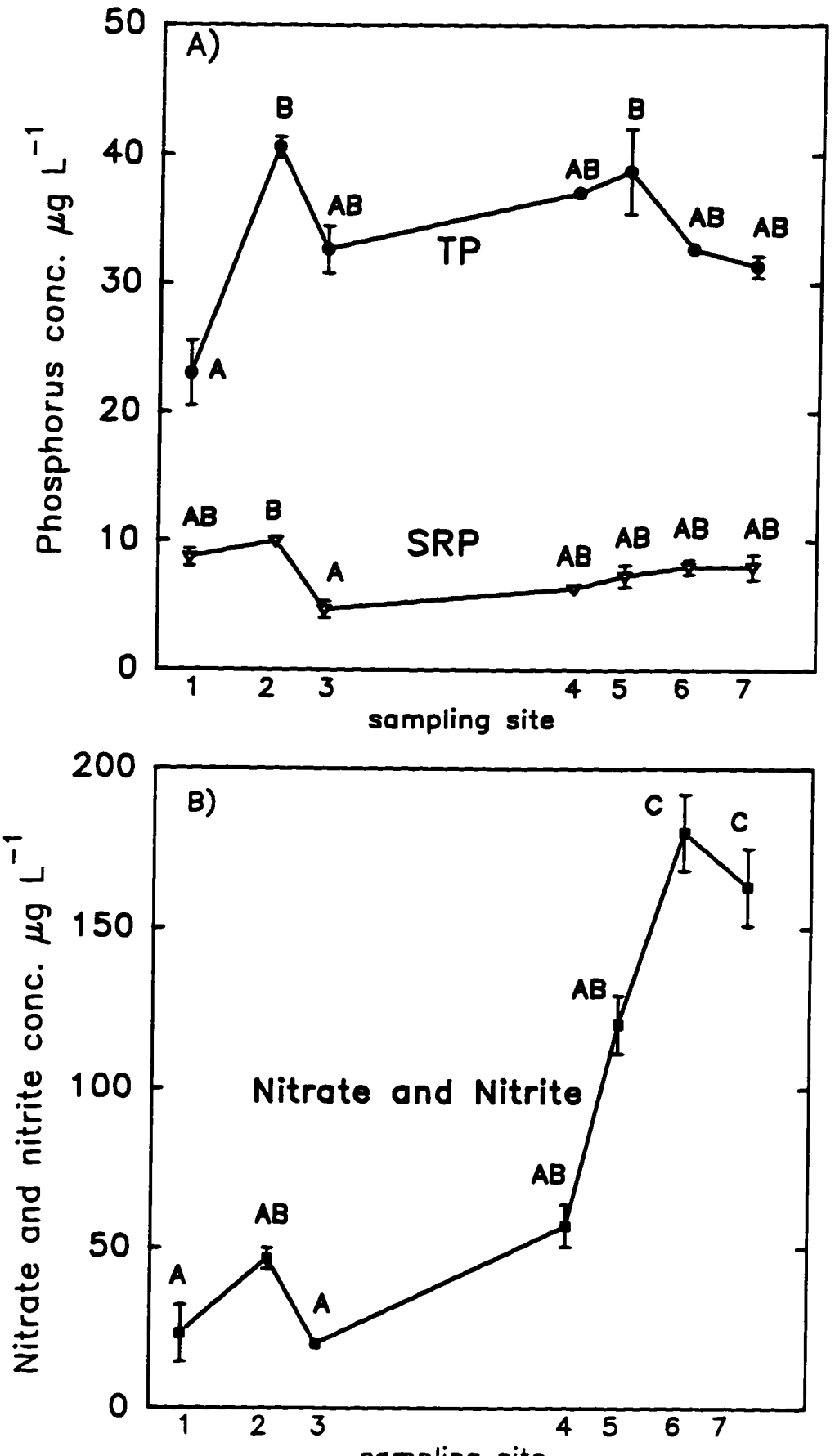


Figure 2.6. Longitudinal variation in (A) total phosphorus (TP) and soluble reactive phosphorus (SRP) concentrations and (B) nitrate and nitrite concentration in the Rideau River during July 1993. Sites are those identified in Figure 2.1. Plotted are means ± standard deviations, n = 3. Means with the same letter are not significantly different at 5%.

Figure 2.6

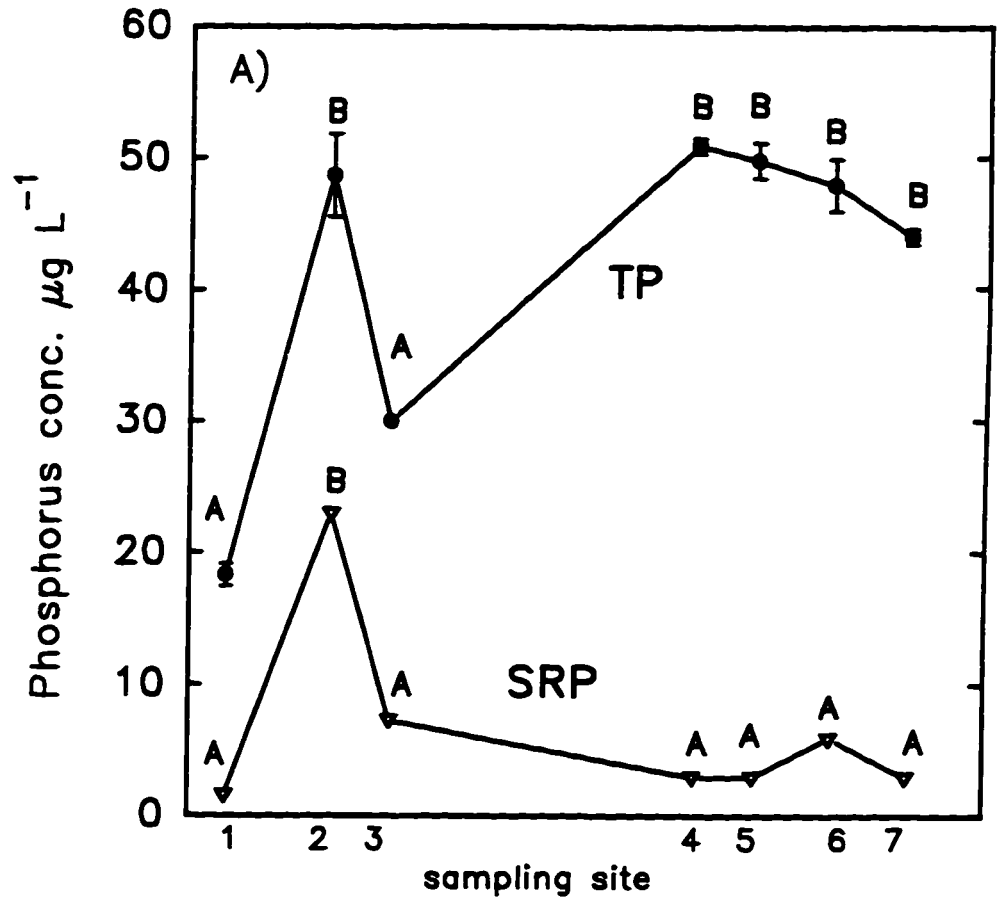

A)
Phosphorus conc. μg L⁻¹
TP
SRP
sampling site
B)
Nitrate and nitrite conc. μg L⁻¹
Nitrate and Nitrite
sampling site

Figure 2.7. Seasonal changes in (A) total phosphorus (TP) and soluble reactive phosphorus (SRP) concentrations and (B) nitrate and nitrite concentration for site 6 on the Rideau River in 1993. Plotted are means ± standard deviations, n = 3. Means with the same letter are not significantly different at 5%.

Figure 2.7

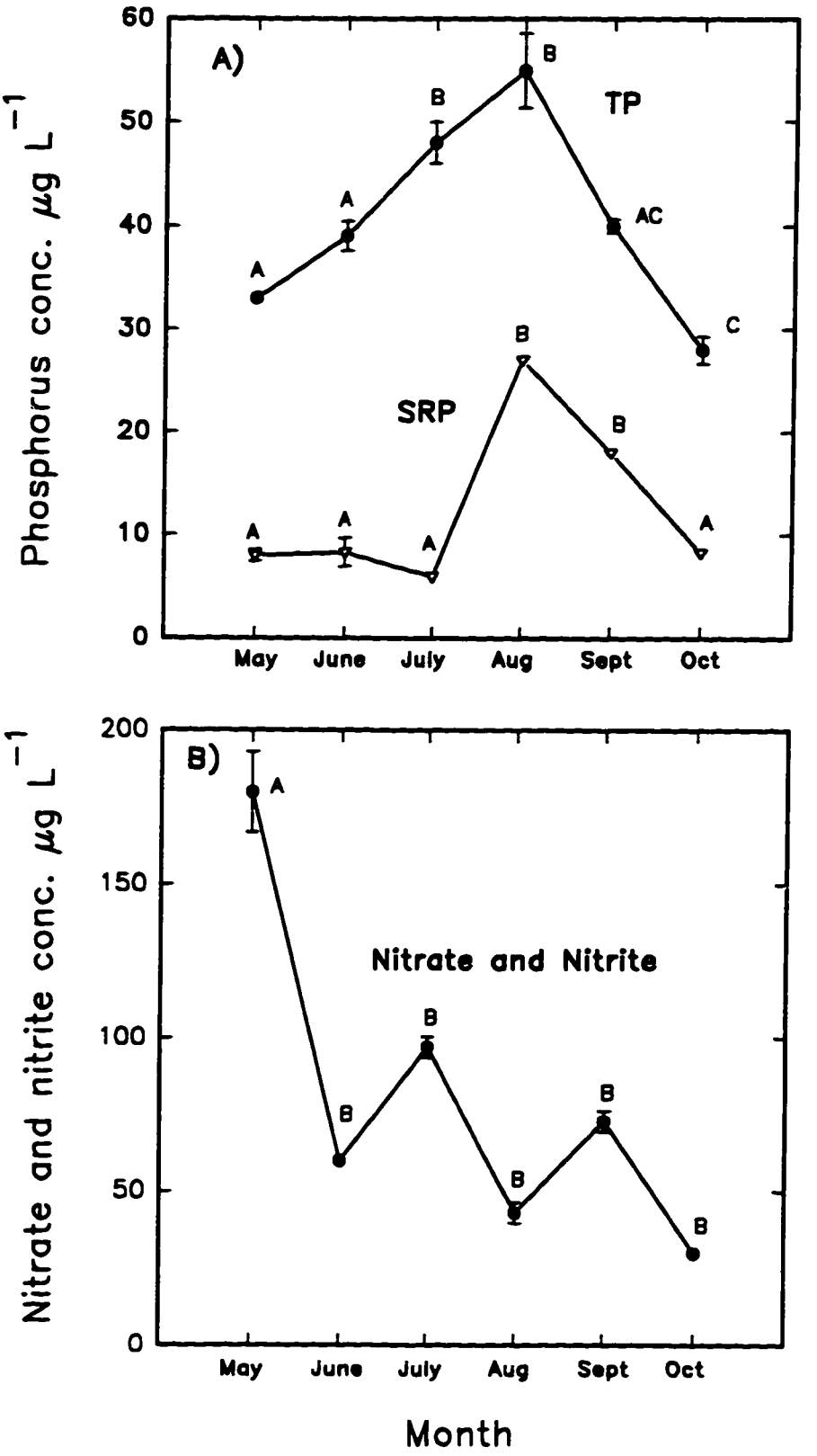
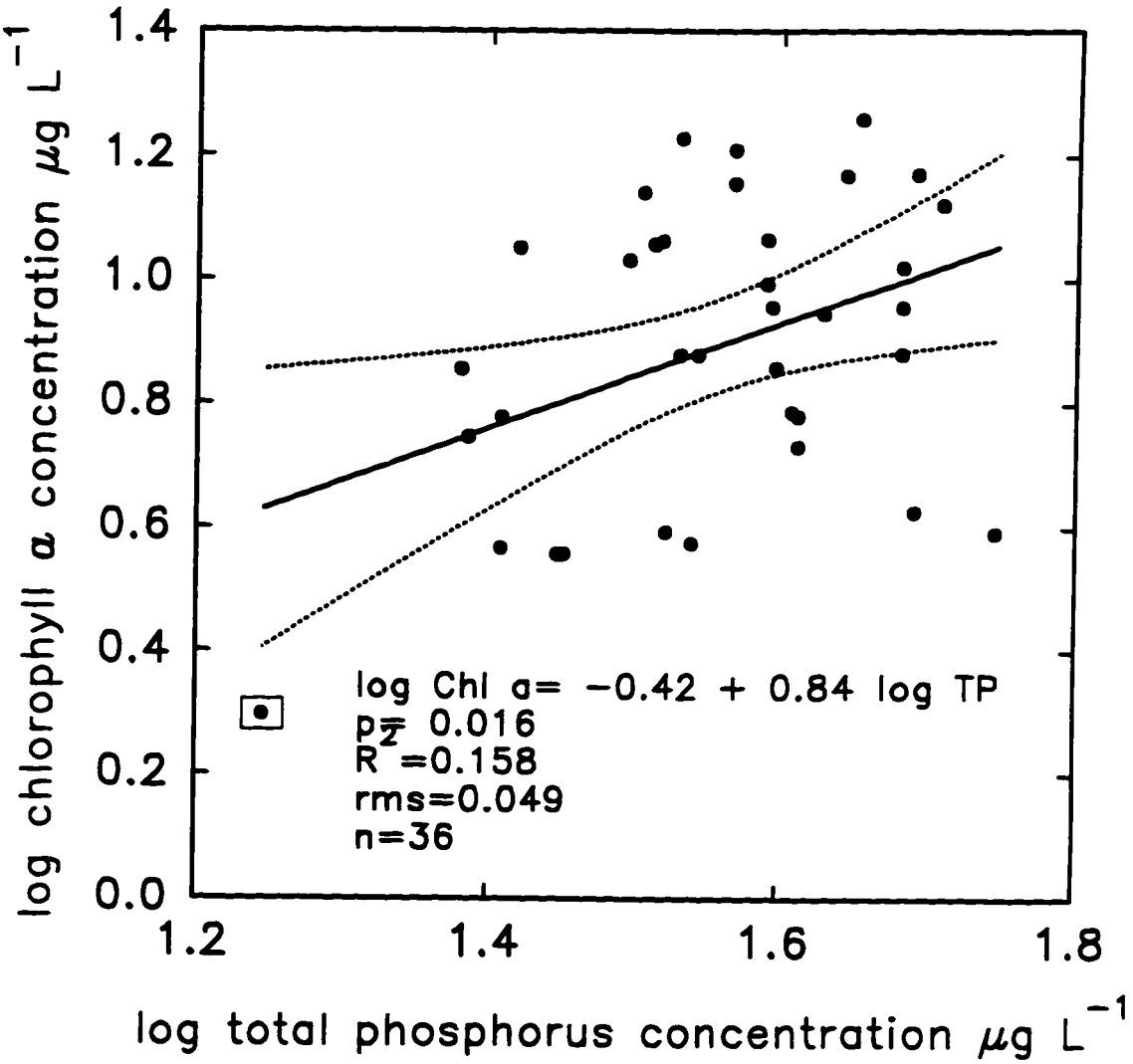

A)
TP
SRP
Phosphorus conc. µg L-1
60
50
40
30
20
10
0
A
A
B
B
AC
C
A
A
A
B
B
A
May
June
July
Aug
Sept
Oct
B)
Nitrate and Nitrite
Nitrate and nitrite conc. µg L-1
200
150
100
50
0
A
B
B
B
B
B
May
June
July
Aug
Sept
Oct
Month

Figure 2.8. Relationship between log TP and log Chl *a* for monthly means of Rideau River sites. Dotted lines are 95% confidence intervals. Relationship is significant only with the inclusion of boxed point (see text).

Figure 2.8


log chlorophyll a concentration μg L⁻¹
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.2
1.4
1.6
1.8
log Chl a= −0.42 + 0.84 log TP
p≤ 0.016
R² =0.158
rms=0.049
n=36
log total phosphorus concentration μg L⁻¹

Chapter 3

Phytoplankton and Zooplankton Development in a Lowland Temperate River

Modified from Basu, B.K. and F.R. Pick. Journal of Plankton Research. 19: 237-253. (with permission)

3.1 Abstract

The longitudinal and seasonal patterns of plankton development were examined over two years in a lowland, temperate river, the Rideau River (Ontario, Canada). Following an initial decrease in phytoplankton and zooplankton biomass as water flowed from the headwaters into the Rideau River proper, there was an increase in chlorophyll *a* (Chl *a*) and zooplankton biomass with downstream travel. At approximately river km 60, both phytoplankton and zooplankton reached their maximum biomass of 27 $\mu g\ L^{-1}$ Chl *a* and 470 $\mu g\ l^{-1}$ dry mass, respectively. Downstream of river km 60 the biomass of both planktonic communities significantly declined despite increased nutrient concentrations and favorable light conditions. At the furthest downstream sites Chl *a* was often less than 10 $\mu g\ L^{-1}$ and zooplankton biomass often less than 50 $\mu g\ L^{-1}$. These downstream declines may be due to the feeding activity of the exotic zebra mussel (*Dreissena polymorpha*) which was of high density in downstream reaches (> 1000 individuals m^{-2}). There was no evidence for longitudinal phasing of phytoplankton and zooplankton in the Rideau River, as increases and decreases in Chl *a* and zooplankton biomass appeared to coincide. Overall, Chl *a* was positively related to total phosphorus concentration ($R^2 = 0.43$) and zooplankton biomass was positively related to Chl *a* ($R^2 = 0.20$). Neither Chl *a* nor zooplankton biomass were significantly related to discharge. A negative relationship between zooplankton and phytoplankton biomass was not observed.

3.2 Introduction

The development of phytoplankton and zooplankton communities in lentic freshwaters (lakes and reservoirs) has been studied extensively. In contrast, comparatively little research has focused on phytoplankton and zooplankton development in lotic waters (rivers) (Reynolds 1988, Kohler 1993, Thorp *et al.* 1994). Potamoplankton (true river plankton) attains significant biomass in large lowland rivers where residence times and low flow rates allow planktonic organisms sufficient time for growth and reproduction (Margalef 1960, Lack 1971, de Ruyter van Steveninck *et al.* 1990a). However, the regulation of both phytoplankton and zooplankton development and the interactions between these two communities in large rivers remain poorly described. It cannot be assumed that conclusions drawn from lentic environments are applicable to lotic environments (Ryder and Pesendorfer 1989, Thorp *et al.* 1994).

Possible factors regulating potamoplankton abundance may be hydrological (discharge, water residence time), chemical (nutrient concentrations), physical (light conditions), and biotic (grazing, competition) (Reynolds 1988, Moss *et al.* 1989, Basu and Pick, 1995). An inverse correlation between phytoplankton biomass and river discharge has been demonstrated (Reynolds 1988, Jones 1984, Jones and Barrington 1985). Increases in river discharge are believed to decrease phytoplankton biomass by shortening the residence time of the water, thereby shortening the time available for potamoplankton to develop (Baker and Baker 1979, Reynolds 1988).

Other researchers have concluded that river phytoplankton is less sensitive to the effect of discharge or water residence time and more strongly regulated by nutrient

concentrations. A significant positive relationship between river phytoplankton abundance or biomass and total phosphorus concentration has been observed in several studies (Soballe and Kimmel 1987, Moss *et al.* 1989, Basu and Pick 1995, 1996, Van Nieuwenhuyse and Jones 1996).

Due to the turbulent and often turbid conditions found in many large rivers, it has also been suggested that light conditions may regulate river phytoplankton development (Krogstad and Lovstad 1989, Cole *et al.* 1992). In deep sections of rivers, when the depth of mixing is greater than the depth of the photic zone, it is possible that the average irradiance to which algal cells are exposed is near or below the threshold for net growth (Lewis 1988, Cole *et al.* 1992).

In comparison to the algal component, there has been less attention devoted to the zooplankton component of the potamoplankton. Pace *et al.* (1992) studying the Hudson River, USA, and Thorp *et al.* (1994) the Ohio River, USA, observed zooplankton abundance to be negatively correlated with river discharge. Basu and Pick (1996) similarly observed that across a range of 31 rivers in Ontario, Canada, zooplankton biomass was positively related to water residence time. In addition, Basu and Pick (1996) observed a positive correlation between zooplankton biomass and phytoplankton biomass suggesting a (weak) resource effect. In contrast, de Ruyter van Steveninck *et al.* (1990a) observed an inverse correlation between zooplankton biomass and phytoplankton biomass in the lower reaches of the River Rhine. They suggested that this was due to a strong grazing effect of zooplankton on phytoplankton; however, the extent of trophic coupling between phytoplankton and zooplankton in rivers remains little explored.

The present study examines the development of phytoplankton and zooplankton biomass longitudinally and seasonally along a large, temperate, lowland river, the Rideau River, Ontario, Canada. Our previous work on the Rideau (Basu and Pick 1995, Chapter 2 of the present thesis) indicated extensive longitudinal changes in phytoplankton biomass, as has been observed in other large rivers (Soballe and Bachman 1984, Chessman 1985, Cole *et al.* 1992, Kohler 1993). We also observed a positive relationship between phytoplankton biomass and total phosphorus concentration and no relationship between biomass and discharge (Basu and Pick 1995. Chapter 2 of the present thesis). However, much of the variation in phytoplankton biomass remained unexplained by either nutrient or physical factors. This suggested the potential role of biotic factors (including zooplankton grazing) in influencing phytoplankton biomass.

The objectives of this study were as follows: i) to describe the longitudinal and seasonal pattern of both phytoplankton and zooplankton development within the Rideau River, ii) to determine the factors most strongly related to phytoplankton biomass, and iii) to determine the factors most strongly related to zooplankton biomass. Variables measured included: chlorophyll *a* concentration (Chl *a*), crustacean zooplankton biomass, rotifer biomass, total phosphorus concentration (TP), soluble reactive phosphorus concentration (SRP), total nitrogen concentration (TN), river discharge, light attenuation, depth and temperature. Invasion of the Rideau River by the exotic zebra mussel (*Dreissena polymorpha*) occurred in 1990 and densities have increased since (years 1990 to 1996, Martel 1995). The potential effect that this benthic suspension feeder could have on plankton densities in the Rideau was also considered.

3.3 Methods

3.3.1 Study Area

The Rideau River is located in southeastern Ontario and flows northeast for 110 km from its headwaters in Lower Rideau Lake before discharging into the Ottawa River at Ottawa (45°N 27'N, 75° 42'W) (Figure 3.1). The watershed area of the Rideau at Ottawa is 3830 km^2. The mean annual discharge of the Rideau River is 38.9 $m^3 s^{-1}$, and the mean discharge from May to October is 19.4 $m^3 s^{-1}$. (Water Survey of Canada, Historical Streamflow Summary, Ontario 1990). Most of the Rideau is wide and slow flowing. Width varies from 60 m to 700 m with a mean width of approximately 150 m. Depth varies from < 1 m to 10 m with a mean depth of approximately 4 m. Only six reaches of shallow, fast flow occur along the Rideau (Andrewsville Rapids, Burritt's Rapids, Manotick Rapids, Black Rapids, Carleton Rapids, and Strathcona Park Rapids). The discharge and water levels of the Rideau River are highly regulated by Parks Canada in order to maintain navigational channels in the summer and fall, and to prevent flooding in the spring. A series of 13 lock stations and weirs are used to regulate river flow and allow for navigation. Being lake-fed and regulated, discharge does not change appreciably along the Rideau's length and there are no major tributaries within the section studied. The two main tributaries are Kemptville Creek and the Jock River with mean annual discharges of 5.1 and 6.5 $m^3 s^{-1}$, respectively. The mean discharge for Kemptville Creek from May to October is 1.9 $m^3 s^{-1}$ and for the Jock River, 2.7 $m^3 s^{-1}$ (Water Survey of Canada, Historical Streamflow Summary, Ontario 1990).

The geology of the region consists of a mixture of sedimentary and Precambrian bedrock with large areas of silty clay and sandy loam (Davidson 1990). Approximately 70% of the watershed area is agricultural land, the remainder is either forested or urban (Davidson 1990). The primary uses of the river are for recreation and water supply and there are no major industries located along the Rideau's course.

Once a month from May to October 1994 and May to September 1995, the Rideau was sampled at 15 sites (numbered 1-15). Site 1 was located in the headwaters, Lower Rideau Lake, while sites 2-15 were located within the river proper, upstream from the city of Ottawa. The sites were evenly spaced approximately 7 km apart (Figure 3.1).

3.3.2 Field Sampling

At each site vertically integrated water samples were taken using a 4 m tube (inner diameter 2.54 cm). It was assumed that the water column was vertically homogenous (Basu and Pick 1995, Chapter 2 of the present thesis). Five 2-L samples were taken for algal Chl *a* and three 300-ml samples were taken for total phosphorus (TP), soluble reactive phosphorus (SRP), and total nitrogen (TN) concentration determinations. Samples were stored in Nalgene plastic bottles and kept cool and dark during transport to Ottawa.

Zooplankton was sampled at sites 1, 3, 5, 7, 9, 12 and 14. Mesozooplankton (cladocerans and copepods) were sampled using an open diaphragm bilge pump (pumping rate of 10-L min^{-1}) (Pace 1984). Triplicate mesozooplankton samples were collected by pumping 30-L of water through a 64-μm Nitex mesh plankton net. Samples

were vertically integrated by raising and lowering the pump intake between the surface and the maximum depth at a constant rate. Triplicate microzooplankton (rotifer) samples were collected by filtering 4-L of water (collected at 0.5-m depth) through a 35-μm Nitex mesh screen. All zooplankton samples were collected mid channel and preserved with a 4% chilled Formalin solution containing 40-g of sucrose L^{-1} (Haney and Hall 1975).

Depth at each site was measured using an LCR 400ID depth sounder (Marine Information Systems) and temperature was measured using a mercury thermometer. Light attenuation coefficients were calculated using irradiance measurements obtained with a LiCor 185B 4Π underwater photometer (LiCor, USA). Euphotic depth (1% light level) to mixing depth ratios were calculated using attenuation coefficients and assuming that mixing depth was equivalent to the total depth. The shallow depth of the Rideau (usually 3 to 5 m) justified this assumption. All depth, temperature and light measurements were taken mid channel.

Daily discharge values were obtained from the Water Survey of Canada, which maintains a continuous gauging site at Ottawa. Discharge for each month was calculated as the average of the daily discharges for the period 7 d prior to and including the sampling date (Pace *et al.* 1992, Basu and Pick 1995).

3.3.3 Laboratory Analysis

Chemical analysis to determine TP, SRP and TN concentration was performed at the Regional Municipality of Ottawa-Carleton, Surface Water Quality Laboratories using

a Skalar auto-analyzer. A detailed description of the methods used to determine TP. SRP and TN is given in Basu and Pick (1995) (Chapter 2 of the present thesis).

For Chl *a* analysis, water samples were filtered through Whatman GF/F filters. Chl *a* was extracted using DMSO and acetone (Burnison 1980) and concentrations (uncorrected for pheaopigments) were calculated using the equations of Jeffrey and Humphrey (1975).

Zooplankton abundance was determined by enumerating either whole samples or counting at least 120 individuals in subsamples of each replicate. Cladocerans and copepods were counted under a dissecting microscope at 50X magnification and rotifers were counted using an inverted microscope at 80X magnification. Crustaceans and rotifers were identified to genus level following Thorp and Covich (1991) and Stemberger (1979). Biomass estimates for crustaceans were determined using measured lengths and length-dry mass relationships of Bottrell *et al.* (1976) and Dumont *et al.* (1975). Biovolume of rotifers was calculated using the volume formulae of Ruttner-Kolisko (1977). Biomass estimates for rotifers were calculated by converting biovolume to dry mass assuming a specific density of 1.0 (Dumont *et al.* 1975) and a dry mass to wet mass ratio of 0.1 (Bottrell *et al.* 1976). Total zooplankton biomass was the sum of crustacean and rotifer biomass.

3.3.4 Statistical Analysis

Statistical analysis was performed using either SAS 6.06 (SAS Institute Inc. USA, 1992) or Systat 5.03 (Systat Inc. USA, 1993) statistical software. Polynomial regression

analysis was used to quantify longitudinal patterns of Chl *a*. The inclusion of site 1 (Lower Rideau Lake, km 0) during polynomial regression analysis created significance at third and fourth order levels. Therefore, because site 1 was not located in the Rideau River proper and the most parsimonious regression models were desired, we did not include site 1 during derivation of polynomial equations. Linear regression and correlation analyses were used to identify relationships between variables. Analysis of covariance was used to compare polynomial regression equations and linear regression equations. Bonferroni correction (significance value of 5% divided by the number of tests) was applied following multiple uses of analysis of covariance. In all other cases the significance value for statistical tests remained at 5%. All parametric tests performed satisfied the assumptions of normality (Wilkes-Shapiro test) and homoscedasticity (plot of residuals against independent variable) following any required logarithmic transformations of the data.

3.4 Results

3.4.1 Longitudinal and Seasonal Development of Chlorophyll *a*

The longitudinal patterns in Chl *a* concentration for the sampling months of 1994 and 1995 are shown in Figure 3.2. In all months for both 1994 and 1995, there was a decrease in Chl *a* concentration as the water flowed from site 1 (Lower Rideau Lake, km 0) into the Rideau River proper at site 2 (km 7). With the exception of May 1994, October 1994 and July 1995, the subsequent development of Chl *a* along the river proper could be described using a second order polynomial including km and km^2 terms as

significant independent variables. Chl *a* concentration appeared to increase with downstream travel, peak, and then decrease (Figure 3.2).

Analysis of covariance (ANCOVA) indicated that there were significant differences among the shapes and elevations of these second order regression equations (for shape, $p < 0.05$, $F_{14, 88} = 2.49$; for elevation, $p < 0.05$, $F_{7, 88} = 12.62$). In order to identify which months differed significantly, a series of Bonferroni corrected ANCOVA's comparing the shape and elevation of pairs of months was conducted. A total of 15 ANCOVA's were performed comparing months in the same year (e.g. June 1994 with July 1994) and the same month in different years (e.g. June 1994 with June 1995) (Table 3.1). Only one significant difference in shape was identified (June 1994 with June 1995, $p < 0.003$, $F_{2, 22} = 11.1$) . The shapes for all other months were not significantly different (Table 3.1).

In contrast, there were numerous differences in elevations among the months. In general, a seasonal pattern was apparent with June and July 1994 having a higher elevation than August, and August 1994 having a higher elevation than September. In 1995, May, June, and August generally had a higher elevation than September (Table 3.1, Figure 3.2).

Examining the second order regressions, the longitudinal kilometer at which the peak in Chl *a* occurred ranged from km 54 to km 76 and was most often located near km 60 (Figure 3.2). To obtain the most general second order polynomial describing the longitudinal development of Chl *a* in the Rideau, the data from all the months (of second order) were combined and an overall second order equation derived (Figure 3.3). The

constant (elevation) for this regression is less meaningful as it changes seasonally. However, the regression coefficients which define overall shape, allow for the prediction that peak Chl *a* occurred at km 59.3 (Figure 3.3). Downstream of km 59.3 Chl *a* concentration decreased.

The longitudinal pattern of Chl *a* in May 1994 and October 1994 was best described using a first order (simple linear) regression. In these months Chl *a* continued to increase with downstream travel (Figure 3.2). The longitudinal pattern of Chl *a* for July 1995 was not predictable even upon trial of a tenth order polynomial (Figure 3.2).

3.4.2 Longitudinal and Seasonal Development of Zooplankton Biomass

The longitudinal development of zooplankton biomass in the Rideau River could not be described using polynomial regressions ($p > 0.05$ for all months up to fifth order). However, several patterns were repeated from month to month and across years (Figure 3.4). For all months of both 1994 and 1995 there was a decrease in total zooplankton biomass from site 1 (Lower Rideau Lake, km 0) to the first riverine zooplankton sampling site (site 3, km 14). This decrease in zooplankton biomass was often very large (Figure 3.4). For example, in August 1994 zooplankton biomass decreased from 193 $\mu g\ L^{-1}$ at site 1 to 5.3 $\mu g\ L^{-1}$ dry mass at site 3 and in June 1995 the decrease was from 273 $\mu g\ L^{-1}$ to 19.7 $\mu g\ L^{-1}$ dry mass.

Following this initial decrease, zooplankton biomass tended to increase with downstream travel from site 3 (km 14) to site 9 (km 56) or to site 12 (km 77) (Figure 3.4).

After peaking at site 9 or site 12, zooplankton biomass usually dropped, often with very low levels recorded at site 14 (km 91).

Seasonally, no trend in zooplankton biomass was evident in 1994. May and June of 1995 tended to have higher levels of zooplankton biomass than the other months of either 1994 or 1995 (Figure 3.4).

3.4.3 Longitudinal and Seasonal Trends in Nutrient Concentrations

The longitudinal pattern in total phosphorus concentration (TP) for the sampling months of 1994 and 1995 is shown in Figure 3.5. In contrast to the second order pattern exhibited by Chl *a* (Figure 3.2), the longitudinal trend in TP for most months was a simple linear increase in TP with downstream travel (Figure 3.5). The exceptions to this pattern occurred in May 1994 (no significant trend) and May 1995 (second order polynomial relationship). ANCOVA indicated that the slopes of the first order, simple linear regression equations between TP and km were not significantly different ($p > 0.05$, $F_{8, 108} = 2.3$). A regression of TP with km for the combined data of all first order relationships had a slope of 0.26. The elevations of the monthly TP-km regressions, however, did differ significantly ($p < 0.05$, $F_{8, 116} = 34.0$). In 1994, the elevations for June and July were higher than those for August and September which, in turn, were higher than the elevation for October. In 1995 the elevations for the TP-km regressions of June, July and August were higher than the elevation for September (Figure 3.5).

In comparison to TP, longitudinal and seasonal patterns in soluble reactive phosphorus concentration (SRP) were less evident (Figure 3.6, note that SRP values for

May 1995 were not available). The most notable feature was the high concentration of SRP measured at sites 13 (km 84), 14 (km 91) and 15 (km 98) in most months.

As with SRP, identifiable longitudinal or seasonal patterns in total nitrogen concentration (TN) were difficult to establish (Figure 3.7). Gradual increases in TN were sometimes observed as were high concentrations at sites 13 (km 84), 14 (km 91), and 15 (km 98) for several months.

3.4.4 Hydrological and Physical Variables

The discharge hydrographs for the Rideau River for 1994 and 1995 are shown in Figure 3.8. In both years peak discharge occurred during spring melt. Peak discharge occurred earlier in 1995 and overall, discharges were lower in 1995 compared with 1994. Two prominent storm events raised discharges in 1995, one in early June (Julian day 157), the other in early August (Julian day 220) (Figure 3.8).

Water temperatures for both 1994 and 1995 displayed the expected seasonal trend (Figure 3.8). In May and October of 1994 water temperatures were below 10°C. Due to the early spring in 1995, the water temperature in May was 13°C and the river reached a midsummer temperature above 25°C.

The euphotic depth to mixing depth ratio for all sites and all dates in the Rideau was usually greater than 0.6 ($Z_{eu} : Z_m > 0.6$ for 153 out of 165 observations). Due to the shallow depths, often the entire water column was euphotic ($Z_{eu} : Z_m >= 1.0$). $Z_{eu} : Z_m$ was never below 0.4.

3.4.5 Determinants of Algal Biomass

Chl *a* concentration in the Rideau River for both 1994 and 1995 was best predicted using a simple linear regression equation including TP concentration as the only independent variable (for 1994, log Chl *a* = -0.72 + 1.1 log TP, $p = 0.001$, $R^2 = 0.53$; for 1995, log Chl *a* = -0.46 + 0.91 log TP, $p = 0.001$, $R^2 = 0.30$). Log Chl *a* was also significantly related to log TN in 1994 ($p = 0.001$, $R^2 = 0.13$) but not in 1995 ($p = 0.32$). In neither year was log Chl *a* significantly related to log SRP concentration (for 1994, $p = 0.12$; for 1995, $p = 0.06$).

ANCOVA indicated that the slopes and elevations for the 1994 and 1995 TP-Chl *a* regressions were not significantly different (for slopes, $p > 0.05$, $F_{1, 161} = 0.94$; for elevations, $p > 0.05$, $F_{1, 162} = 0.44$). Therefore, we derived a TP-Chl *a* relationship for the pooled 1994 and 1995 data as shown in Figure 3.9 (log Chl *a* = -0.62 + 1.02 log TP, $p = 0.001$, $R^2 = 0.43$). We did not derive a multiple regression equation predicting Chl *a* from all the nutrient variables due to high multicollinearity between TP and TN ($p = 0.001$, $R = 0.72$, pooled data), TP and SRP ($p = 0.001$, $R = 0.54$, pooled data), and SRP and TN ($p = 0.001$, $R = 0.56$, pooled data).

Chl *a* was not significantly related to temperature (for 1994, $p = 0.57$; for 1995, $p = 0.25$) and mean Chl *a* for each month was not related to discharge for each month (for 1994, $p = 0.10$; for 1995, $p = 0.89$).

3.4.6 Determinants of Zooplankton Biomass

In both 1994 and 1995 zooplankton biomass in the Rideau was best predicted using a simple linear regression equation including Chl *a* as the independent variable (for 1994, log zooplankton biomass = 0.61 + 1.06 log Chl *a*, $p = 0.001$, $R^2 = 0.29$; for 1995, log zooplankton biomass = 0.96 + 0.88 log Chl *a*, $p = 0.001$, $R^2 = 0.13$). ANCOVA indicated that 1994 data could be pooled with 1995 data (for slopes, $p > 0.05$, $F_{1,72} = 0.16$; for elevations, $p > 0.05$, $F_{1,73} = 3.17$). The pooled relationship is shown in Figure 3.10 (log zooplankton biomass = 0.78 + 0.97 log Chl *a*, $p = 0.001$, $R^2 = 0.20$). Zooplankton biomass was not significantly related to TP in either year (for 1994, $p = 0.37$; for 1995, $p = 0.58$). Zooplankton biomass was also not significantly related to temperature (for 1994, $p = 0.95$; for 1995, $p = 0.52$) and mean monthly zooplankton biomass was not significantly related to discharge for each month (for 1994, $p = 0.15$; for 1995, $p = 0.67$).

3.5 Discussion

A distinct longitudinal pattern in Chl *a* concentration within the Rideau River was observed for most months of 1994 and 1995. The initial decrease in Chl *a* as water flowed from Lower Rideau Lake (site 1, km 0) into the Rideau River proper (site 2, km 7) has been previously observed (Basu and Pick 1995, Chapter 2 of the present thesis). Other researchers have observed similar decreases in algal biomass during such lentic to lotic transitions. Kohler (1993) suggests that algae that develop in lentic waters are ill-suited to lotic conditions and Uehlinger (1993) observed that phytoplankton flowing out

of a lake incurred physiological damage upon entering a river. Dense growths of submerged macrophytes at the outflow of Lower Rideau Lake may also contribute to losses of phytoplankton by intercepting and enhancing sedimentation of suspended algae (Talling and Rzoska 1967, Petticrew and Kalff 1992).

Following the initial decrease in algal biomass, Chl *a* concentrations were observed to increase with downstream travel from km 7 (site 2) until concentrations peaked at approximately km 60 (site 10). Basu and Pick (1995) outlined how the longitudinal development of Chl *a* within the Rideau was characterized by certain river reaches which act as planktonic "sources" (net increases in plankton) and others which act as planktonic "sinks" (net decreases in plankton) (*sensu* Pace *et al.* 1992, Basu and Pick 1995). Close examination of Figure 3.2 reveals certain reaches from km 7 to km 60 over which Chl *a* regularly increased (e.g. from site 3 (km 14) to site 4 (km 21)) and others over which Chl *a* regularly decreased (e.g. from site 5 (km 28) to site 6 (km 35) in most months). From km 7 to km 60 there appeared to be more reaches which acted as planktonic sources than reaches which acted as planktonic sinks. As a result, there was an overall pattern of increasing Chl *a* concentration as water flowed from km 7 to km 60. The increasing Chl *a* concentrations indicated the development of a true river potamoplankton, as algal concentrations in the river were not simply a reflection of concentrations in Lower Rideau Lake (Basu and Pick 1995).

Increases in algal biomass with downstream travel have been observed in many other river studies (Greenberg 1964, Capblancq and Descamps 1978, Holmes and Whitton 1981, Jones 1984, Descy *et al.* 1987, de Ruyter van Steveninck *et al.* 1990a, b)

and generally these increases have been associated with an increased time available for plankton to develop. However, nutrient concentrations in rivers also increase with downstream travel (Moss *et al.* 1984, Jones 1984, Jones and Barrington 1985, de Ruyter van Steveninck *et al.* 1992, Garnier *et al.* 1995). Total phosphorus in the Rideau continued to increase along the entire section of river sampled while maximum SRP and TN values were recorded at the most downstream sites. Downstream increases in nutrients may be attributed to continuous loading from agricultural and municipal sources as well as a high degree of association between the river and its watershed. Therefore, increasing algal biomass in the Rideau (and other rivers) with downstream travel is not surprising, given that the increasing time for development coincides with increasing nutrient concentrations.

In the Rideau, however, Chl *a* concentration only increased until km 60. From km 60 to km 98 Chl *a* concentrations decreased in most months. This decrease occurred despite a lengthening residence time and still increasing nutrient concentrations. At the furthest downstream sites, Chl *a* concentration was often less than 10 $\mu g\ L^{-1}$ even though TP concentration was greater than 30 $\mu g\ L^{-1}$. Downstream decreases in plankton biomass are less frequently reported than are downstream increases (de Ruyter van Steveninck *et al.* 1990a, b, 1992). The observed second order pattern of Chl *a* concentration in the Rideau combined with the observed increase in nutrient concentrations with downstream travel led us to examine what factors may have contributed to the decrease in algal biomass downstream of km 60.

Cole *et al.* (1992) concluded that in deep sections of a large, turbid river (Hudson River, USA), the depth of mixing was greater than the depth of the euphotic zone ($Z_{euphotic} : Z_{mixing} \sim 0.2$). This resulted in phytoplankton cells remaining below the 1% light level for a period of time long enough to make net algal growth impossible. Alpine and Cloern (1988) suggested that net negative growth (as reflected in a decrease in biomass) should be considered when $Z_{eu} : Z_m$ is less than 0.2. In the Rideau, $Z_{eu} : Z_m$ was usually greater than 0.6 and due to shallow depths (3 - 5 m) often the entire water column was euphotic. No large decrease in $Z_{eu} : Z_m$ occurred downstream of km 60, indicating that this type of light limitation of phytoplankton growth, leading to a decrease in algal biomass, was unlikely.

Various researchers have suggested that grazing by zooplankton may contribute to observed decreases in phytoplankton biomass in the downstream reaches of large rivers (Nusch 1978, de Ruyter van Steveninck *et al.* 1990a, b; Gosselain *et al.* 1994). Descy *et al.* (1987) using a simulation model concluded that zooplankton grazing could account for 46% of phytoplankton loss within the River Meuse (Belgium). Similarly, de Ruyter van Steveninck *et al.* (1990a, b) observed that in the downstream reaches of the River Rhine (Netherlands) the grazing activity of zooplankton contributed to an observed decrease in phytoplankton biomass. De Ruyter van Steveninck *et al.* (1990a, b, 1992) further suggested that plankton communities in rivers are " spatially phased". River phytoplankton with a higher intrinsic rate of growth will develop further upstream in a river, while zooplankton will lag behind phytoplankton and develop further downstream.

This may result in significant grazing occurring in the downstream reaches of large rivers once a high biomass of zooplankton had developed.

In the Rideau River, however, there was no evidence for phasing of the plankton communities. The pattern of zooplankton development resembled the pattern of Chl *a* development with no lags observed. Zooplankton biomass decreased (often dramatically) as water flowed from Lower Rideau Lake (km 0, site 1) to km 14 (site 3) within the river proper. This decrease may be associated with the lentic to lotic transition, as discussed with respect to phytoplankton (Talling and Rzoska 1967, Basu and Pick 1995) and observed by Kohler (1993) for the River Spree (Germany). As was the case for phytoplankton, a true river zooplankton community then developed in the Rideau. There was an overall increase in zooplankton biomass as water flowed downstream from km 14 (site 3) to km 56 (site 9) or km 77 (site 12). This increase in zooplankton biomass was subsequently followed by large downstream decreases in biomass. The increases and decreases in the biomass of phytoplankton and zooplankton appeared to coincide. In order for zooplankton grazing to significantly contribute to the decrease in Chl *a* concentration, a high biomass of large-bodied zooplankton at the downstream sites would be required (as was observed in the Rhine by de Ruyter van Steveninck *et al.* (1990a, b)). Instead, we observed decreases in zooplankton biomass downstream of km 60 and the zooplankton community was dominated by rotifers and smaller crustaceans (e.g. *Bosmina* sp.). Large zooplankton taxa (e.g. *Daphnia* sp.) were much less abundant (mean *Daphnia* sp. biomass at river sites 12 and 14 was 17.2 $\mu g\ L^{-1}$ dry mass).

To determine the potential impact of zooplankton grazing in the downstream reaches of the Rideau, theoretical filtration rates (volume filtered individual^{-1} d^{-1}) were multiplied by zooplankton densities (individuals L^{-1}). The densities of crustaceans and rotifers were calculated as the mean densities from site 12 and site 14 for both 1994 and 1995. For a mean density of 65 individuals L^{-1} and a mean filtration rate of 1 ml individual^{-1} d^{-1} (Mazumder *et al.* 1992), crustacean zooplankton could filter approximately 6.5% of the water column d^{-1}. Rotifers, with a mean density of 500 individuals L^{-1} and a mean filtration rate of 60 µL individual^{-1} d^{-1} (Mazumder *et al.* 1992), could filter approximately 3% of the water column d^{-1}. Combined, crustaceans and rotifers could therefore filter approximately 10% of the water column d^{-1}. This level of filtration was unlikely to have caused the substantial decrease in phytoplankton biomass downstream of km 60. In addition, low levels of zooplankton biomass were often recorded at the sites furthest downstream (< 50 µg L^{-1} dry mass). Thus, we were led to inquire about what factors may have contributed to the decreases in **both** algal biomass **and** zooplankton biomass downstream of km 60.

Colonization of the Rideau River by the exotic zebra mussel (*Dreissena polymorpha*) began in 1990. Since then densities of this benthic filter feeder have increased dramatically (Martel 1995). There is a distinct longitudinal pattern in the distribution of *D. polymorpha* within the Rideau (Figure 3.11) (Martel 1995). In both 1994 and 1995 relatively low densities were recorded at upstream sites, whereas densities at downstream sites (km 60 to km 98) were several orders of magnitude higher (Figure 3.11) (Martel 1995, A. Martel unpubl. data). This longitudinal pattern may be attributed

to an increased availability of hard, rocky substrates in the downstream reaches of the Rideau (Martel 1995).

Could the downstream colonization of the Rideau River by zebra mussels be the major factor which contributed to the downstream decreases in Chl *a* and zooplankton biomass? To address this possibility, the following conservative assumptions were made: i) the average density of zebra mussels in the Rideau from km 60 to km 98 was 1200 individuals m^{-2} (Figure 3.11) (Martel 1995), ii) the average length of individuals was 11 mm (Martel 1995), iii) the average filtration rate was 1 L $individual^{-1}$ day^{-1} (Kryger and Riisgard 1988, MacIsaac *et al.* 1992, Leach 1993), and iv) the coverage of total benthic area was 25%. Based on these assumptions the zebra mussel community could theoretically filter 14.5 m^3 s^{-1}. Therefore, a substantial percentage of total river discharge could be filtered by the zebra mussels from km 60 to km 98, from 30% to over 100% in both 1994 and 1995 (Table 3.2). On an aerial basis zebra mussels could filter 1.2 m^3 m^{-2} d^{-1}, which assuming a 3 m water column, is 40% d^{-1}. Such high filtration capacities have often been reported for *D. polymorpha* populations. MacIsaac *et al.* (1992) calculated that a 7 m water column in Lake Erie could be filtered between 3.5 and 18.8 times d^{-1}. Reeders *et al.* (1989) reported that the entire contents of two Dutch lakes could be filtered in approximately 15 d by *Dreissena* populations at densities of about 180 individuals m^{-2}. Our results indicate that zebra mussels have a filtration impact four times greater that of the zooplankton community (40% d^{-1} versus 10% d^{-1}). MacIsaac *et al.* (1992) similarly concluded that the filtering impact of *D. polymorpha* greatly exceeded that of herbivorous zooplankton in Lake Erie.

Suspended phytoplankton comprise a large component of the diet of *D. polymorpha* (Sprung and Rose 1988, Jorgenson 1990). As has been reported numerous times for lakes, Chl *a* concentration can be severely depleted in the presence of *D. polymorpha* beds (Reeders and Bij de Vaate 1990, MacIsaac *et al.* 1992, Bunt *et al.* 1993, Leach 1993). *D. polymorpha* can decrease zooplankton biomass through competition with zooplankton for suspended algal food resources and results from Ten Winkel and Davids (1982), Sprung and Rose (1988), MacIsaac *et al.* (1991) and Bunt *et al.* (1993) suggest that zebra mussels can also be direct predators on rotifers and small crustaceans.

Mackie (1991) hypothesized that reductions in phytoplankton and zooplankton biomass should occur following zebra mussel colonization. Bunt *et al.* (1993) suggested that the filtering impacts of zebra mussels should be maximized in shallow, well-mixed water columns due to increased contact between the benthic filter feeders and suspended food particles. In the downstream sections of the Rideau River, warm, shallow, well-mixed waters with rocky substrates appear favorable habitat for zebra mussels (Martel 1995). Given that densities of *D. polymorpha* increased in 1995 (densities from km 60 to km 98 were often over 50 000 individuals m^{-2} in 1995, A. Martel unpubl. data), and that zebra mussels could filter a large proportion of river discharge, it seems likely that zebra mussel filtration had significant impacts on planktonic development downstream of km 60 in both 1994 and 1995. We believe these impacts were manifested in decreases in both Chl *a* concentration and zooplankton biomass.

In the Seneca River (New York), Effler *et al.* (1996) observed that Chl *a* concentration decreased from a mean of 47 to 3.4 $\mu g\ L^{-1}$ while dissolved nutrient

concentrations increased (SRP from 1.8 to 40.3 μg L^{-1} and NH_3 from 31 to 160 μg L^{-1}) following zebra mussel infestation. The increase in dissolved nutrient concentrations was attributed to zebra mussel excretions (which are rich in ammonia and phosphorus), as well as to a decreased demand for dissolved nutrients due to reduced phytoplankton concentrations (Effler *et al.* 1996). Effler *et al.* (1996) concluded that the infestation of the Seneca by zebra mussels converted the river from "a turbid, phytoplankton-rich, (dissolved) nutrient depleted system, to a river with high clarity, low phytoplankton concentrations and enriched in dissolved nutrients".

Observations from the Rideau River exemplify a situation similar to the Seneca. Upstream from the area of infestation, the Rideau is a phytoplankton and zooplankton-rich system, whereas in downstream reaches plankton concentrations are greatly reduced. Furthermore, large increases in SRP and TN concentrations were observed in the downstream reaches of the Rideau (Fig. 3.6, Fig. 3.7). This may reflect the conversion of particulate forms of nutrients to dissolved forms due to zebra mussel feeding and excretion, combined with a lowered demand for dissolved nutrients due to decreased phytoplankton density.

In May and October 1994, a decrease in Chl *a* concentration downstream of km 60 was not observed (Figure 3.2). In these months water temperatures were less than 10°C. The effect of temperature on zebra mussel filtration rate remains unclear. Reeders and Bij de Vaate (1990) reported that filtration activity of *D. polymorpha* was temperature indifferent between 5 and 20°C. However, a positive linear relationship between bivalve filtration rate and temperature has also been demonstrated between

approximately 8 and 25°C (Jorgenson 1990, Fisher *et al.* 1993). This allows for the possibility that in May and October 1994 (due to cold water temperatures) filtration rates of the resident *D. polymorpha* community were not high enough to cause a decrease in Chl *a* and as a result, Chl *a* concentrations continued to increase downstream.

Previous work on the Rideau and other rivers has demonstrated that algal biomass and abundance can be predicted from TP concentration (Soballe and Kimmel 1987, Moss *et al.* 1989, Basu and Pick 1995, Van Nieuwenhuyse and Jones 1996). Though benthic grazing may have created conditions of low Chl *a* despite high TP in the downstream reaches of the Rideau, overall, Chl *a* was best predicted by TP concentration in 1994 and 1995 (as was the case in 1993 (Basu and Pick 1995)). The seasonal increase in TP concentration in the Rideau was paralleled by a seasonal increase in Chl *a*. TP tended to be higher in the summer months (June, July, August) possibly due to low dilution (i.e. low discharges) and internal loading. In downstream sections of the Rideau, bottom waters are known to become anoxic during periods of the summer (Stuart Dean, Regional Municipality of Ottawa-Carleton, personal communication). Chlorophyll *a* concentrations tended to be higher in summer possibly due to high nutrient concentrations (as well as warm temperatures and favorable light conditions). The low coefficient of determination for the TP-Chl *a* relationship ($R^2 = 0.43$), however, indicates that additional factors (such as benthic filtration) contribute to the regulation of algal biomass in the Rideau River.

We did not observe a significant negative relationship between Chl *a* and river discharge as has been reported in other studies (summarized by Reynolds 1988). As discussed by Basu and Pick (1995) the absence of a relationship between Chl *a*

concentration and discharge may be due to a limited range of discharges over which sampling was conducted. We sampled when the Rideau was open for navigation during the relatively low discharge period from May until October. Bothar and Kiss (1990) concluded that from May until October, discharge conditions were always favorable for potamoplankton development in the River Danube (Hungary). The same conclusion seems applicable to the Rideau.

Despite the possible influence of zebra mussel filtration on zooplankton biomass in the Rideau, zooplankton biomass was best related to Chl *a* concentration. No significant relationship between zooplankton biomass and discharge was observed. The positive relationship between Chl *a* and zooplankton biomass is indicative of a resource effect of phytoplankton biomass on zooplankton biomass. A negative relationship between phytoplankton and zooplankton biomass was not observed. The biomass of zooplankton in rivers tends to be lower than in lakes and river zooplankton communities tend to be dominated by smaller taxa (e.g. rotifers, nauplii, and bosminids) (Sheil *et al.* 1982, Ferrari *et al.* 1989, Bothar and Kiss 1990, Pace *et al.* 1992, Thorp *et al.* 1994, this study). Larger cladocerans (e.g. *Daphnia* sp.) and calanoid copepods appear much less abundant within riverine zooplankton communities (Basu and Pick 1996). McQueen *et al.* (1986) concluded that large-bodied zooplankton taxa (especially cladocerans) are required for zooplankton to decrease phytoplankton biomass. Considering the low overall biomass of zooplankton and the dominance of small taxa, significant grazing effects of zooplankton on phytoplankton may not occur with regularity in rivers. Very large rivers,

such as the Rhine or Meuse may be the exception (Descy *et al.* 1987, de Ruyter van Steveninck 1990a, b, 1992, Gosselain *et al.* 1994).

As discussed with respect to the TP-Chl *a* relationship, the low coefficient of determination for the Chl *a*-zooplankton relationship ($R^2 = 0.20$) indicates that additional factors regulate zooplankton biomass in the Rideau. One of these now appears to be benthic filtration by zebra mussels.

3.6 Summary

Following an initial decrease in phytoplankton and zooplankton biomass as water flowed from Lower Rideau Lake into the Rideau River proper, there was a downstream increase in the biomass of these two communities. Peak biomass for both phytoplankton and zooplankton occurred at approximately km 60. In the downstream reaches (from km 60 to km 98) the biomass of both phytoplankton and zooplankton significantly declined. Light conditions and nutrient levels appeared favorable for continued planktonic development in these downstream reaches. Therefore, these downstream declines may be attributed to high levels of grazing activity by the exotic zebra mussel (*D. polymorpha*). There was no evidence of longitudinal phasing of phytoplankton and zooplankton communities in the Rideau River. Chlorophyll *a* concentration was best predicted by total phosphorus concentration and zooplankton biomass was best predicted by Chl *a* concentration. A negative relationship between zooplankton and phytoplankton biomass was not observed.

Table 3.1. Pairwise ANCOVA's comparing second order regressions between Chl *a* and river km. F-test for shapes, numerator degrees of freedom = 2, denominator degrees of freedom = 22: F-test for elevations, numerator degrees of freedom = 1, denominator degrees of freedom = 24. Bonferroni corrected critical F value(s) = 9.61 for shapes; F_{crit} = 12.0 for elevations.

Comparison	F (shapes)	F (elevations)
June 1994 with July 1994	1.95	0.56
June 1994 with Aug. 1994	4.26	24.20*
June 1994 with Sept. 1994	9.25	56.68*
July 1994 with Aug. 1994	1.32	3.50
July 1994 with Sept. 1994	2.68	19.04*
Aug. 1994 with Sept. 1994	0.63	10.69
May 1995 with June 1995	1.04	3.05
May 1995 with Aug. 1995	4.16	0.21
May 1995 with Sept. 1995	1.20	16.04*
June 1995 with Aug. 1995	2.18	3 .17
June 1995 with Sept. 1995	0.20	6.26
Aug. 1995 with Sept. 1995	0.74	15.23*
June 1994 with June 1995	11.11*	do not test
Aug. 1994 with Aug. 1995	1.93	4.80
Sept. 1994 with Sept. 1995	1.75	0.34

* denotes significance following Bonferroni correction.

Table 3.2. Proportion of Rideau River discharge filtered from km 60 to km 98 given a zebra mussel community filtration capacity of 14.5 $m^3 s^{-1}$ (see assumptions in text). Discharges are means for the period 7 d prior to and including the sampling date (see methods).

Month	River Discharge $m^3 s^{-1}$	Proportion Filtered %
May 1994	47.0	30
June 1994	46.3	31
July 1994	21.3	68
Aug. 1994	17.0	85
Sept. 1994	9.4	100+
Oct. 1994	19.2	76
May 1995	16.1	90
June 1995	30.6	47
July 1995	4.0	100+
Aug. 1995	30.4	48
Sept. 1995	2.6	100+

Figure 3.1. Location of sampling sites (numbered 1 to 15) in the Rideau River, Ontario. Distances in parentheses refer to the number of kilometers downstream from site 1 in Lower Rideau Lake (km 0).

Figure 3.1

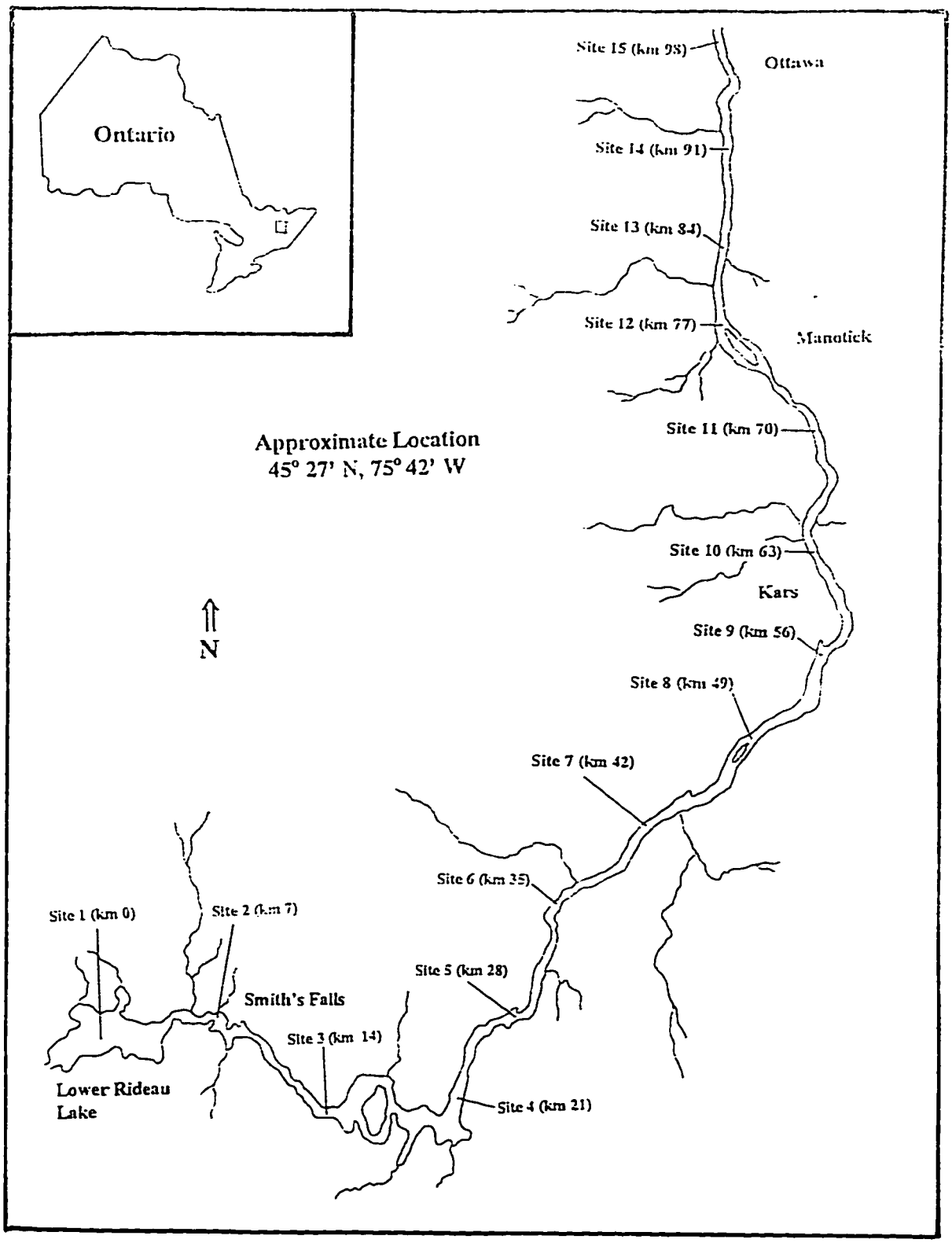

Ontario
Site 15 (km 98)
Ottawa
Site 14 (km 91)
Site 13 (km 84)
Site 12 (km 77)
Manotick
Site 11 (km 70)
Approximate Location
45° 27' N, 75° 42' W
Site 10 (km 63)
Kars
N
Site 9 (km 56)
Site 8 (km 49)
Site 7 (km 42)
Site 6 (km 35)
Site 1 (km 0)
Site 2 (km 7)
Site 5 (km 28)
Smith's Falls
Site 3 (km 14)
Lower Rideau Lake
Site 4 (km 21)

Figure 3.2. Longitudinal pattern of Chl *a* concentration in the Rideau River for the sampling months of 1994 (A-F) and 1995 (G-K). Plotted are means for each site ± standard deviation. Significant first or second order regressions between Chl *a* and river km are indicated by solid lines with 95% confidence intervals (dotted lines). Site 1 (Lower Rideau Lake, km 0) was not included in regression analysis (see text) and is represented by an asterisk (*).

Figure 3.2

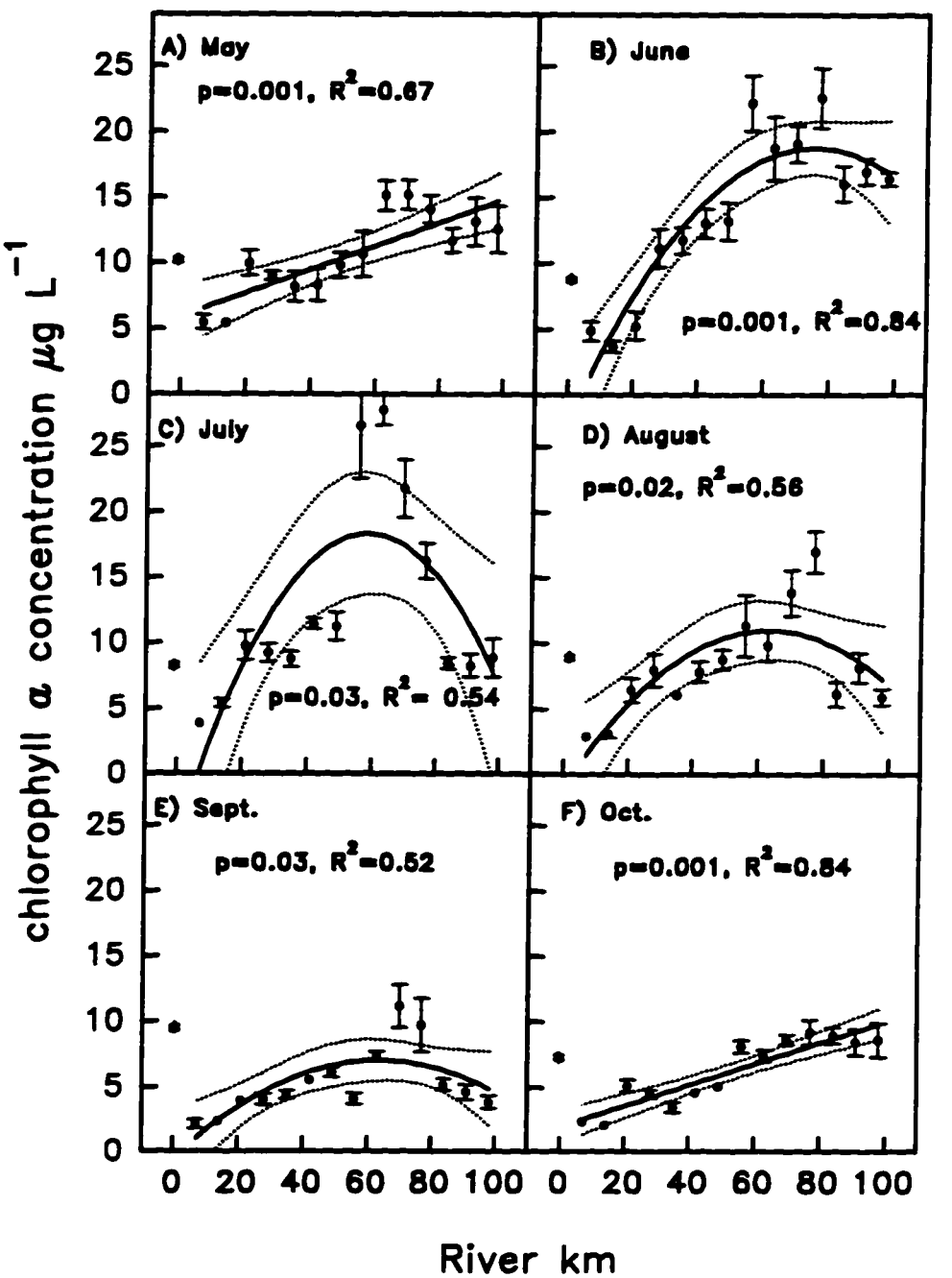

A) May
p=0.001, R²=0.67
B) June
p=0.001, R²=0.84
C) July
p=0.03, R²= 0.54
D) August
p=0.02, R²=0.56
E) Sept.
p=0.03, R²=0.52
F) Oct.
p=0.001, R²=0.84
chlorophyll a concentration μg L⁻¹
River km
0 20 40 60 80 100
0 5 10 15 20 25

Figure 3.2 cont.

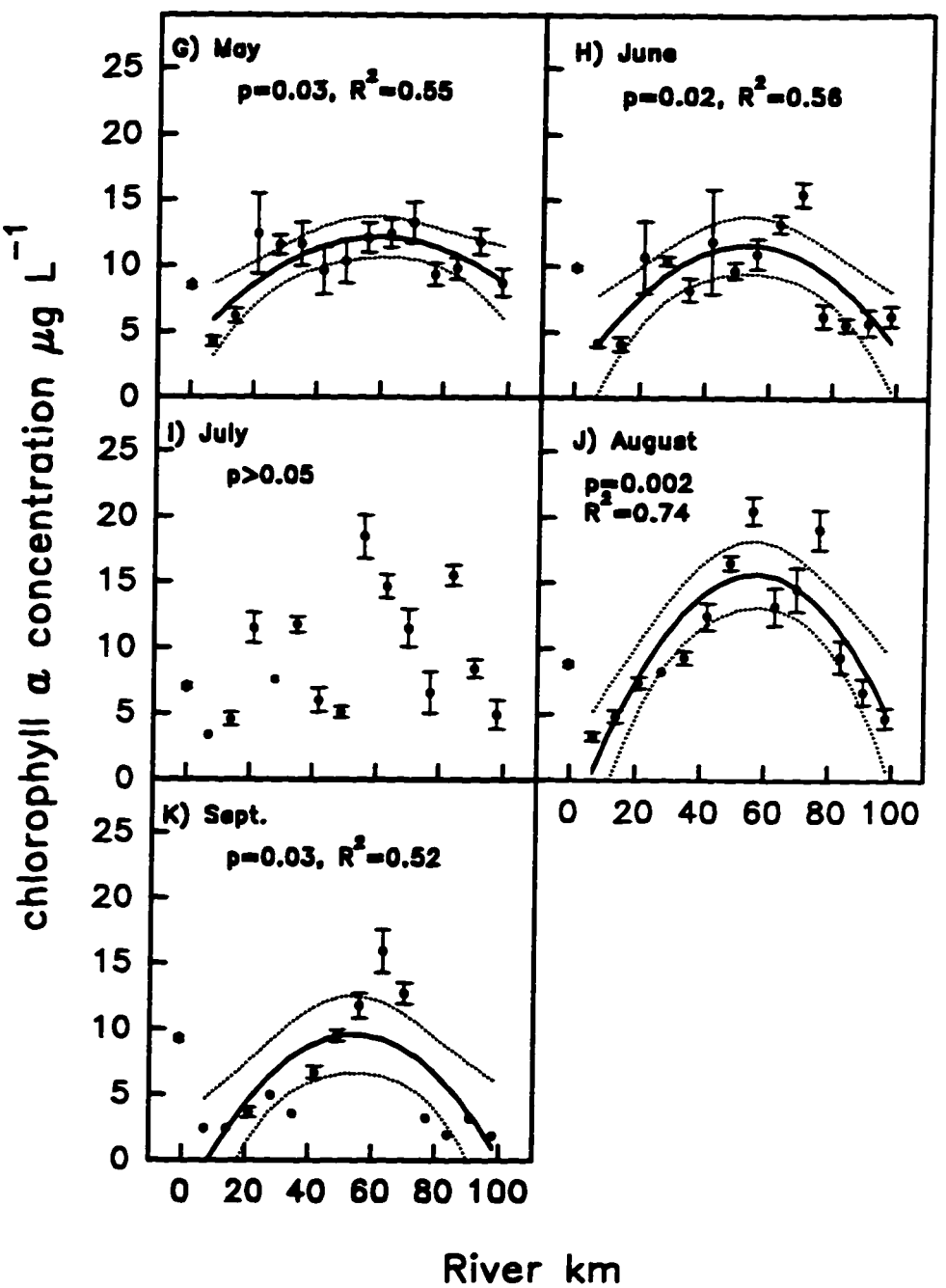


Figure 3.3. Overall second order relationship between Chl *a* and river km derived by pooling the data from all second order relationships indicated in Figure 3.2 (Chl *a* = -1.29 + 0.47 km - 0.004 km^2). Site 1 (Lower Rideau Lake, km 0) was not included in regression analysis and is represented by asterisks (*).

Figure 3.3

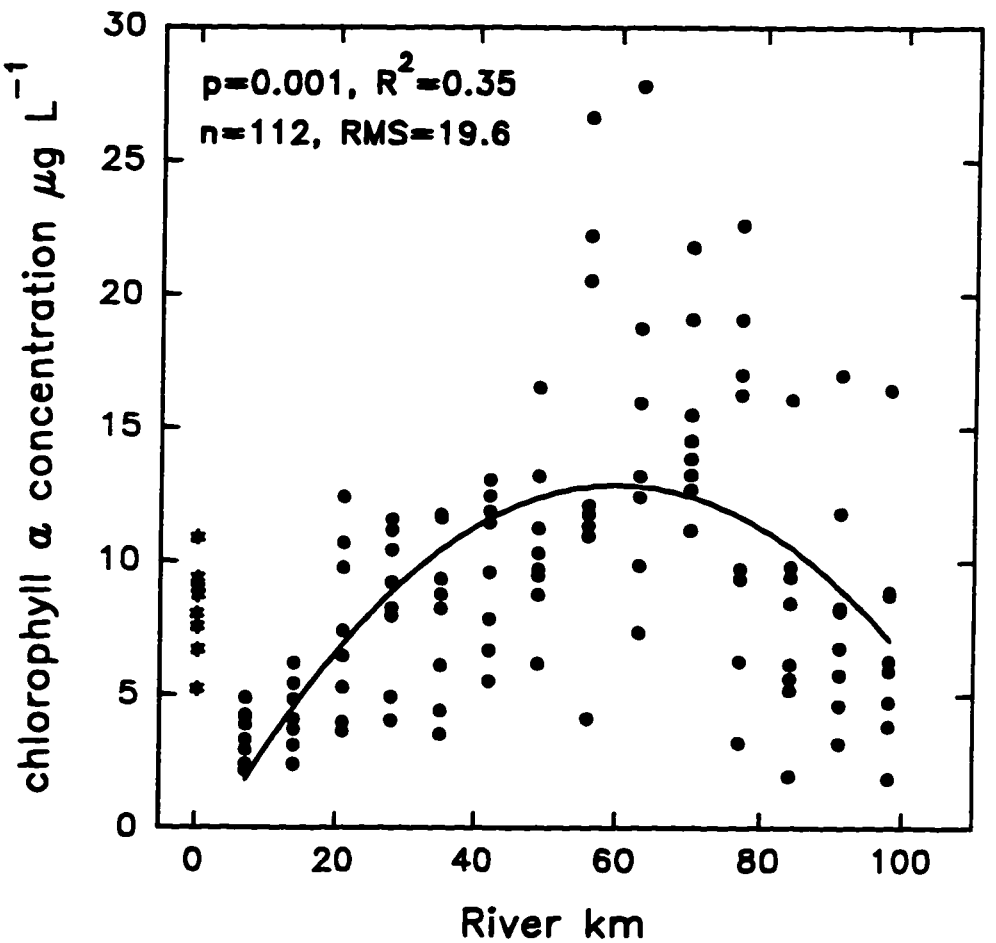

p=0.001, R^2=0.35
n=112, RMS=19.6
chlorophyll a concentration μg L^{-1}
River km
0
5
10
15
20
25
30
0
20
40
60
80
100

Figure 3.4. Longitudinal pattern of zooplankton biomass in the Rideau River for the sampling months of 1994 (A-C) and 1995 (D-F). Plotted are means ± standard deviation. Note the change in scale between panels (y-axis). (Data for site 14, October 1994 were not available.)

Figure 3.4

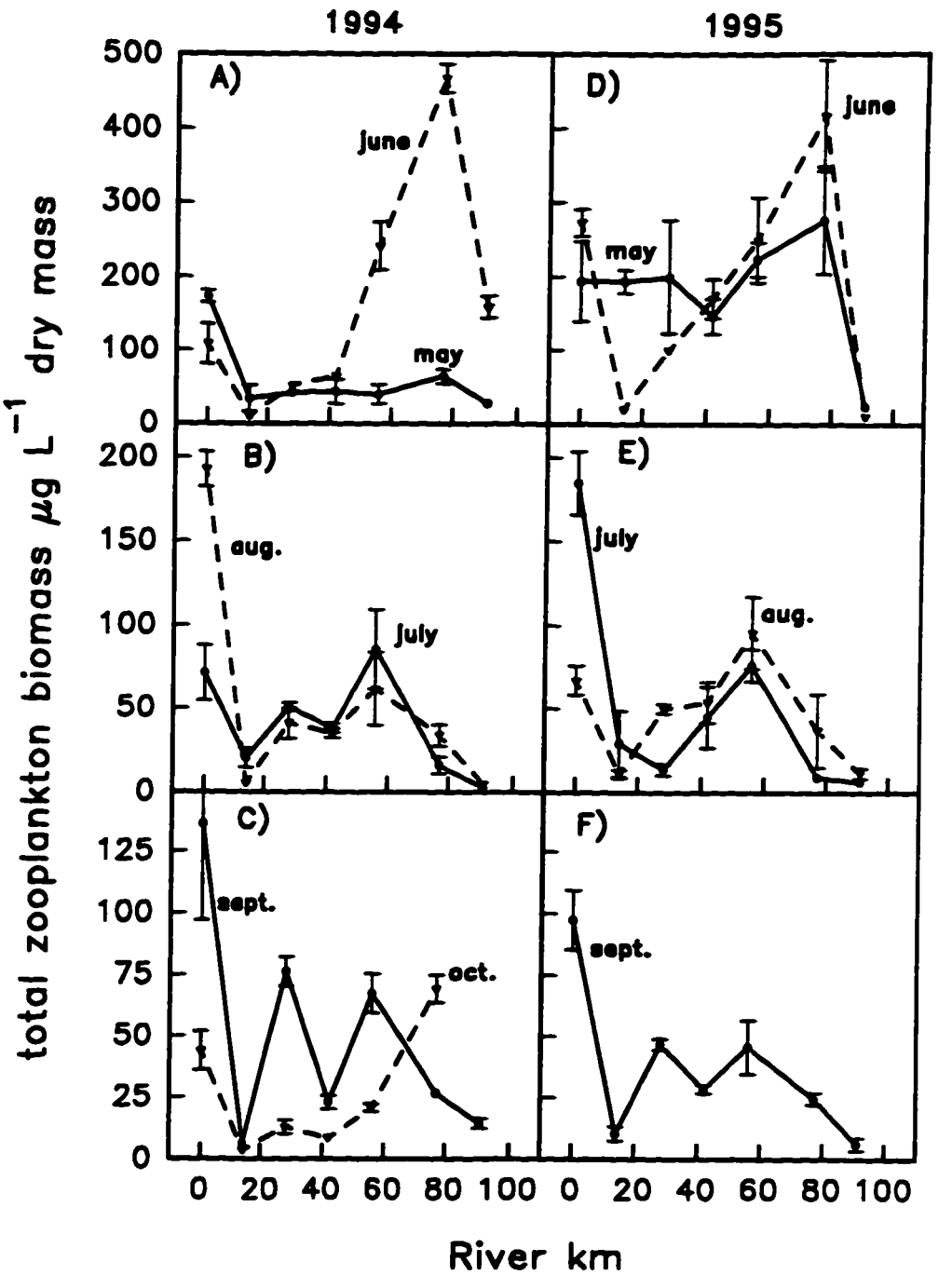

1994
1995
A)
B)
C)
D)
E)
F)
june
may
aug.
july
sept.
oct.
total zooplankton biomass µg L⁻¹ dry mass
River km
0
20
40
60
80
100
0
25
50
75
100
125
0
50
100
150
200
0
100
200
300
400
500

Figure 3.5. Longitudinal pattern of TP concentration in the Rideau River for the sampling months of 1994 (A-F) and 1995 (G-K). Plotted are means for each site ± standard deviation. Significant first or second order regressions between TP and river km are indicated by solid lines with 95% confidence intervals (dotted lines). Note the change in scale between panels (y-axis).

Figure 3.5

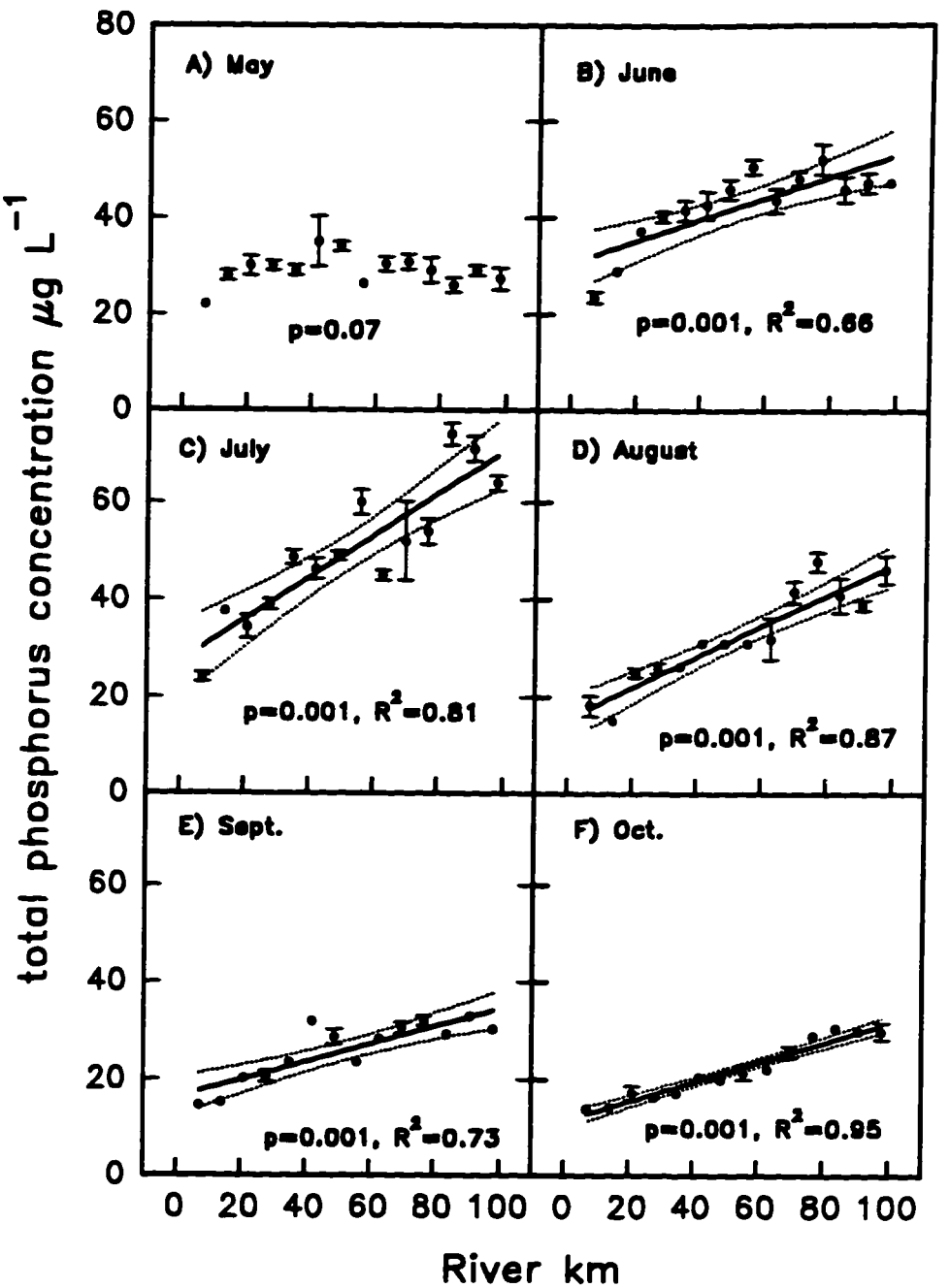

A) May
p=0.07
B) June
p=0.001, R²=0.66
C) July
p=0.001, R²=0.81
D) August
p=0.001, R²=0.87
E) Sept.
p=0.001, R²=0.73
F) Oct.
p=0.001, R²=0.95
total phosphorus concentration µg L⁻¹
River km
0
20
40
60
80
100

Figure 3.5 cont.

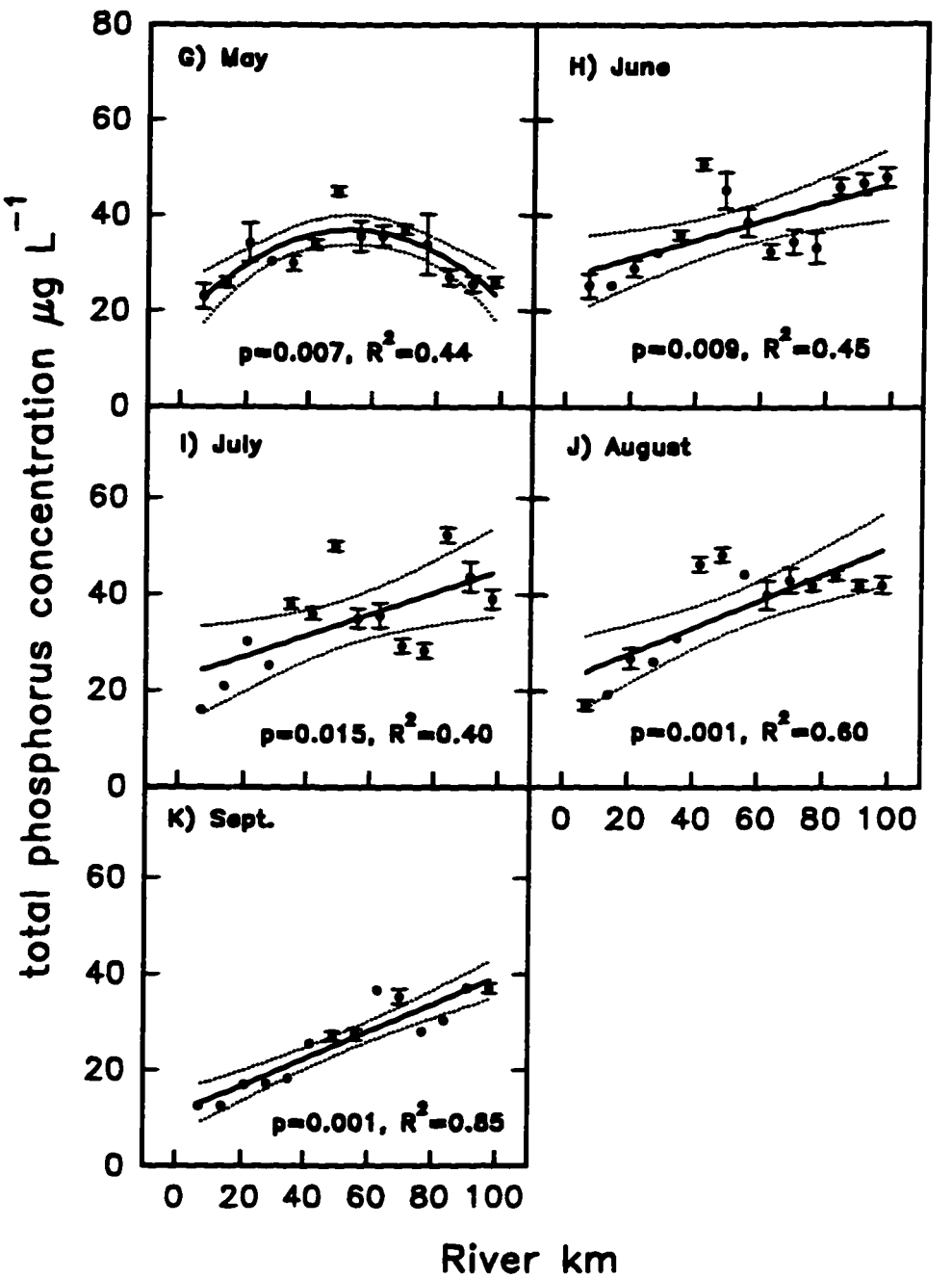


Figure 3.6. Longitudinal pattern of SRP concentration in the Rideau River for the sampling months of 1994 (A and B) and 1995 (C and D). Plotted are means ± standard deviation. (Data for May 1995 were not available).

Figure 3.6

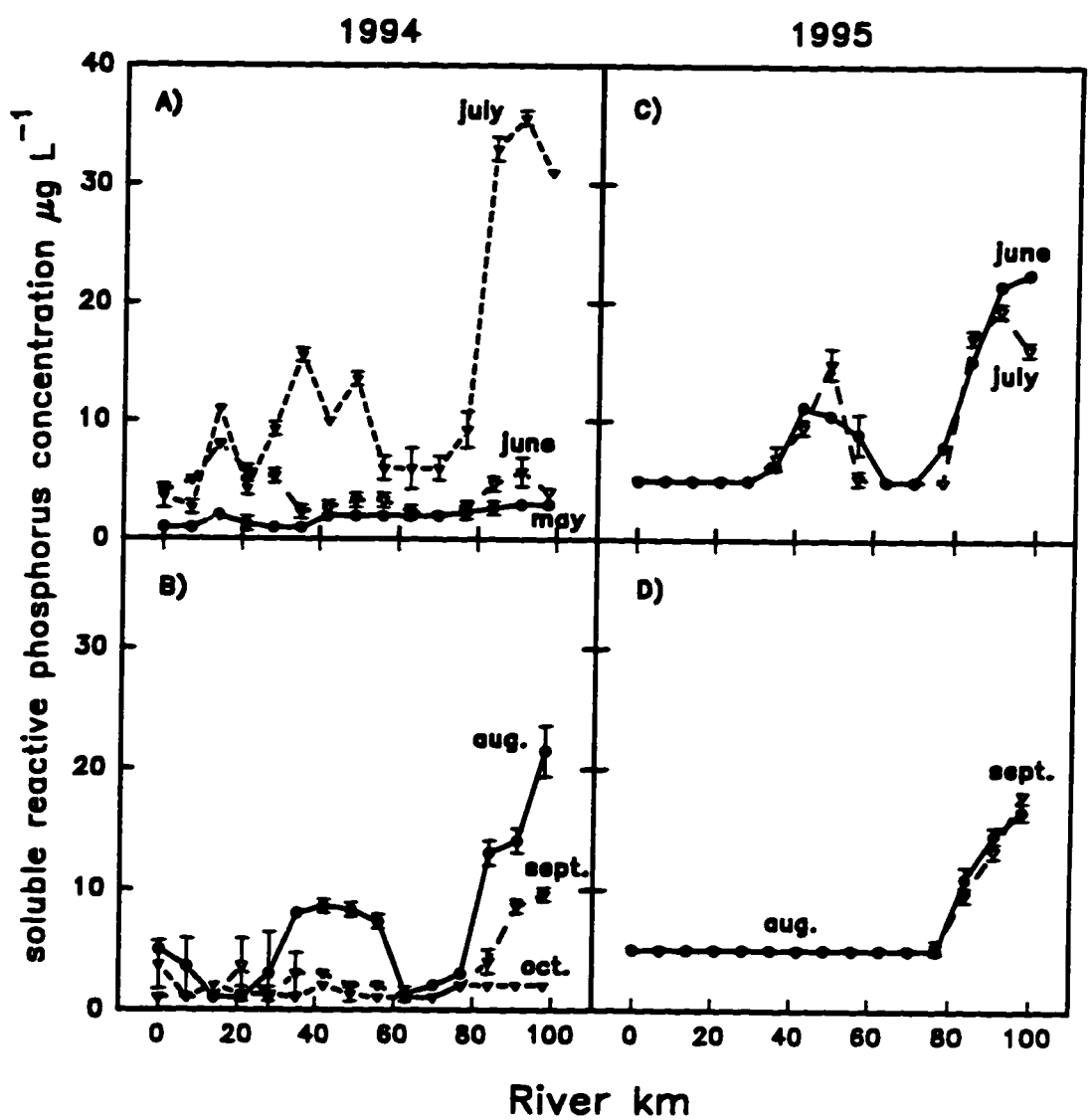

1994
1995
A)
B)
C)
D)
July
June
may
aug.
sept.
oct.
soluble reactive phosphorus concentration µg L⁻¹
River km
0
10
20
30
40
0
20
40
60
80
100

Figure 3.7. Longitudinal pattern of TN concentration in the Rideau River for the sampling months of 1994 (A and B) and 1995 (C and D). Plotted are means ± standard deviation. Note the change in scale between panels (y-axis).

Figure 3.7

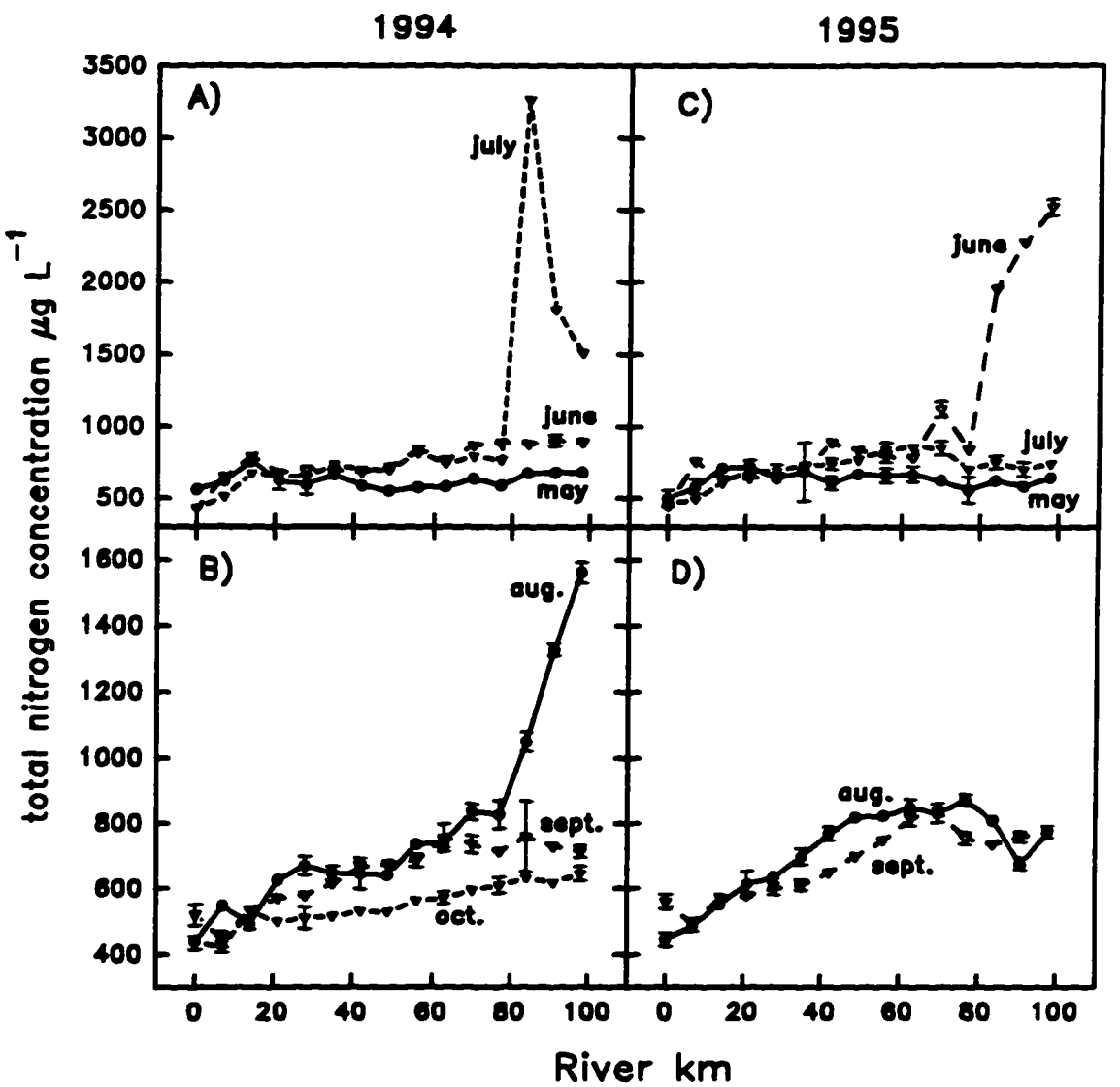

1994
1995
A)
B)
C)
D)
july
june
may
aug.
sept.
oct.
total nitrogen concentration μg L⁻¹
River km
3500
3000
2500
2000
1500
1000
500
1600
1400
1200
1000
800
600
400
0
20
40
60
80
100

Figure 3.8. Discharge hydrograph (solid line) and monthly temperature measurements (dashed line) for the Rideau River in 1994 (A) and 1995 (B).

Figure 3.8

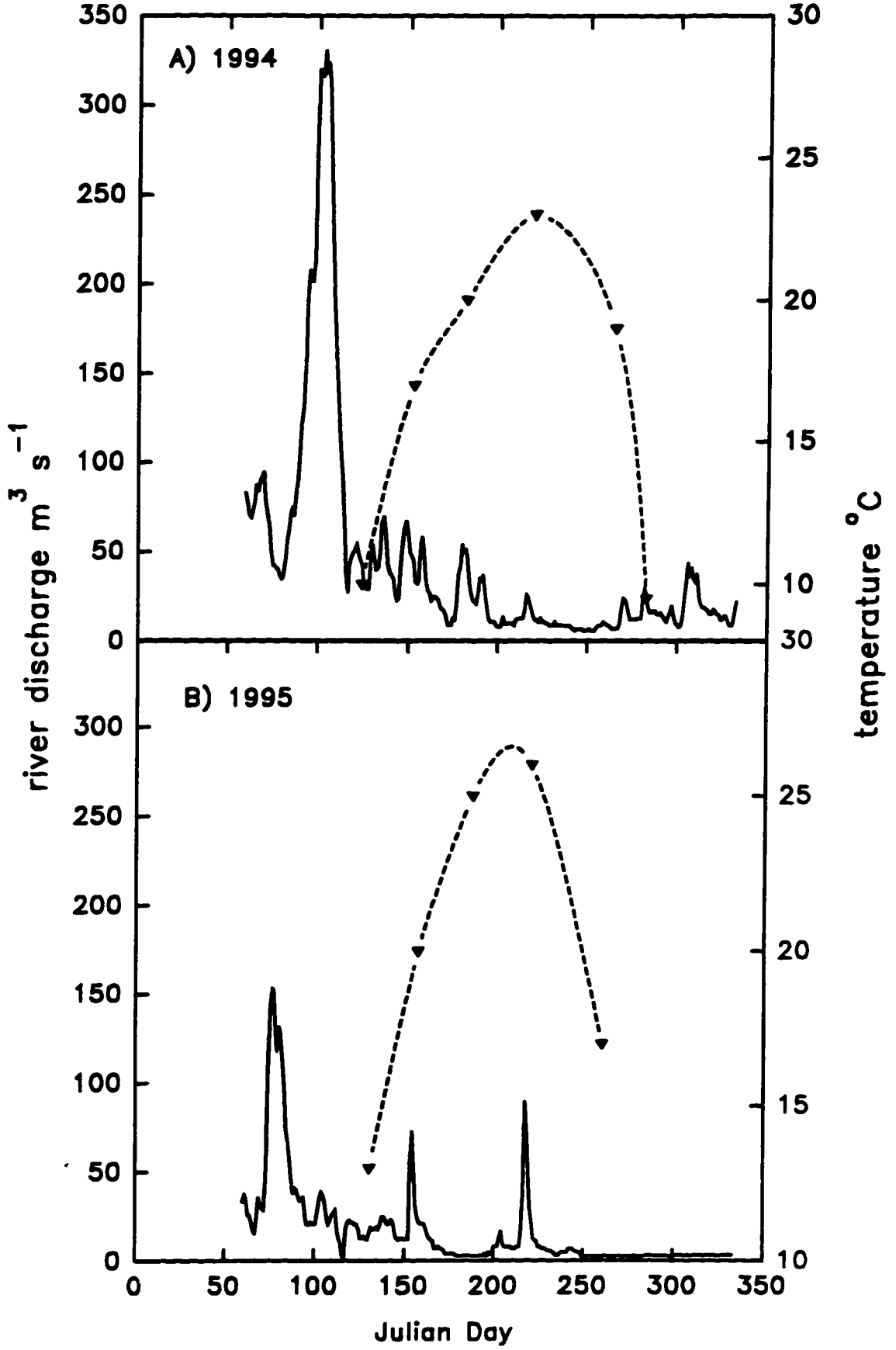

A) 1994
B) 1995
river discharge m3 s-1
temperature °C
Julian Day
0
50
100
150
200
250
300
350
10
15
20
25
30

Figure 3.9. Relationship between Chl *a* concentration and TP concentration for the Rideau River (combined 1994 and 1995 data) (log Chl *a* = -0.62 + 1.02 log TP). Dashed line indicates 95% confidence interval.

Figure 3.9

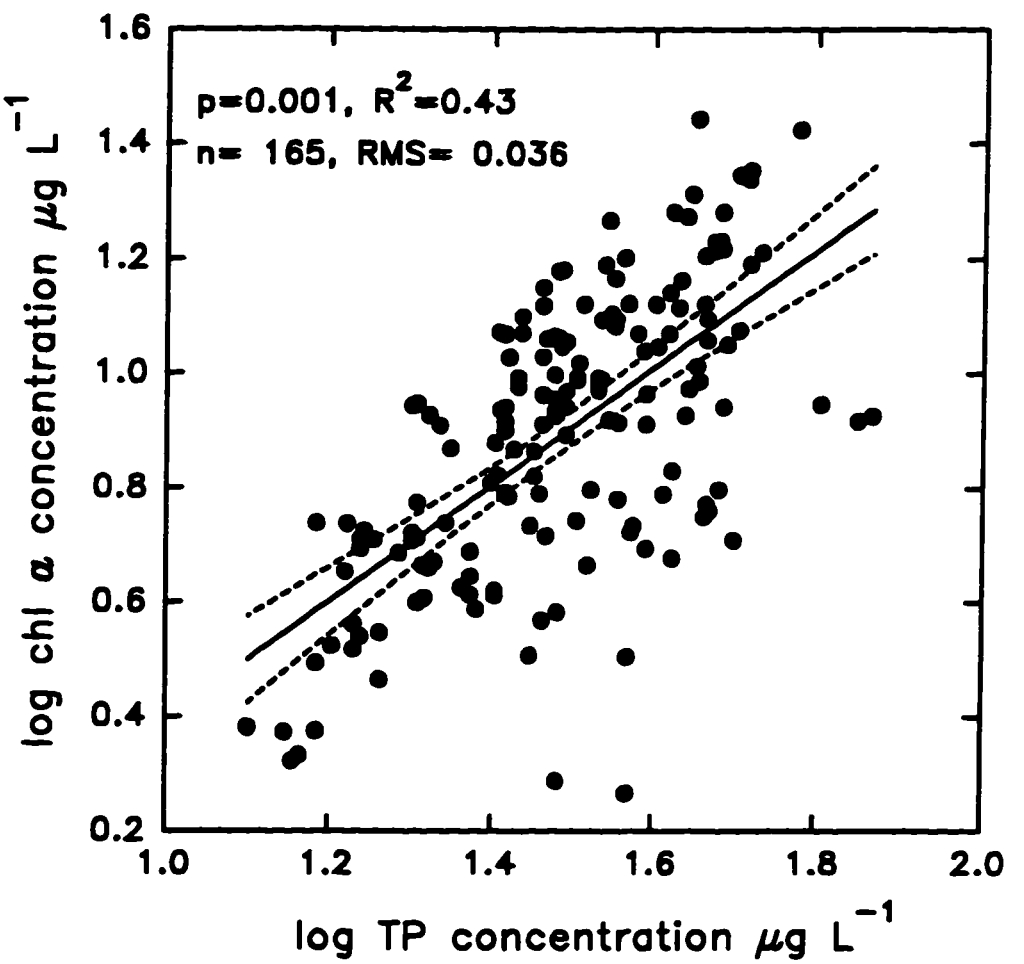

p=0.001, R^2=0.43
n= 165, RMS= 0.036
log chl a concentration μg L^{-1}
log TP concentration μg L^{-1}
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1.0
1.2
1.4
1.6
1.8
2.0

Figure 3.10. Relationship between zooplankton biomass and Chl *a* concentration for the Rideau River (combined 1994 and 1995 data) (log zooplankton biomass = 0.76 + 0.97 log Chl *a*). Dashed line indicates 95% confidence interval.

Figure 3.10

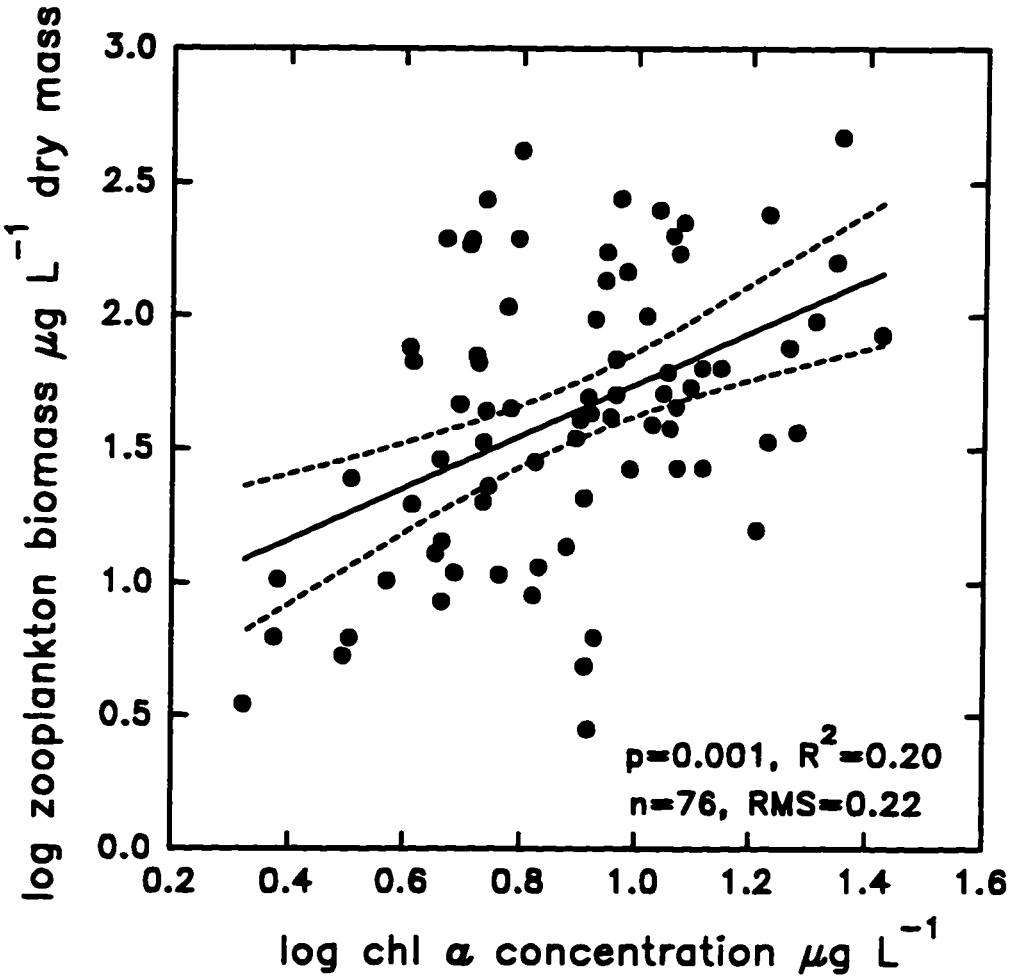
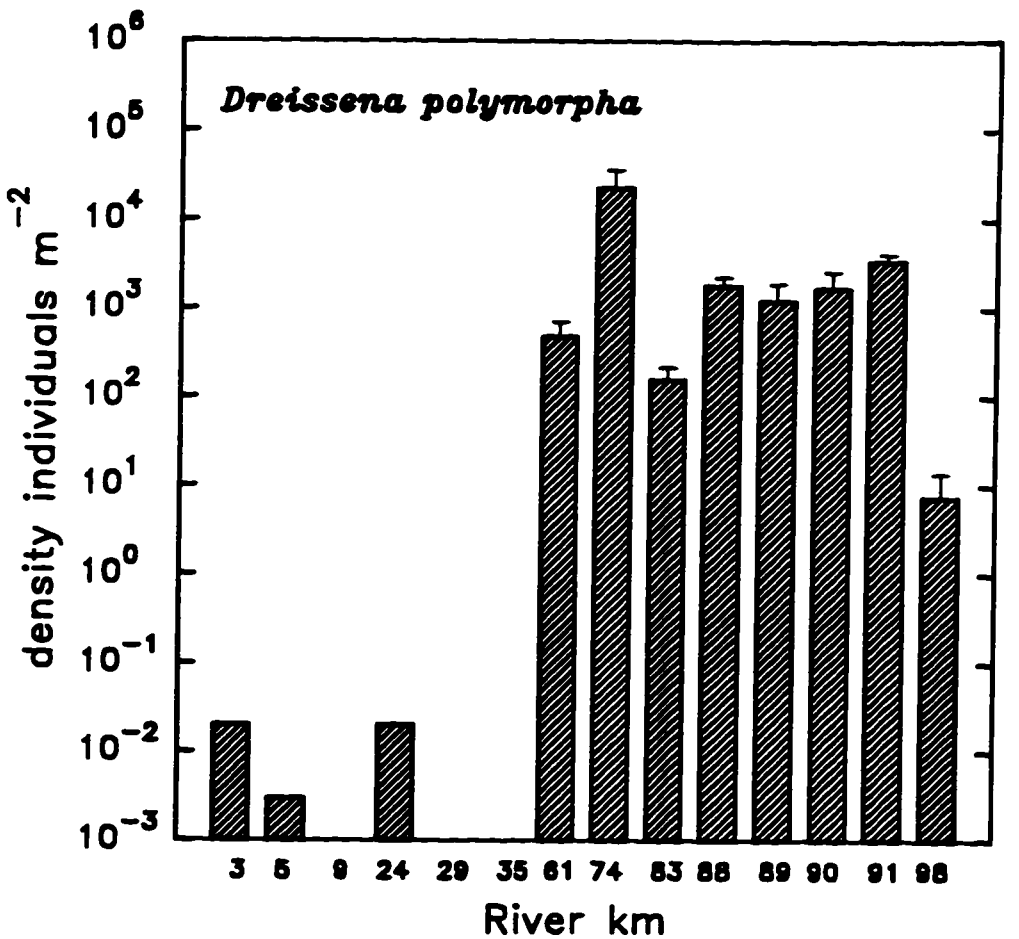

log zooplankton biomass μg L⁻¹ dry mass
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
log chl a concentration μg L⁻¹
p=0.001, R²=0.20
n=76, RMS=0.22

Figure 3.11. Longitudinal pattern of the density of *Dreissena polymorpha* in the Rideau River in 1994 (mean ± standard deviation). Data from Martel (1995) replotted. Note that x-axis is not to scale.

Figure 3.11


Dreissena polymorpha
density individuals m^{-2}
10^{6}
10^{5}
10^{4}
10^{3}
10^{2}
10^{1}
10^{0}
10^{-1}
10^{-2}
10^{-3}
3 5 9 24 29 35 61 74 83 88 89 90 91 98
River km

Chapter 4

Factors Regulating Phytoplankton and Zooplankton Biomass in Temperate Rivers

Modified from Basu, B.K. and F.R. Pick. 1996. Limnology and Oceanography. 41: 1572-1577. (with permission)

4.1 Abstract

By measuring chlorophyll *a* concentration (Chl *a*), zooplankton biomass, nutrient concentrations (total nitrogen (TN) and total phosphorus (TP)), water residence time, depth, and light attenuation coefficients within 31 rivers in Ontario and Quebec, Canada. we tested the following hypotheses: i) Chl *a* concentration is positively related to nutrient concentrations and water residence time, ii) zooplankton biomass is positively related to Chl *a* (and/or TP) concentration and water residence time, and iii) relationships between phytoplankton biomass and zooplankton biomass are weak due to overriding physical factors. In the rivers, Chl *a* ranged from 1.8 to 27.6 $\mu g\ L^{-1}$ and TP concentration ranged from 7.3 to 212.3 $\mu g\ L^{-1}$. Water residence time at the river sampling sites ranged from 3.3 to 19.4 d. There was a highly significant and positive relationship between Chl *a* and TP ($R^2 = 0.76$). There was no significant relationship between Chl *a* and water residence time. In contrast, crustacean biomass, rotifer biomass and total zooplankton biomass were significantly and positively related to water residence time (for total zooplankton biomass, $R^2 = 0.33$). After controlling for the effect of water residence time on zooplankton biomass, there was a weak positive relationship between phytoplankton biomass and zooplankton biomass. A negative relationship between zooplankton and phytoplankton biomass was not observed. Mean total zooplankton biomass in the rivers was low (11.26 $\mu g\ L^{-1}$ dry mass) and the zooplankton was dominated by rotifers and small crustaceans.

4.2 Introduction

Phytoplankton and zooplankton dynamics have been studied extensively in lentic freshwaters (lakes and reservoirs), yet comparatively little research has focused on lotic waters (rivers) (Reynolds 1988, Murakami *et al.* 1992). As a result, basic biological information concerning riverine plankton (potamoplankton) is lacking. The existence of truly planktonic organisms in large (greater than fifth order) rivers has been recognized for many decades (e.g. Zacharius 1898, Margalef 1960, Lack 1971, Jones 1984, Pace *et al.* 1992), yet there is no general consensus as to what factors regulate both phytoplankton and zooplankton biomass in large rivers. Furthermore, the relationships between phytoplankton and zooplankton in rivers have rarely been described.

Possible factors regulating river plankton abundance may be physical (light), chemical (nutrient concentrations), hydrological (discharge, water residence time), and biotic (predation, competition) (Reynolds 1988, Moss *et al.* 1989a). It is generally believed that hydrological and physical factors such as discharge or water residence time will be of greater importance to planktonic development in rivers than in comparison to lakes (Reynolds 1988, Cole *et al.* 1992, Pace *et al.* 1992, Reynolds 1994).

Soballe and Bachman (1984) working on the Des Moines River, U.S.A. and Sabater and Munoz (1990) working on the River Ebro, Spain have shown that river phytoplankton abundance is less dependent on nutrient concentrations than lentic phytoplankton abundance. Soballe and Kimmel (1987) using the NASQUAN (National Stream and Water Quality Accounting Network) data base concluded that algal

abundance in U.S. rivers could be predicted from total phosphorus concentrations though much variability in abundance remained unexplained (for TP-algal abundance relationship, $R^2 = 0.24$). Furthermore, algal abundance per unit phosphorus increased in the sequence: rivers < impoundments < natural lakes. This sequence paralleled differences in water residence times, indicating that rivers in general had lower algal abundances, possibly due to shorter water residence times (Soballe and Kimmel 1987). However, as most other studies have focused on phytoplankton dynamics within individual rivers (e.g. Lack 1971, Chessman 1985, Moss *et al.* 1989a, Jones 1984, Kohler 1993, Basu and Pick 1995), general knowledge of the most significant factors regulating algal biomass development across a wide range of rivers remains lacking.

In comparison to the algal component of the river plankton, there has been much less attention devoted to the zooplankton component of river plankton. Thorp *et al.* (1994) described the biological knowledge concerning riverine zooplankton as being "abysmal". From the few published studies it appears that zooplankton biomass and abundance in rivers is much lower than zooplankton biomass and abundance in lakes of comparable nutrient and chlorophyll concentrations (Bothar and Kiss 1990, Pace *et al.* 1992, Thorp *et al.* 1994). Pace *et al.* (1992) suggested that this difference, once again, may be due to the shorter residence times of rivers, but they did not have direct estimates of water residence times. The significance of water residence time should be more important for zooplankton in comparison to phytoplankton due to their longer generation time. Phytoplankton in rivers may be more controlled by nutrient concentrations than by hydrologic conditions (such as residence time) because of their higher growth rates, and

lower susceptibility to advective loss. Slower reproducing zooplankton may be more susceptible to advective loss in short residence systems.

Apart from these few speculations, however, the factors regulating zooplankton biomass in rivers are virtually unknown and no empirical relationship between zooplankton biomass and water residence time has been demonstrated. In addition, the relationships between zooplankton and phytoplankton in rivers and how these relationships compare with those observed in lakes remain unexplored. In lakes zooplankton biomass has either been positively related to phytoplankton biomass (or total phosphorus concentration)- a resource effect (e.g. McCauley and Kalff 1981, Hanson and Peters 1984, Canfield and Watkins 1984) or negatively related to phytoplankton biomass- a grazing effect (e.g. McQueen *et al.* 1986, Quiros 1990). It is not known whether resource or grazing interactions between phytoplankton and zooplankton are of importance in rivers.

The present study examines the biomass of phytoplankton and the biomass of zooplankton (both rotifers and crustaceans) across a range of mid-sized to large rivers in central and southern Ontario and western Quebec, Canada. Variables measured included chlorophyll *a* concentration (Chl *a*), crustacean zooplankton biomass, rotifer biomass, total phosphorus concentration (TP), total nitrogen concentration (TN), river discharge, watershed area, water residence time, light attenuation, and depth.

First, we considered the hypothesis that river phytoplankton biomass, as measured by chlorophyll *a* concentration, is positively related to nutrient (TP and TN) concentrations and to a measure of water residence time.

Secondly, we considered the hypothesis that zooplankton biomass would be positively related to Chl *a* and/or TP concentrations and positively related to a measure of water residence time. We expected a stronger relationship between biomass and residence time for zooplankton in comparison to phytoplankton- zooplankton being more susceptible to advective loss.

Finally, we examined the relationship between zooplankton biomass and phytoplankton biomass and compared this to what has been observed in lakes with respect to either resource or grazing interactions. If hydrological factors primarily regulate phytoplankton or zooplankton biomass in rivers, we expect interactions between phytoplankton and zooplankton to be weaker than in lakes.

4.3 Methods

4.3.1 Study Rivers

Thirty-one rivers in central, southern, and eastern Ontario and western Quebec, Canada, were sampled in July 1994 (Table 4.1). The rivers have a low gradient (< 1%) and drain areas located on either the Canadian Shield (granitic, igneous bedrock) or the Great Lakes, St. Lawrence Lowlands (sedimentary bedrock). The watersheds of the rivers range from completely forested to agricultural. All the rivers are fifth order or larger and have mean annual discharges greater than 8.0 $m^3 s^{-1}$ (Water Survey of Canada, Historical Streamflow Summary, Ontario and Quebec, 1990). The sampling sites on the rivers were located close to Water Survey of Canada gauging stations and not near any inflowing

tributaries or within 10 km of headwater lakes. Only two rivers (the Temagami and the Veuve) did not have operational gauging sites located along their courses during 1994.

4.3.2 Field Sampling

At each river site water samples were taken using a 4-m vertically integrated tube across a bank to bank transect. Samples were taken at the one-third, one-half (mid channel), and two-thirds distances across (Shaw 1987). Across each transect, five 2-L samples (one at the one-third and two-third distances, and three mid channel) were taken for algal Chl *a* concentration and three 300-ml samples (one at each distance across) were taken for measurements of total phosphorus (TP) and total nitrogen (TN) concentrations. Samples were stored in Nalgene plastic bottles and kept cool and dark during transport back to the laboratory.

Mesozooplankton (cladocerans and copepods) were sampled using an open diaphragm bilge pump (pumping rate of 10-L min^{-1}) (Pace 1984). Triplicate mesozooplankton samples were collected by pumping 30-L of water through a 64-μm Nitex mesh plankton net. Vertically integrated samples were collected by raising and lowering the pump intake between the surface and the maximum depth at a constant rate during sampling. Triplicate microzooplankton (rotifer) samples were collected by filtering 4-L of water (collected in a Nalgene bottle at 0.5-m depth) through a 35-μm Nitex mesh screen. All zooplankton samples were collected mid channel and preserved with a 4% chilled Formalin solution containing 40-g of sucrose L^{-1} (Haney and Hall 1975).

Light attenuation coefficients were calculated using irradiance measurements obtained with a LiCor 185B 4Π underwater photometer (LiCor, U.S.A.). Depth was measured using an LCR 400ID depth sounder (Marine Information Systems). All light and depth measurements were taken mid channel.

Discharge values for all the rivers except the Temagami and Veuve were obtained from Water Survey of Canada gauging sites. Discharge was calculated as the average of the daily discharges for the period seven days prior to and including the sampling date in a manner similar to that of Pace *et al.* (1992). For the Temagami and the Veuve rivers, discharge was inferred by averaging historical July data from 1960 to 1990 (Temagami River, mean discharge = 24.7 $m^3 s^{-1}$, standard deviation = 12.7) and 1973 to 1990 (Veuve River, mean discharge = 1.8 $m^3 s^{-1}$, standard deviation = 1.0) (Water Survey of Canada, Historical Streamflow Summary, Ontario, 1990). Watershed area for each river was obtained from the Water Survey of Canada which calculates upstream watershed area at each gauging site (Water Survey of Canada, Historical Streamflow Summary, Ontario, Quebec, 1990). Water residence time for each river was calculated using geomorphometric relationships developed by Leopold *et al.* (1964). Water residence time (an estimate of the time the water has been in the river system or in other words its "age" at the sampling site) was calculated using the formula:

$$R = 0.08\ A_d\ 0.6/\ Q\ 0.1 \qquad (1)$$

where R represents water residence time at the sampling site (d), A_d represents watershed area upstream of the sampling site (km^2), and Q represents river discharge ($m^3 s^{-1}$) (Soballe and Kimmel 1987).

4.3.3 Laboratory Analysis

Water samples were filtered through Whatman GF/F filters for Chl *a* analysis. Chl *a* was extracted using DMSO and acetone (Burnison 1980) and concentrations (uncorrected for phaeopigments) were calculated using the equations of Jeffrey and Humphrey (1975).

Chemical analysis was performed at the Regional Municipality of Ottawa-Carleton, Surface Water Quality Laboratories using a Skalar auto-analyzer. TP concentration was determined by acid digestion to orthophosphorus followed by reaction with ammonium molybdate and ascorbic acid. Nitrate and nitrite concentration was determined by reducing nitrate to nitrite, diazotizing the nitrite with sulfanilimide and coupling with ethylenediamine dihydrochloride. Total Kjeldahl nitrogen (TKN) concentration was determined by converting organic nitrogen to ammonium sulphate through acid digestion. Total nitrogen (TN) was the sum of nitrate, nitrite and TKN concentrations.

Zooplankton abundance was determined by enumerating either whole samples or counting at least 120 individuals in subsamples of each replicate. Cladocerans and copepods were counted under a dissecting microscope at 50X magnification and rotifers were counted using an inverted microscope at 80X magnification. Crustaceans and rotifers were identified to the genus level following Thorp and Covich (1991) and Stemberger (1979). Biomass estimates for crustaceans were determined using measured lengths and length-dry mass relationships of Bottrell *et al.* (1976) and Dumont *et al.*

(1975). Biovolume of rotifers was calculated using the volume formulae of Ruttner-Kolisko (1977). Biomass estimates for rotifers were calculated by converting biovolume to dry mass assuming a specific density of 1.0 (Dumont *et al.* 1975) and a dry mass to wet mass ratio of 0.1 (Bottrell *et al.* 1976). Total zooplankton biomass was the sum of crustacean dry mass and rotifer dry mass.

4.3.4 Statistical Analysis

Statistical analysis was performed using either SAS 6.04 (SAS Institute Inc. Cary N.C., 1987) or Sigmastat 1.01 (Jandel Scientific, San Rafael CA., 1992) statistical software. All tests performed were parametric (linear regression, multiple linear regression) and satisfied the assumptions of normality (Wilkes-Shapiro test) and homoscedasticity (plot of residuals against independent variable) following any required logarithmic transformations of the data. The significance value for all statistical tests was 5% ($p = 0.05$).

4.4 Results

There was a large range for all the variables measured in the 31 rivers. (Table 4.2) The mean Chl *a* concentration was 6.62 ± 1.17 μg L^{-1} (mean ± standard error) with the lowest Chl *a* measured in the Moira River (1.77 ± 0.34 μg L^{-1}) and the highest in the Thames River (27.62 ± 0.76 μg L^{-1}). Mean rotifer and crustacean zooplankton biomass values were low. Mean rotifer biomass was 2.27 ± 0.85 μg L^{-1} with the lowest biomass observed in the Salmon River (0.016 ± 0.003 μg L^{-1}) and the highest biomass of rotifers

observed in the South Nation River (22.6 ± 2.18 μg L^{-1}). The highest biomass of crustaceans was observed in the Trent River (196.0 ± 26.3 μg L^{-1}) while the lowest biomass was observed in the Salmon River (< 0.1 μg L^{-1}). Mean crustacean biomass was 8.99 ± 6.38 μg L^{-1} (Table 4.1, 4.2). Among the rotifers, *Synchaeta* sp., *Keratella* sp. and *Polyarthra* sp. were most common, occurring in more than 70% of the samples. Among the crustacean zooplankton, copepod nauplii, cyclopoid copepods and *Bosmina* sp. were most common, occurring in more than 60% of the samples (Table 4.3)

Mean TP and TN concentrations were high (mean TP = 32.0 ± 7.6 μg L^{-1}, mean TN = 1117.6 ± 219.5 μg L^{-1}). The highest TP concentration was observed in the Thames River (212.3 ± 7.8 μg L^{-1}), the lowest in the Temagami River (7.3 ± 0.3 μg L^{-1}). The highest TN concentration was observed in the Thames River (5318 ± 22.6 μg L^{-1}), the lowest in the Picanoc River (272.0 ± 4.9 μg L^{-1}). The TN:TP ratio for all the rivers sampled was never below 20, with an average ratio of 40.16 ± 4.15 (Table 4.2).

Among the hydrological variables measured (discharge, watershed area, depth and water residence time) there was also a large range. The largest river sampled was the Gatineau River (discharge = 250 m^3 s^{-1}, watershed area = 23,620 km^2). The river with the lowest discharge for the sampling period was the Ausable River (discharge = 0.9 m^3 s^{-1}) and the river with the smallest watershed area was the Maitland River (watershed area = 548 km^2) (Table 4.2). The river with the shortest water residence time was also the Maitland River (3.28 d) and the river with the longest water residence time was the Gatineau River (19.38 d). The average water residence time for the 31 rivers was 7.32 ± 0.70 d. The French River had the lowest attenuation coefficient (0.64 m^{-1}) while the

Ausable River had the highest attenuation coefficient (5.36 m^{-1}). For replicate samples of Chl *a*, TP and TN, the mean coefficient of variation (C.V.) for the 31 rivers was less than 10%. The mean C.V.'s for discharge and total zooplankton biomass were 11% and 33%, respectively.

Linear regression equations were derived in order to predict the biomasses of the dependent variables log Chl *a* and log zooplankton biomass (crustaceans and rotifers) from the independent variables log TP, log TN, attenuation coefficient, depth and water residence time. Discharge and watershed area were not entered as independent variables due to obvious multicollinearity with water residence time (water residence time was calculated from discharge and watershed area values). The "best" regression equations were defined as having the highest R^2, all regressors significant and limited multicollinearity ($R < 0.60$ between any pair of independent variables).

The linear regression equation best predicting log Chl *a* concentration included only the log TP term as an independent variable. There was a significant positive relationship between log Chl *a* and log TP ($p < 0.001$, $R^2 = 0.76$) (Figure 4.1). Log Chl *a* was also positively related to log TN ($p < 0.001$, $R^2 = 0.66$) and attenuation coefficient ($p < 0.001$, $R^2 = 0.64$); however, in comparison with log TP, these regressors accounted for less of the variation in Chl *a*. Both log TN and attenuation coefficient were highly positively correlated with log TP (log TP with log TN, $p < 0.001$, $R = 0.90$, log TP with attenuation coefficient, $p < 0.001$, $R = 0.86$). There was no significant relationship between log Chl *a* and log water residence time ($p = 0.47$, $R^2 = 0.02$) (Figure 4.2a). Furthermore, a plot of the residuals of the TP-Chl *a* relationship against water residence

time also indicated no significant effect of water residence time on Chl *a* concentration after controlling for the effect of TP concentration ($p = 0.87$, $R^2 = 0.007$) (Figure 4.2b).

In contrast, there was a significant positive relationship between log total zooplankton biomass and water residence time ($p < 0.001$, $R^2 = 0.33$) (Figure 4.3). The positive relationship between biomass and water residence time applied to both rotifers and crustaceans (for rotifers: $p = 0.002$, $R^2 = 0.30$, log rotifer biomass = -1.15 + 0.12 water residence time, for crustaceans: $p = 0.003$, $R^2 = 0.28$, log crustacean biomass = -1.66 + 0.15 water residence time).

With respect to possible relationships between zooplankton biomass and phytoplankton biomass, there were no significant relationships between log total zooplankton biomass and either log Chl *a* or log TP concentrations (for log Chl *a*, $p = 0.26$, $R^2 = 0.04$, for log TP, $p = 0.98$, $R^2 = 0.006$) (Figure 4.4). There were also no significant relationships between log rotifer biomass and log Chl *a* ($p = 0.494$, $R^2 = 0.016$), log rotifer biomass and log TP ($p = 0.650$, $R^2 = 0.007$), log crustacean biomass and Chl *a* ($p = 0.718$, $R^2 = 0.005$) or log crustacean biomass and log TP ($p = 0.656$, $R^2 = 0.007$). However, there was a significant (albeit weak) positive relationship between the residuals of the total zooplankton biomass- water residence time relationship and log Chl *a* concentration ($p = 0.038$, $R^2 = 0.14$) (Figure 4.5). Only after controlling for the effect of water residence time, did the resource effect of Chl *a* upon zooplankton biomass become more apparent.

Accordingly, the best equation predicting total zooplankton biomass included both water residence time and Chl *a* concentration as independent variables (log total

zooplankton biomass = -1.72 + 0.15 water residence time + 0.89 log Chl *a*, $p < 0.001$, $R^2 = 0.43$). The inclusion of the Chl *a* term increased the R^2 from 0.33 for the simple regression including only water residence time to 0.43 for the multiple regression.

Potential grazing effects of zooplankton upon Chl *a* were evaluated by plotting the residuals of the TP-Chl *a* relationship against log total zooplankton biomass. A significant positive relationship was observed ($p = 0.014$. $R^2 = 0.19$) (Figure 4.6). The significant positive relationship between zooplankton biomass and Chl *a* after controlling for TP (Figure 4.6) combined with the significant positive relationship between zooplankton biomass and Chl *a* after controlling for water residence time (Figure 4.5) suggests a significant (although weak) resource effect and no negative relationship between zooplankton and phytoplankton biomass.

4.5 Discussion

Knowledge of the factors regulating plankton development in large rivers is lacking. Such basic ecological information is required before more complex and applied issues such as maintenance of river water quality, fisheries management, contaminant dynamics, and the effects of river impoundment can be addressed. Principles learned through examination of lentic systems may not be applicable to large river systems (Ryder and Pesendorfer 1989). The objectives of the present research were to determine which factors are most strongly related to plankton development across a wide range of rivers and to explore the relationship between zooplankton biomass and phytoplankton biomass.

The significant positive relationship that we observed between Chl *a* concentration and total phosphorus concentration was anticipated (Figure 4.1). Other studies on individual rivers have demonstrated postitive relationships between algal biomass and nutrients (Moss *et al.* 1989, Basu and Pick 1995, Chapter 2 and 3 of the present thesis) and Soballe and Kimmel (1987) observed a significant positive relationship between algal abundance and TP for numerous rivers in the U.S. Although discharge and turbidity have been correlated with phytoplankton abundance more than nutrient concentrations in some rivers (e.g. Lack 1971, Jones 1984, Krogstad and Lovstad 1989), our results and those of Soballe and Kimmel (1987) show that total phosphorus concentration is most strongly correlated with Chl *a* and algal abundance. It is unlikely that total nitrogen concentration regulates Chl *a* concentration in our study rivers, as the TN:TP ratio was always greater than 20 with a mean of 40. Under such conditions TP is more likely the limiting nutrient (Smith 1982).

In comparison to the algal abundance-TP relationship of Soballe and Kimmel (1987), our regression predicting Chl *a* from TP concentrations in rivers is more directly comparable to TP-Chl *a* relationships derived for lakes. The amount of variance in Chl *a* accounted for by TP is similar in both large rivers ($R^2 = 0.76$ for this study) and lakes (R^2 from 0.64 to 0.95) (Dillon and Rigler 1974, Canfield 1983, Riley and Prepas 1985, Pridmore *et al.* 1985). In addition, a higher amount of the variance in Chl *a* was accounted for by TP ($R^2 = 0.76$) in comparison to the amount of variance in algal abundance accounted for by TP ($R^2 = 0.24$) (Soballe and Kimmel 1987).

Our results suggest no effect of water residence time on Chl *a* concentrations in rivers. This conflicts with the results of Soballe and Kimmel (1987) who observed algal abundance per unit TP increasing in the sequence rivers < impoundments < natural lakes- a sequence which paralleled differences in water residence time. The lack of a relationship between water residence time and Chl *a* and the higher R^2 between Chl *a* and TP in comparison to algal abundance and TP may be the result of algal biomass (Chl *a*) not necessarily being equivalent to algal abundance. In rivers, small algae such as picocyanobacteria (0.2 to 2.0 μm) are abundant (Pick and Basu unpubl. data); their fast doubling times being an advantage in short residence systems. These algae and other small species of phytoplankton are not enumerated when using traditional cell count methods to estimate algal abundance; however, they contribute to algal biomass (Chl *a*). The minimum water residence time for our study rivers was 3.3 d. This length of time is sufficient for many species of phytoplankton (e.g. small species of Chlorophyta and Cryptophyta with doubling times less than 48 hours and picocyanobacteria with doubling times of less than 24 hours, Pick and Berubé 1992) to be regulated by nutrient concentrations rather than by water residence times. Our results indicate that, in rivers, algal biomass (Chl *a*) rather than algal abundance is better predicted from TP concentrations and is not related to water residence time. It seems likely that when the residence time is greater than 3 d, planktonic algal biomass (Chl *a*) is regulated by nutrient concentrations rather than by water residence time. This may not apply to smaller rivers with shorter water residence times.

In contrast to Chl *a* concentration, we observed a significant positive relationship between zooplankton biomass and water residence time. As water residence time increased, total zooplankton biomass increased (Figure 4.3). This was also the case for both rotifer biomass and crustacean biomass separately. That water residence time should have a direct effect upon zooplankton biomass in comparison to phytoplankton biomass was expected. As mentioned, phytoplankton with short generation times (hours to days) are less susceptible to advective loss when compared to zooplankton. Zooplankton with longer generation times (days to months) appear more susceptible to advective loss (Pace *et al.* 1992).

We detected a weak effect of Chl *a* upon zooplankton biomass (Figure 4.5). This resource effect became apparent only after controlling for the much stronger effect of water residence time on zooplankton biomass. This result suggests that water residence time rather than resources (Chl *a* or TP) primarily limits zooplankton biomass in rivers, although much variability remains unexplained. In contrast, lake zooplankton biomass, without temporal restrictions, is strongly related to measures of overall lake productivity (e.g. Chl *a* or TP) (McCauley and Kalff 1981, Hanson and Peters 1984, Canfield and Watkins 1984, Pace 1984, McQueen *et al.* 1986).

The zooplankton taxa with the highest relative occurrence in our study included the rotifers *Synchaeta* sp., *Keratella* sp., and *Polyarthra* sp. as well as nauplii, cyclopoid copepods and *Bosmina* sp. Rotifers were clearly numerically dominant over crustaceans, an average of 20 times more abundant. These results are similar to results of the few previous studies conducted on individual rivers. Rotifers tend to be the most abundant

zooplankton in rivers followed by nauplii, bosminids and cyclopoid copepods (Shiel *et al.* 1982, Ferrari *et al.* 1989, Bothar and Kiss 1990, Pace *et al.* 1992, Thorp *et al.* 1994). Larger cladocerans (e.g. *Daphnia* sp.) and calanoid copepods are much less abundant within riverine zooplankton communities. Pace *et al.* (1992) hypothesized that smaller zooplankton species, such as rotifers and bosminids, are favoured in rivers due to their shorter generation times which reduce the impacts of advective loss.

Our results indicate that compared to lakes, rivers have a much lower biomass of zooplankton. Mean biomass for the sampled rivers was 11.3 $\mu g\ L^{-1}$. In comparison, Wilson and Currie (submitted) observed a mean zooplankton biomass of 164 $\mu g\ L^{-1}$ for 33 lakes located in the same geographic area as the rivers, and sampled during the same time period (July-August 1994) (Wilson and Currie submitted). In addition, the same equations were used to determine total zooplankton biomass for both the lake data and river data.

The mean zooplankton biomass : Chl *a* ratio for the 31 rivers was 1.65. We compared this ratio to the mean zooplankton biomass : Chl *a* ratio for the 33 lakes sampled by Wilson and Currie (submitted) combined with 12 eastern Quebec lakes sampled by Pace (1984). Pace's (1984) data was included to achieve a similar range in Chl *a* for the river and lake data sets (range in Chl *a* for rivers: 1.8 to 27.6 $\mu g\ L^{-1}$, for lakes: 0.9 to 28.6 $\mu g\ L^{-1}$). The average zooplankton : Chl *a* ratio for the lake data was 63.4. A one tailed Mann-Whitney test indicated that the mean ratio for the river data was significantly lower than the mean ratio for the lake data ($p < 0.001$). The lower ratio of

zooplankton biomass : Chl *a* is due to the overall lower biomass of zooplankton in rivers possibly a result of temporal limitations imposed on their development.

Considering the low overall biomass of zooplankton in our rivers and the dominance of small taxa, it is not surprising that we observed no negative relationship between zooplankton biomass and Chl *a* concentration. McQueen *et al.* (1986) and Pace (1984) concluded that when large zooplankton taxa (especially cladocerans) are absent, zooplankton cannot significantly reduce phytoplankton biomass.

4.6 Summary

As in lakes, the biomass of phytoplankton in large (greater than fifth order) rivers is strongly correlated with nutrient concentrations (TP), but not with water residence time. In contrast, zooplankton biomass in rivers is more strongly correlated with water residence time than with Chl *a* or TP concentrations. Zooplankton biomass in rivers is much lower than in lakes and zooplankton populations in rivers are dominated by rotifers and small crustaceans. Zooplankton populations, with longer generation times, seem more susceptible than phytoplankton to advective loss in short residence river systems.

Table 4.1. River locations with mean chemical, physical, and biotic variables for July 1994 sampling. (S) denotes rivers located on the Canadian Shield, (L) denotes rivers located in the Great Lakes/ St. Lawrence Lowlands. Light attenuation coefficient not available - na.

River	N lat, W long	TP ($\mu g\ liter^{-1}$)	TN ($\mu g\ liter^{-1}$)	Water residence time (d)	Light attenuation coefficient (m^{-1})	Chl *a* ($\mu g\ liter^{-1}$)	Total zooplankton biomass ($\mu g\ liter^{-1}$)
Madawaska (S)	45° 30', 77° 10'	10.3	412.3	10.6	0.9	6.7	9.3
Bonnechere (S)	45° 30', 76° 50'	16.0	411.3	5.6	1.1	3.0	0.6
Mississippi (S/L)	45° 20', 76° 15'	19.6	606.3	7.9	1.0	3.8	0.9
Rouge (S)	45° 50', 74° 40'	15.0	316.3	9.2	1.3	3.4	0.6
du Lievre (S)	45° 40', 75° 35'	11.3	335.0	10.9	1.1	2.4	2.9
South Nation (L)	45° 20', 75° 5'	96.0	3,059.0	6.2	4.6	12.7	24.5
Gatineau (S)	45° 40', 75° 55'	11.6	354.3	19.4	1.3	2.3	3.6
Picanoc (S)	45° 43', 75° 55'	8.6	272.3	4.5	0.9	2.5	0.5
Magnetewan (S)	45° 46', 80° 35'	8.6	358.6	6.6	1.1	3.5	2.1
French (S)	46° 2', 80° 43'	9.3	325.0	14.1	0.6	3.6	29.2
Mattawa (S)	46° 20', 78° 45'	11.6	360.0	7.5	1.0	3.2	3.7
Temagami (S)	46° 38', 80° 8'	7.3	358.0	6.9	0.9	2.4	0.4
Sturgeon (S)	46° 26', 79° 58'	8.0	280.3	11.1	1.0	2.1	0.6
Amable (S)	46° 20', 77° 15'	8.6	295.0	4.0	2.1	3.6	1.3
Veuve (S)	46° 26', 80° 10'	42.0	845.0	3.6	2.7	10.6	0.2
Trent (L)	44° 20', 77° 55'	18.3	470.6	13.5	0.9	8.4	205.3
Napanee (L)	44° 20', 76° 50'	15.3	493.4	3.8	1.5	1.9	< 0.1
Salmon (L)	44° 15', 77° 5'	13.0	490.3	3.4	na	2.1	< 0.1
Moira (L)	44° 20', 77° 20'	8.0	441.3	5.9	na	1.8	0.2
Burnt (S/L)	44° 30', 78° 42'	8.6	397.3	4.9	0.8	3.4	1.4
Otonabee (S/L)	44° 25', 78° 15'	13.3	387.0	12.1	0.7	4.3	14.5
Skootamata (S/L)	44° 30', 77° 15'	15.0	520.3	4.1	1.1	5.4	0.2
Saugeen (L)	44° 12', 81° 11'	18.3	1,243.3	6.1	na	4.0	0.1
Ausable (L)	43° 3', 81° 38'	80.6	3,239.0	4.7	5.4	23.1	0.3
North Thames (L)	43° 14', 81° 12'	61.6	3,029.0	4.7	na	21.1	2.1
Nith (L)	43° 25', 80° 43'	92.3	2,222.0	3.6	5.0	11.5	0.8
Thames (L)	42° 51', 81° 25'	212.3	5,317.6	7.6	4.8	27.6	0.2
Conestogo (L)	43° 36', 80° 40'	28.3	2,008.7	3.4	na	4.5	0.1
Maitland (L)	43° 51', 81° 15'	12.3	1,783.2	3.3	na	5.1	0.9
Grand (L)	43° 6', 80° 11'	46.3	2,506.3	9.8	2.2	6.4	0.2
Rideau (L)	45° 27', 75° 42'	64.0	1,510.0	7.8	1.5	8.8	43.0

Table 4.2. Means (± standard errors) and ranges of measured variables for rivers sampled in Ontario and Quebec during July 1994. n = 31 sampled rivers.

Variable	Mean (± SE)	Range
Chl *a* (μg liter^{-1})	6.62 (±1.17)	1.77 - 27.62
Rotifer biomass (μg liter^{-1} dry mass)	2.27 (±0.85)	0.016 - 22.6
Crustacean biomass (μg liter^{-1} dry mass)	8.99 (±6.38)	< 0.1 - 196.0
Total zooplankton biomass (μg liter^{-1} dry mass)	11.26 (±6.71)	0.016 - 205.3
TP (μg liter^{-1})	32.00 (±7.60)	7.3 - 212.3
TN (μg liter^{-1})	1,117.6 (±219.5)	272.0 - 5,318.0
TN : TP ratio	40.16 (±4.15)	20.1 - 144.6
Discharge (m^3 s^{-1})	34.1 (±10.7)	0.9 - 250.0
Depth (m)	3.9 (±0.8)	1.0 - 24.0
Watershed area (km^2)	3,953 (±861)	548 - 23, 620
Water residence time (d)	7.32 (±0.70)	3.28 - 19.38
Attenuation coefficient (m^{-1})	1.83 (±0.30)	0.64 - 5.36

Table 4.3. Relative occurrence (percentage of samples in which the taxon occurred) of major zooplankton taxa for rivers sampled in Ontario and Quebec, July 1994.

Rotifers	Relative Occurrence	Crustaceans	Relative Occurrence
Synchaeta sp.	89	nauplii	94
Keratella sp.	79	cyclopoid copepods	71
Polyarthra sp.	73	*Bosmina* sp.	61
Monostyla sp.	43	*Diaphanosoma* sp.	40
Trichocerca sp.	29	calanoid copepods	29
Colurella sp.	25	*Daphnia* sp.	21
Lecane sp.	27	*Chydorus* sp.	16
Pleosoma sp.	15	*Acoperus* sp.	4
Gastropus sp.	14	*Eurycerus* sp.	3

Table 4.3 (continued)

Rotifers	Relative Occurrence	Crustaceans	Relative Occurrence
Brachionus sp.	12	others (*Holopedium* sp. *Leptodora* sp.)	< 2
Kellicottia sp.	8		
Filinia sp.	8		
Ascomorpha sp.	5		
Cephaodella sp.	3		
Euchlanis sp.	3		
Testudinella sp.	3		
Conochilus sp.	2		
others (digononts and unknowns)	< 2		

Figure 4.1. Significant relationship between total phosphorus concentration and Chl *a* concentration for rivers sampled during July 1994 (log Chl *a* = -0.26 + 0.73 log TP). Dashed lines represent 95% confidence intervals.

Figure 4.1

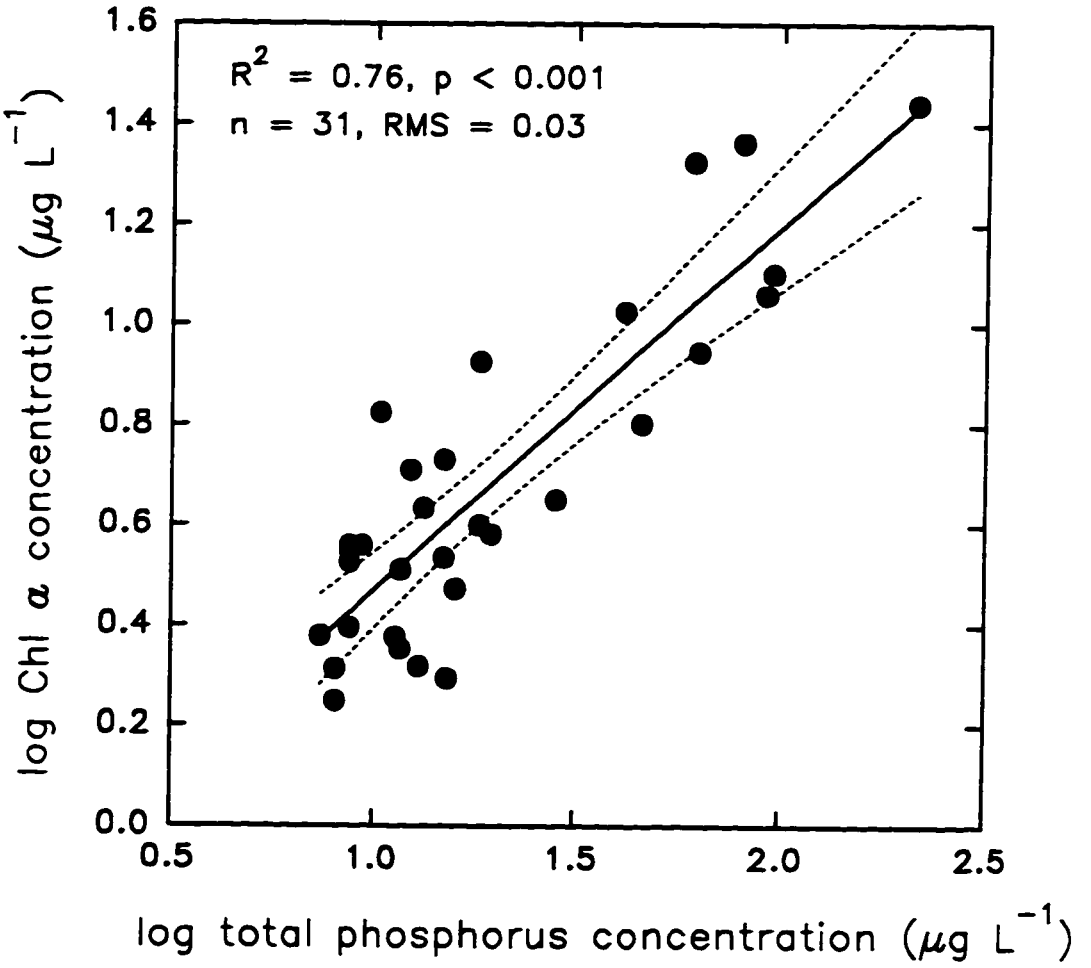

R^2 = 0.76, p < 0.001
n = 31, RMS = 0.03
log Chl a concentration (μg L^{-1})
log total phosphorus concentration (μg L^{-1})
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.5
1.0
1.5
2.0
2.5

Figure 4.2. Scatterplots demonstrating no significant relationship between water residence time and Chl *a* concentration (A), and water residence time and Chl *a* concentration after controlling for the effect of total phosphorus concentration (B) (for rivers sampled during July 1994).

Figure 4.2A

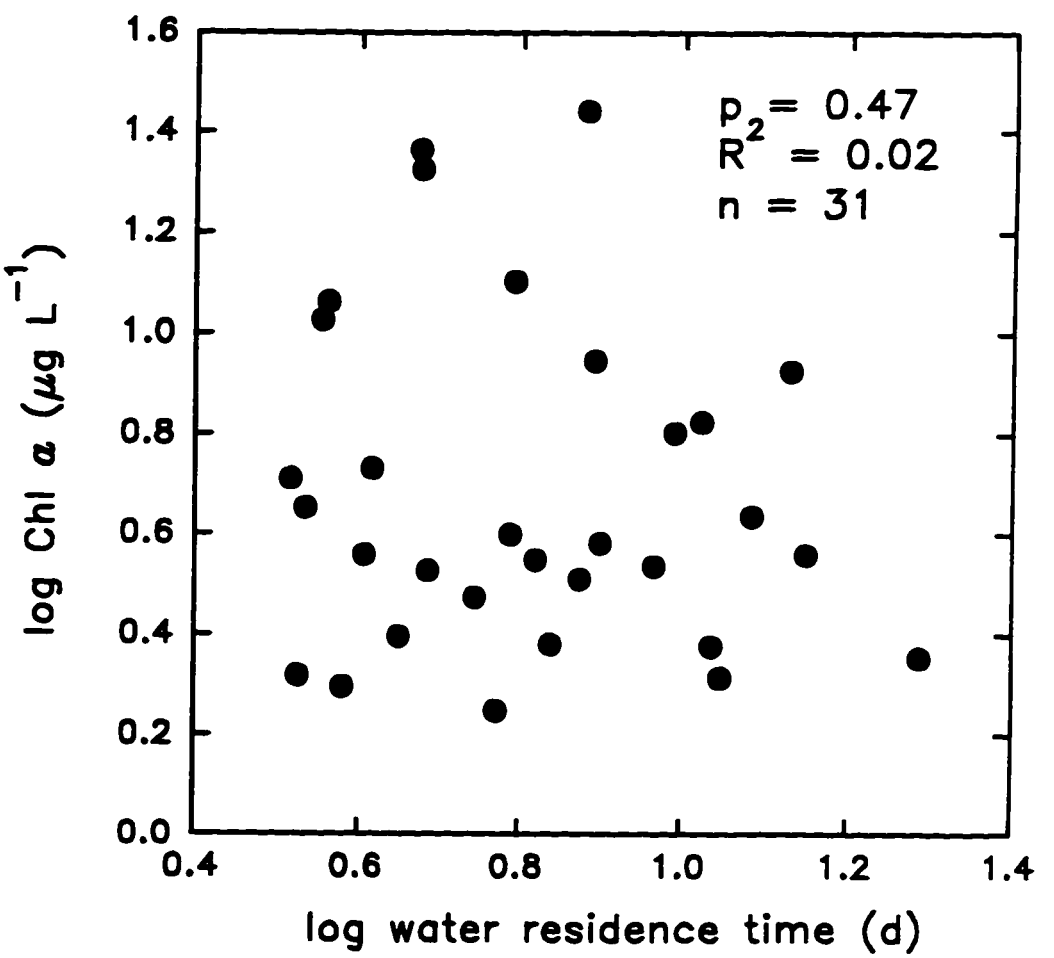

1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.4
0.6
0.8
1.0
1.2
1.4
log Chl a (μg L⁻¹)
log water residence time (d)
p2 = 0.47
R2 = 0.02
n = 31

Figure 4.2B

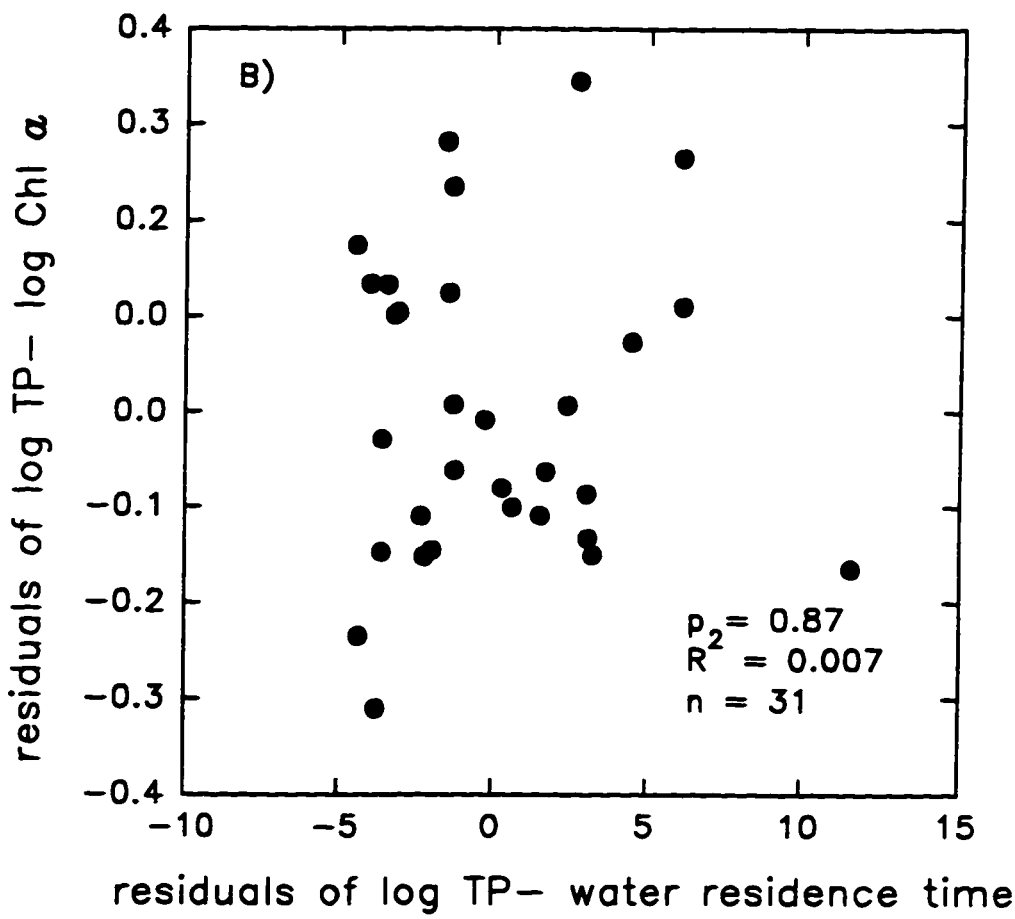

B)
0.4
0.3
0.2
0.0
0.0
−0.1
−0.2
−0.3
−0.4
−10
−5
0
5
10
15
p_2= 0.87
R^2 = 0.007
n = 31
residuals of log TP− log Chl a
residuals of log TP− water residence time

Figure 4.3. Significant relationship between water residence time and total zooplankton biomass (rotifers and crustaceans) for rivers sampled during July 1994 (log zooplankton biomass = -1.02 + 0.14 water residence time). Dashed lines represent 95% confidence intervals.

Figure 4.3

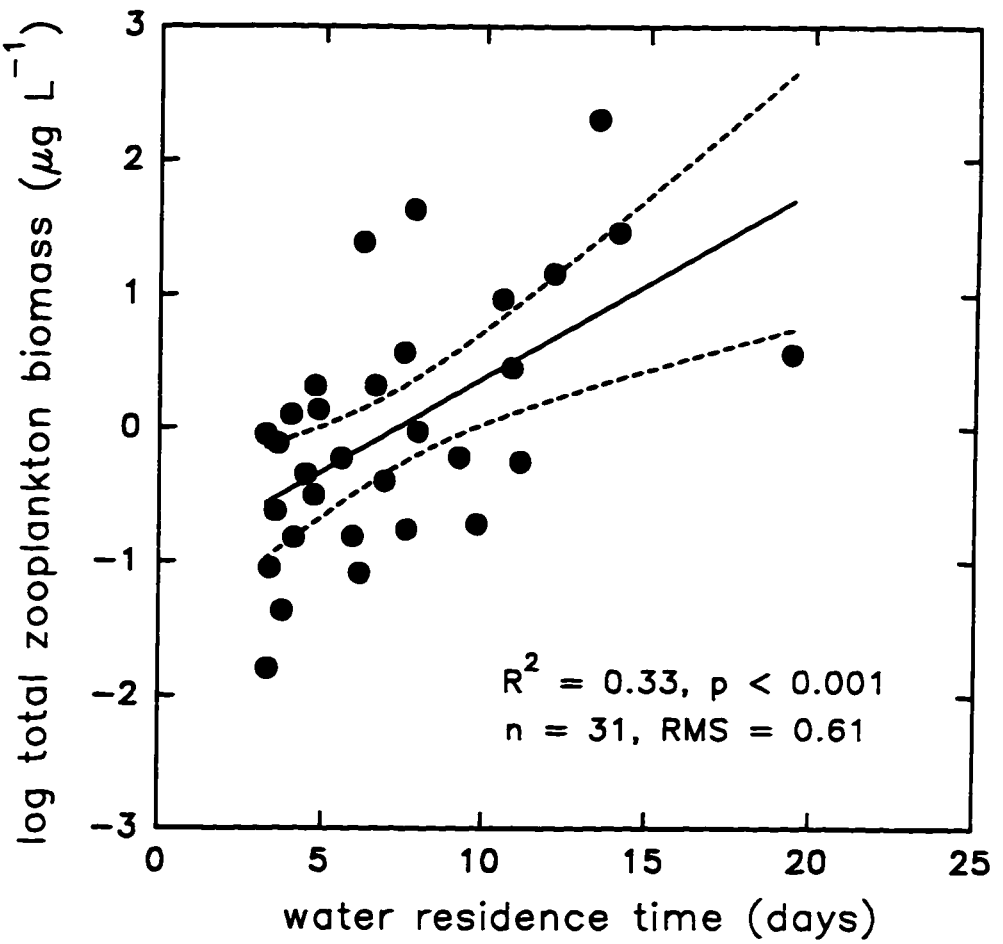

log total zooplankton biomass ($\mu g\ L^{-1}$)
water residence time (days)
R^2 = 0.33, p < 0.001
n = 31, RMS = 0.61
3
2
1
0
−1
−2
−3
0
5
10
15
20
25

Figure 4.4. Scatterplots demonstrating no significant relationship between Chl *a* concentration and total zooplankton biomass (A) and total phosphorus concentration and total zooplankton biomass (B) (for rivers sampled during July 1994).

Figure 4.4A

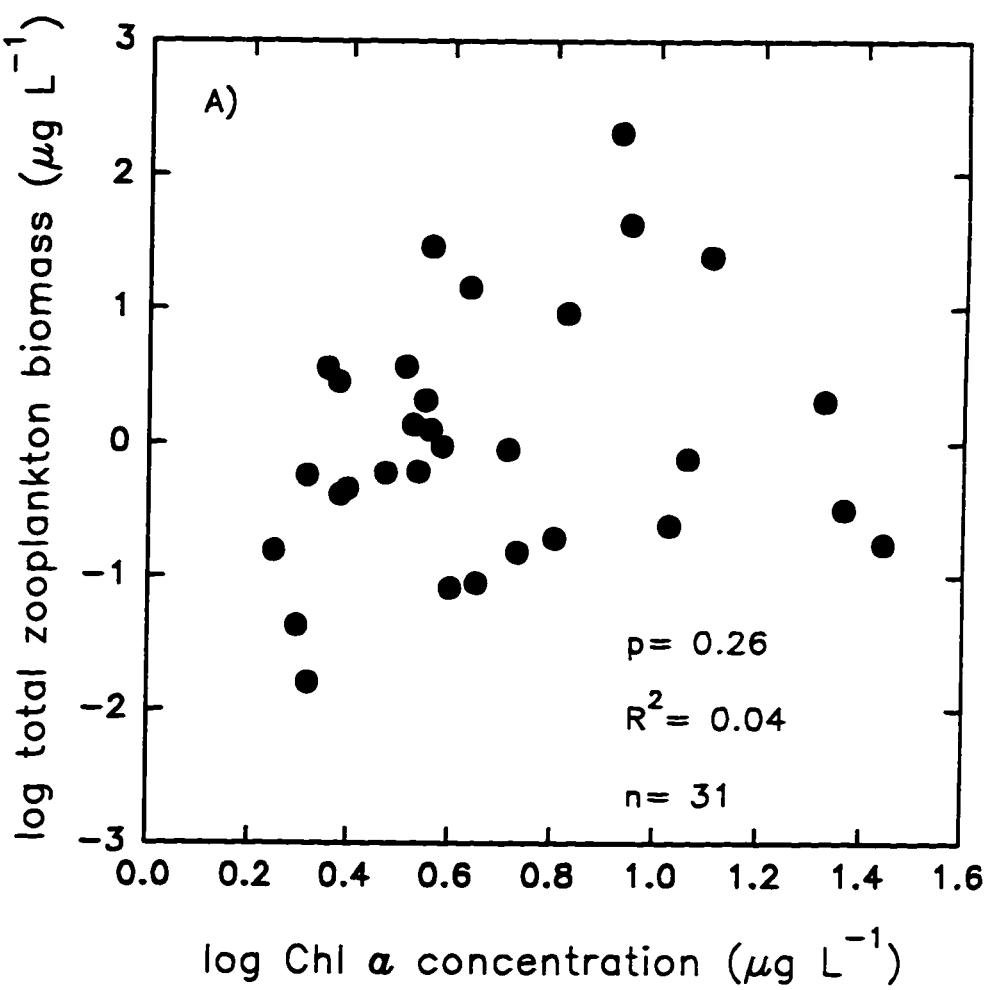

A)
p= 0.26
R^2= 0.04
n= 31
log total zooplankton biomass (μg L^{-1})
log Chl *a* concentration (μg L^{-1})
3
2
1
0
−1
−2
−3
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6

Figure 4.4B

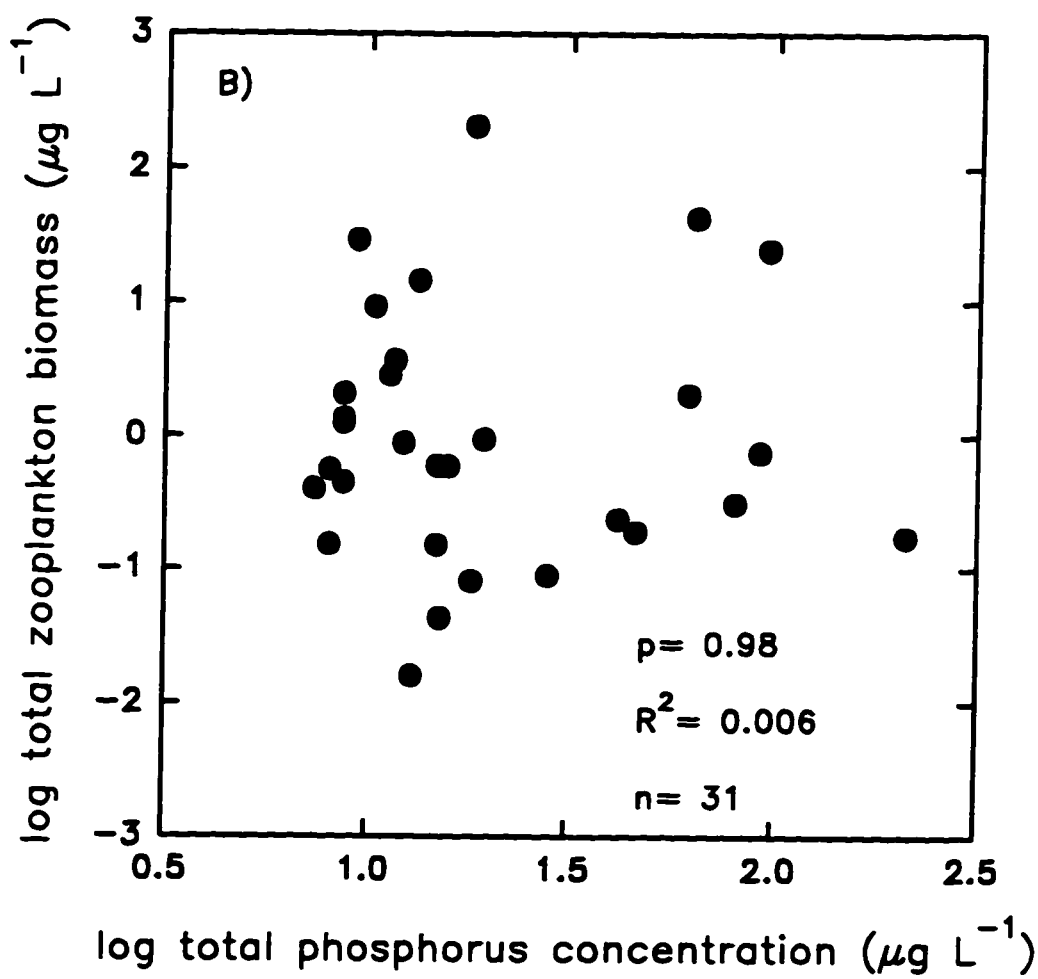

B)
p= 0.98
R^2= 0.006
n= 31
log total zooplankton biomass (μg L^{-1})
log total phosphorus concentration (μg L^{-1})
3
2
1
0
−1
−2
−3
0.5
1.0
1.5
2.0
2.5

Figure 4.5. Significant relationship between Chl *a* concentration and total zooplankton biomass after controlling for the effect of water residence time (for rivers sampled during July 1994). Dashed lines represent 95% confidence intervals.

Figure 4.5

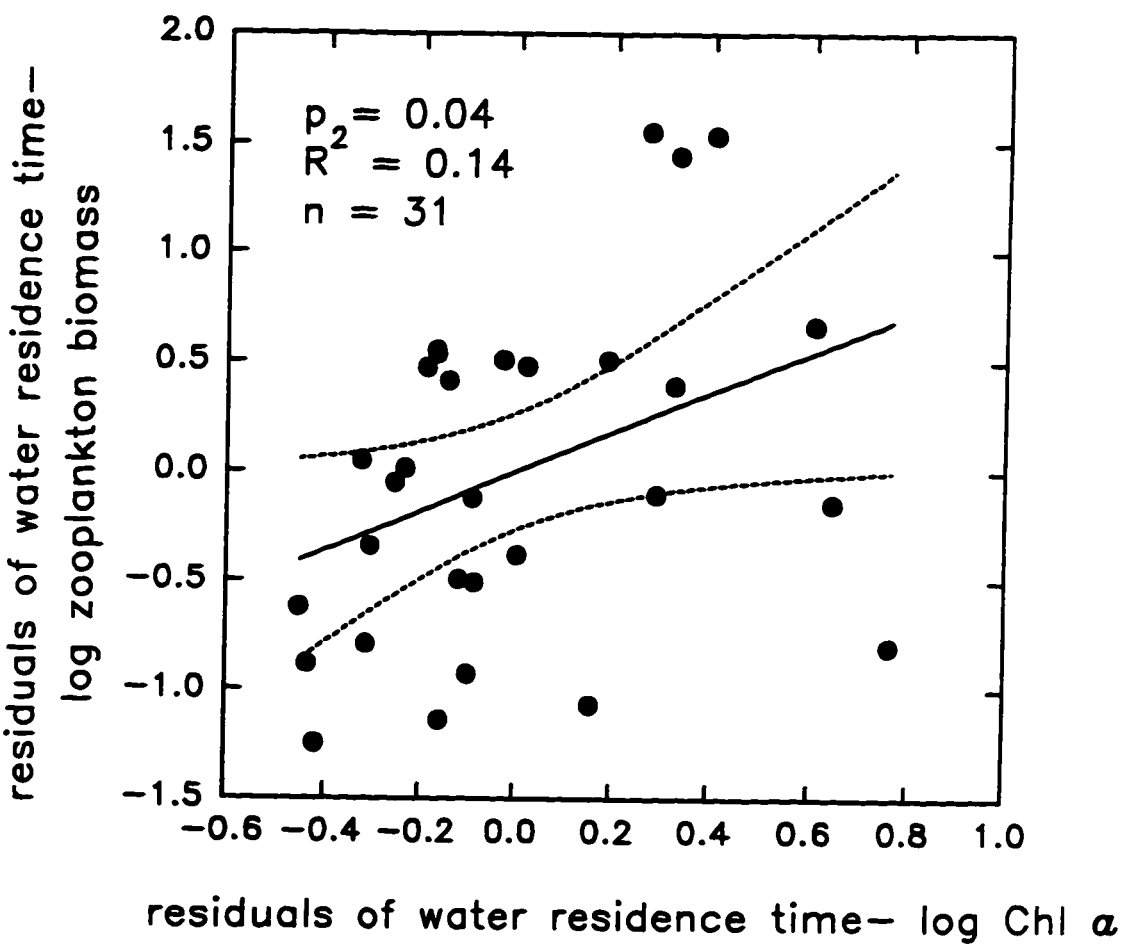
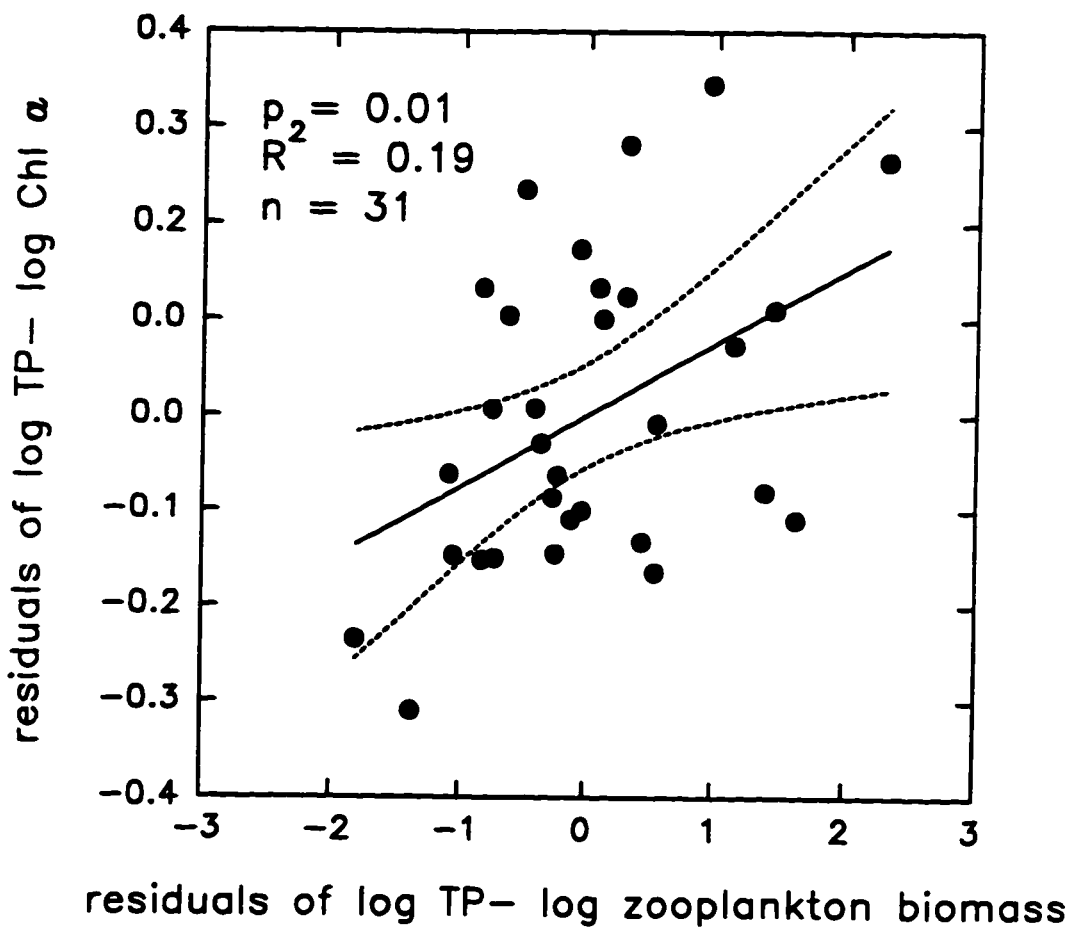

2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−0.6 −0.4 −0.2 0.0 0.2 0.4 0.6 0.8 1.0
p2= 0.04
R2 = 0.14
n = 31
residuals of water residence time– log zooplankton biomass
residuals of water residence time– log Chl a

Figure 4.6. Significant relationship between total zooplankton biomass and Chl *a* concentration after controlling for the effect of total phosphorus concentration (for rivers sampled during July 1994).

Figure 4.6


0.4
0.3
0.2
0.0
0.0
−0.1
−0.2
−0.3
−0.4
−3
−2
−1
0
1
2
3
p_2= 0.01
R^2 = 0.19
n = 31
residuals of log TP− log Chl a
residuals of log TP− log zooplankton biomass

Chapter 5

Factors Related to Heterotrophic Bacterial and Flagellate Abundance in Temperate Rivers

Modified from Basu, B.K. and F.R. Pick. Aquatic Microbial Ecology. 11: in press. (with permission)

5.1 Abstract

Thirty-one rivers of varying trophic status located in Ontario and Quebec, Canada were sampled in order to determine the factors related to heterotrophic bacterial and flagellate abundance. Bacterial abundance ranged from 1.80×10^6 to 9.92×10^6 cells ml^{-1} and flagellate abundance ranged from 1.18×10^3 to 17.4×10^3 cells ml^{-1}. There was a highly significant, positive relationship between bacterial abundance and both total phosphorus ($R^2 = 0.55$) and chlorophyll *a* ($R^2 = 0.55$). Bacterial abundance was not related to dissolved organic carbon concentration which ranged from 4.6 to 13.0 mg L^{-1}. A significant positive relationship was observed between heterotrophic flagellate abundance and both heterotrophic bacterial abundance ($R^2 = 0.46$) and total phosphorus ($R^2 = 0.52$). Neither bacterial nor flagellate abundance was significantly related to water residence time. No relationship between zooplankton biomass and bacterial or flagellate abundance was observed, possibly because of the low biomass of zooplankton in the rivers (mean = 11.3 μg L^{-1} dry mass). It seems likely that in rivers there is little transfer of energy from the planktonic microbial food web to the pelagic food web due to the scarcity of metazoan zooplankton.

5.2 Introduction

The importance of microbial food webs in marine and lentic freshwaters has been recognized for the past decade (Azam *et al.* 1983, Fenchel 1986, Cole *et al.* 1988). These webs can be visualized as "microbial loops" (Azam *et al.* 1983), in which heterotrophic bacteria convert dissolved organic matter of autochthonous or allochthonous origin into particulate organic carbon (Azam *et al.* 1983, Berninger *et al.* 1991, Findlay *et al.* 1991). The heterotrophic bacteria are then grazed by heterotrophic flagellates and small ciliates (Porter *et al.* 1985, Berninger *et al.* 1991). In turn, the bactivorous flagellates and ciliates may be consumed by larger ciliates, microzooplankton (rotifers) and cladocerans (Gasol and Vaqué 1993).

The microbial loop can contribute energy to the classical food web (i.e. phytoplankton ---> zooplankton ---> fish) by packaging dissolved organic matter into larger particles (heterotrophic bacteria, flagellates and ciliates) which are directly available for consumption by metazoan zooplankton (Azam *et al.* 1983, Vaqué *et al.* 1992, Gasol and Vaqué 1993). However, the role of the microbial loop as an energy link to higher trophic levels remains controversial. Respiration and trophic transfers within microbial food webs may lead to significant energy losses (Pomeroy and Weibe 1988). Instead, the major importance of the microbial loop may be associated with the remineralization of organic matter into small nutrient molecules (CO_2, PO_4^{3-}, NH_4^+) required for phytoplankton growth (Goldman and Caron 1985, Pomeroy and Weibe

1988). Regardless of whether its major role is energy transfer or nutrient mineralization, the microbial loop appears to be an important component of planktonic food webs.

In temperate lakes heterotrophic bacterial abundance has been related to measures of overall lake productivity such as chlorophyll *a*, total phosphorus or dissolved organic carbon concentrations (Bird and Kalff 1984, Currie 1990, Tranvik 1989, Tzaras and Pick 1994). This suggests that predatory control of bacteria may be of minor importance (Gasol and Vaqué 1993). Heterotrophic flagellate abundance has been positively correlated with heterotrophic bacterial abundance, flagellates being the primary consumers of bacteria (Berninger *et al.* 1991). In some lake studies, however, it has been speculated that zooplankton predation on heterotrophic flagellates weakens or eliminates the positive relationship between flagellates and bacteria (Gasol and Vaqué 1993, Tzaras and Pick 1994).

The overwhelming majority of studies concerning microbial food webs have been conducted in marine and lentic freshwater environments. Comparatively little research has focused on heterotrophic bacteria and protozoa in lotic (flowing water) environments (Edwards and Meyer 1986, Carlough and Meyer 1990, Dolan and Gallegos 1991, Findlay *et al.* 1991). The abundance of heterotrophic bacteria in rivers can be high. For example, Edwards (1987) observed an average abundance of 1.5×10^{10} cells L^{-1} in the blackwater Ogeechee River (USA). As in lakes, the primary consumers of heterotrophic bacteria in rivers appear to be heterotrophic flagellates (Meyer 1990, Carlough and Meyer 1990). In addition, benthic filter-feeding invertebrates may be significant consumers of planktonic bacterial biomass in rivers (Meyer 1990). Meyer (1990) hypothesized that high levels of

secondary production by benthic invertebrates may be supported through the direct consumption of bacterial biomass.

The microbial food web could be particularly important to carbon and nutrient dynamics in river systems due to the often high loadings of allochthonous organic matter (Edwards and Meyer 1986, Findlay *et al.* 1991, Sabater *et al.* 1993), and low zooplankton abundances (Pace *et al.* 1992, Basu and Pick 1996, Chapter 4 of the present thesis). Under such conditions, significant carbon flow to benthic invertebrates and/or nutrient regeneration may occur via the microbial food web. Determining the factors related to the abundance of heterotrophic bacteria and flagellates in lotic waters represents the first step in examining microbial food webs in rivers.

The objective of the present study was to determine the factors most strongly related to heterotrophic bacterial and flagellate abundance in north-temperate rivers. Thirty-one temperate Canadian rivers of varying trophic status were sampled and the following variables measured: heterotrophic bacterial abundance, heterotrophic flagellate abundance, rotifer biomass, crustacean zooplankton biomass, chlorophyll *a* concentration (Chl *a*), total phosphorus concentration (TP), total nitrogen concentration (TN), dissolved organic carbon concentration (DOC) and water residence time (Basu and Pick 1996). Correlation and regression analyses were performed in order to determine which variables were most strongly related to, and hence potentially regulate, bacterial and flagellate abundances in these rivers.

5.3 Methods

Thirty-one rivers in southern Ontario and western Quebec, Canada, were sampled in July 1994 (Table 5.1). The rivers drain areas located on either the Canadian Shield (granitic bedrock) or the Great Lakes, St. Lawrence Lowlands (sedimentary bedrock). The watersheds of the rivers range from completely forested to agricultural. All the rivers are fifth order or larger and have mean annual discharges greater than 8.0 $m^3 s^{-1}$ (Water Survey of Canada, Historical Streamflow Summary, Ontario and Quebec, 1990). The sampling sites on the rivers were located close to Water Survey of Canada gauging stations and not near any inflowing tributaries or within 10 km of headwater lakes.

Heterotrophic bacteria and heterotrophic flagellate samples were collected mid-channel at each river site using a 4-m vertically integrated tube. Usually the entire water column was sampled, as river depths rarely exceeded 4 m. Sub-samples (100-ml) of whole river water were preserved immediately with 10% glutaraldehyde buffered with 0.1 M sodium cacodylate and stored at 4°C in the dark until enumeration. Bacterial and flagellate abundance was determined by staining samples with 4'6 diamidino-2-phenylindole (DAPI) added at a 3:1 sample to DAPI ratio. Enumeration was performed using epifluorescence microscopy at 1500 X magnification (Porter and Feig 1980). Heterotrophic bacteria were filtered onto 0.2-µm Irgalan black stained Nuclepore filters and heterotrophic flagellates onto similarly stained 1.0-µm Nuclepore filters. At least 500 cells from approximately 10 randomly selected fields were enumerated for bacterial abundance. For heterotrophic flagellates, between 70 and 120 cells were counted from random transects (Tzaras and Pick 1994). Samples containing large amounts of inorganic

particulate material were diluted in 10-ml of filtered (0.2-μm) distilled water and subsampled prior to enumeration.

Dissolved organic carbon (DOC) concentration was determined using methods outlined in the Analytical Methods Manual of Environment Canada (1979).

Details of the sampling procedures and methods to determine chlorophyll *a* (Chl *a*), total phosphorus (TP), total nitrogen (TN), crustacean biomass, and rotifer biomass are described in Basu and Pick (1996) (Chapter 4 of the present thesis). Briefly, for Chl *a* vertically integrated water samples were filtered through Whatman GF/F filters and Chl *a* was extracted using DMSO and acetone (Burnison 1980). Chl *a* concentrations were calculated using the equations of Jeffrey and Humphrey (1975). Chemical analyses for TP and TN were performed at the Regional Municipality of Ottawa-Carleton, Surface Water Quality Laboratories using standard methods described in RMOC (1993) and Basu and Pick (1995) (Chapter 2 of the present thesis). Vertically integrated crustacean zooplankton samples were collected mid channel by pumping 30-L of water through a 64-μm Nitex mesh plankton net using an open diaphragm bilge pump (Pace 1984). Rotifer samples were collected by filtering 4-L of water (collected in a Nalgene bottle at 0.5-m depth) through a 35-μm Nitex mesh screen. Zooplankton samples were preserved with 4% chilled Formalin sucrose (Haney and Hall 1975). Crustaceans were enumerated under a dissecting microscope, and rotifers under an inverted microscope. Biomass estimates for crustaceans were determined using length-dry mass relationships (Bottrell *et al.* 1976, Dumont *et al.* 1975) and biomass estimates for rotifers were determined using

biovolume-dry mass relationships (Ruttner-Kolisko 1977, Dumont *et al.* 1975). Further details are described in Basu and Pick (1996) (Chapter 4 of the present thesis).

Discharge values for the rivers were obtained from Water Survey of Canada gauging sites. Discharge was calculated as the average of the daily discharges for the period seven days prior to and including the sampling date in a manner similar to that of Pace *et al.* (1992). Watershed area for each river was obtained from the Water Survey of Canada which calculates upstream watershed area at each gauging site (Water Survey of Canada, Historical Streamflow Summary, Ontario, Quebec, 1990). Water residence time (an estimate of the time the water has been in the river system or in other words its "age" at the sampling site) was calculated using the formula:

$$R = 0.08\ A_d^{\ 0.6} / Q^{\ 0.1} \qquad (1)$$

where R represents water residence time at the sampling site (d), A_d represents watershed area upstream of the sampling site (km^2) and Q represents river discharge ($m^3\ s^{-1}$) (Soballe and Kimmel 1987).

5.3.1 Statistical Analysis

Statistical analysis was performed using either SAS 6.06 (SAS Institute Inc. USA, 1992) or Systat 5.03 (Systat Inc. USA, 1993) statistical software. Linear regression and correlation analyses were used to identify relationships between variables. The significance value for statistical tests was 5%. All parametric tests performed satisfied the assumptions of normality (Wilkes-Shapiro test) and homoscedasticity (plot of residuals

against independent variable) following any required logarithmic transformations of the data.

5.4 Results

In the 31 rivers sampled, bacterial abundance ranged from 1.80 X 10^6 to 9.92 X 10^6 cells ml^{-1} and mean bacterial abundance was 4.46 ± 0.38 X 10^6 cells ml^{-1} (mean ± standard error) (Table 5.1). Flagellates ranged from 1.18 X 10^3 to 17.40 X 10^3 cells ml^{-1} and mean flagellate abundance was 4.07 ± 0.70 X 10^3 cells ml^{-1} (Table 5.1).

Chl *a* ranged from 1.77 to 27.62 µg L^{-1} and mean Chl *a* was 6.62 ± 1.17 µg L^{-1}. TP ranged from 7.3 to 212.0 µg L^{-1} and TN ranged from 272.0 to 5318.0 µg L^{-1}. Mean TP and TN concentrations were 32.0 ± 7.6 and 1117.6 ± 219.5 µg L^{-1}, respectively (Basu and Pick 1996, Chapter 4 of the present thesis). DOC ranged from 4.6 to 13.0 mg L^{-1} and mean DOC was 6.6 ± 0.4 mg L^{-1} (Table 5.1).

Rotifer biomass ranged from < 0.1 to 22.6 µg L^{-1} (dry mass) and crustacean zooplankton biomass from < 0.1 to 196.0 µg L^{-1} (dry mass). Mean rotifer and crustacean biomass were 2.27 ± 0.85 and 8.99 ± 6.38 µg L^{-1} (dry mass), respectively (Basu and Pick 1996).

Water residence time ranged from 3.28 d to 19.38 d and mean water residence time was 7.32 ± 0.70 d (Basu and Pick 1996).

There was a highly significant positive relationship between bacterial abundance and both TP and Chl *a* (Figure 5.1, Figure 5.2). Bacterial abundance was also positively related to TN, however, the coefficient of determination (R^2) for this relationship was

lower than those for the TP-bacteria or Chl *a*-bacteria relationships (for TN: $P < 0.001$, $R^2 = 0.47$). There was no significant relationship between bacterial abundance and DOC ($p = 0.89$) (Figure 5.3).

Bacterial abundance was not significantly related to rotifer biomass ($p = 0.47$) (Figure 5.4), crustacean zooplankton biomass ($p = 0.69$) or total zooplankton biomass (rotifer + crustacean biomass) ($p = 0.89$). Bacterial abundance was also not significantly related to water residence time ($p = 0.22$).

There was a highly significant positive relationship between heterotrophic flagellate abundance and both bacterial abundance and TP (Figure 5.5, Figure 5.6). Flagellate abundance was also significantly related to Chl *a* ($p < 0.001$, $R^2 = 0.50$) and TN ($p < 0.001$, $R^2 = 0.44$). There was no significant relationship between flagellate abundance and DOC ($p = 0.52$) or water residence time ($p = 0.98$).

There were no significant relationships between flagellate abundance and rotifer biomass ($p = 0.25$), (Figure 5.7), crustacean biomass ($p = 0.97$), or total zooplankton biomass (rotifer + crustacean biomass) ($p = 0.26$). Furthermore, there were no significant relationships between the residuals of the flagellate-bacteria regression and any zooplankton variables ($P > 0.05$ for rotifer, crustacean, and total zooplankton biomass). Similarly, there were no correlations of zooplankton with flagellate abundance after controlling for the flagellate-TP relationship ($p > 0.05$ for rotifer, crustacean, and total zooplankton biomass).

5.5 Discussion

In freshwater lakes, heterotrophic bacterial abundance has been positively correlated with Chl *a* and TP concentrations (Bird and Kalff 1984, Currie 1990, Tzaras and Pick 1994). We observed similar results for the temperate rivers of this study. A link between planktonic bacteria and algae was postulated by Bird and Kalff (1984). Bacterial growth was believed to be carbon limited and algae were hypothesized to be the main suppliers of dissolved organic carbon used by bacteria. However, Currie (1990) and Tzaras and Pick (1994) observed that the relationship between bacterial abundance and TP was often stronger (higher R^2) than that between bacterial abundance and Chl *a*. Bacteria can compete effectively with algae for the uptake of phosphorus (Lean and White 1983, Currie and Kalff 1984). Currie (1990) argued that phosphorus directly influences both algal and bacterial abundance.

The positive relationships we observed between bacterial abundance and both Chl *a* and TP (with equal R^2's), indicates that similar processes may occur in temperate rivers, with bacteria responding directly to TP, as well as to organic carbon produced by phytoplankton. Overall, bacterial abundances in our study rivers were similar to abundances recorded by Currie (1990) and Tzaras and Pick (1994) for lakes in the same geographic area.

Though we observed a positive relationship between bacterial abundance and Chl *a*, we did not observe a significant relationship between bacterial abundance and DOC. This result contrasts with many lake studies in which a positive DOC-bacteria relationship has been observed (Tranvik 1989, Currie 1990, Berninger *et al.* 1991, Tzaras

and Pick 1994). A positive relationship between bacterial abundance and DOC may only be evident when a high fraction of total DOC is labile and available for bacterial consumption. In rivers, a large proportion of total DOC may be refractory and unavailable for bacterial use. Most of this non-labile DOC could be allochthonous, of terrestrial origin (Findlay *et al.* 1991). Wetzel and Manny (1977) concluded that 70% of total DOC inputs to streams is refractory to bacterial degradation. In a blackwater river (Ogeechee River, USA), Sabater *et al.* (1993) concluded that there was a good correspondence between low molecular weight (MW) DOC and bacterial abundance. They suggested that low MW fractions of DOC are more readily utilized by bacteria and that medium and high MW DOC fractions are taken up more slowly and may be inhibitory. In the temperate rivers we examined, it is possible that a large proportion of the total DOC was of a high MW, refractory nature. This would preclude any relationship between bacterial abundance and DOC (range in DOC concentration from 4.6 to 13.0 mg L^{-1}). In comparison, the DOC of temperate lakes may be more labile (e.g. low MW algal exudates (Meyer 1990)) and as a result, a DOC-bacteria relationship is often observed (e.g. Tzaras and Pick (1994) in which DOC ranged from 2.4 to 7.6 mg L^{-1}).

Heterotrophic flagellate abundance in our study rivers was of similar magnitude but of wider range in comparison to abundance in lakes, as reported by Tzaras and Pick (1994). A positive relationship was observed between heterotrophic flagellate abundance and bacterial abundance for the 31 rivers. Berninger *et al.* (1991) observed similar results across a range of freshwater lakes and more extreme environments (e.g. glacier fed streams and sediments). The positive correlation between flagellates and bacteria is

indicative of a predator-prey relationship (Berninger *et al.* 1991). Heterotrophic flagellates are the primary consumers of bacteria in freshwaters (Porter *et al.* 1985). However, other studies have concluded that in lakes the relationship between flagellates and bacteria is often weak or eliminated due to metazoan grazing on the flagellates (Gasol and Vaqué 1993, Tzaras and Pick 1994). In the rivers examined, metazoan zooplankton biomass was often very low, as both rotifer and crustacean zooplankton biomass was regulated by water residence time (Basu and Pick 1996, Chapter 4 of the present thesis). This likely means that there was little or no grazing control of flagellates by metazoans. As a result, positive resource control of heterotrophic flagellates by bacteria dominated, as the bacteria-flagellate relationship indicates (Figure 5.5).

Though we observed a positive relationship between flagellates and bacteria, the relationship between flagellates and total phosphorus was of similar strength ($R^2 = 0.46$ for bacteria-flagellates, $R^2 = 0.52$ for TP-flagellates). As Tzaras and Pick (1994) indicate, bacterial turnover can be very rapid and standing stock of bacteria may be a poor indicator of actual supply rates of bacteria to flagellates. Since TP may partially regulate bacterial abundance, TP may represent a less variable measure of bacterial supply rates to heterotrophic flagellates (Tzaras and Pick 1994). Alternatively, the positive relationship between flagellates and TP may result from the protozoans directly responding to nutrients, though this possibility remains little explored (Pace and Funke 1991).

We observed no effect of water residence time on heterotrophic bacterial or flagellate abundances. In contrast, water residence time directly influenced metazoan zooplankton biomass (Basu and Pick 1996, Chapter 4 of the present thesis). As water

residence time increased both rotifer and crustacean zooplankton biomass increased. The relatively long generation time of metazoan zooplankton (days to weeks) makes them more susceptible to advective loss in short residence systems (Pace *et al.* 1992, Basu and Pick 1996). In comparison, the generation times of bacteria and protists are much shorter (hours to days). The average water residence time at the river sites was 7.3 d and the minimum was 3.3 d. There appeared to be sufficient time for bacteria and protozoans to develop in the rivers studied and, as a result, no relationship with residence time was observed.

The limitation of zooplankton development due to short water residence times meant that overall zooplankton biomass in the studied rivers was low (mean = 11.3 $\mu g\ L^{-1}$ dry mass of total zooplankton). In addition, the dominant zooplankton in the rivers were rotifers and small crustaceans (e.g. *Bosmina* sp.). Large cladocerans such as *Daphnia* sp. (which can exert significant grazing pressure on flagellates, Pace and Funke 1991) were much less abundant (Basu and Pick 1996, Chapter 4 of the present thesis). The lack of any relationships between zooplankton biomass and either flagellate or bacterial abundance may be due to these low levels of zooplankton biomass and the dominance of small taxa. Zooplankton biomass, whether rotifers or crustaceans, appeared to be too limited to significantly affect flagellate or bacterial abundances.

As mentioned, this contrasts with studies conducted on lakes and estuaries in which metazoan zooplankton grazing was observed to have significant effects on flagellate and bacterial abundances (Dolan and Gallegos 1991, Pace and Funke 1991, Gasol and Vaqué 1993). In lakes, the microbial loop may be coupled to the classical food

web, with metazoan grazing of flagellates and bacteria serving as the link. In rivers, however, with low zooplankton abundance, there may be little or possibly no transfer of energy from the planktonic microbial food web to planktonic metazoans. Instead, the microbial loop in rivers may support benthic metazoan production and nutrient remineraliztion (Meyer 1990). At present, the study of river food webs lags a decade behind that of lake food webs. It is hoped that ongoing research will help determine the significance of the microbial loop to the overall structure of river food webs.

Table 5.1. River locations with dissolved organic carbon (DOC), heterotrophic bacteria, and heterotrophic flagellate concentrations for July 1994 sampling. (S) denotes rivers located on the Canadian Shield, (L) denotes rivers located in the Great Lakes/ St. Lawrence Lowlands. Further physical, chemical and biotic variables can be found in Table 4.1.

river	latitude north	longitude west	DOC mg L^{-1}	bacteria cells ml^{-1} ($X 10^6$)	flagellates cells ml^{-1} ($X 10^3$)
Madawaska (S)	45° 30'	77° 10'	6.0	3.05	3.10
Bonnechere (S)	45° 30'	76° 50'	6.5	3.80	3.95
Mississippi (S/L)	45° 20'	76° 15'	7.0	3.43	4.95
Rouge (S)	45° 50'	74° 40'	5.8	3.56	1.26
du Lievre (S)	45° 40'	75° 35'	5.7	1.80	1.55
South Nation (L)	45° 20'	75° 5'	12.6	3.95	8.94
Gatineau (S)	45° 40'	75° 55'	6.5	2.12	2.01
Picanoc (S)	45° 43'	75° 55'	5.3	3.24	1.58
Magnetewan (S)	45° 46'	80° 35'	5.1	2.95	2.05
French (S)	46° 2'	80° 43'	4.8	3.18	2.33
Mattawa (S)	46° 20'	78° 45'	5.5	3.01	3.04
Temagami (S)	46° 38'	80° 8'	5.8	2.25	1.55
Sturgeon (S)	46° 26'	79° 58'	5.3	2.86	2.40
Amable (S)	46° 20'	77° 15'	5.5	3.42	2.01
Veuve (S)	46° 26'	80° 10'	13.0	5.14	2.51
Trent (L)	44° 20'	77° 55'	6.7	7.69	2.77
Napanee (L)	44° 20'	76° 50'	9.9	4.33	1.18
Salmon (L)	44° 15'	77° 5'	8.4	3.66	1.21
Moira (L)	44° 20'	77° 20'	8.2	3.21	3.03
Burnt (S/L)	44° 30'	78° 42'	5.5	3.57	4.10
Otonabee (S/L)	44° 25'	78° 15'	6.1	5.88	3.88
Skootamata (S/L)	44° 30'	77° 15'	8.6	3.16	1.60
Saugeen (L)	44° 12'	81° 11'	6.0	4.67	3.33
Ausable (L)	43° 3'	81° 38'	4.6	7.93	17.40
North Thames (L)	43° 14'	81° 12'	5.4	9.92	11.50
Nith (L)	43° 25'	80° 43'	5.8	9.10	13.90
Thames (L)	42° 51'	81° 25'	5.8	7.47	7.70
Conestogo (L)	43° 36'	80° 40'	5.9	5.17	1.47
Maitland (L)	43° 51'	81° 15'	6.1	2.66	1.42
Grand (L)	43° 6'	80° 11'	5.5	7.58	4.66
Rideau (L)	45° 27'	75° 42'	6.7	4.44	3.80

Figure 5.1. Significant relationship between total phosphorus concentration and heterotrophic bacterial abundance for rivers sampled during July 1994 (log bacterial abundance = 6.15 + 0.36 log TP). Dashed lines represent 95% confidence intervals.

Figure 5.1

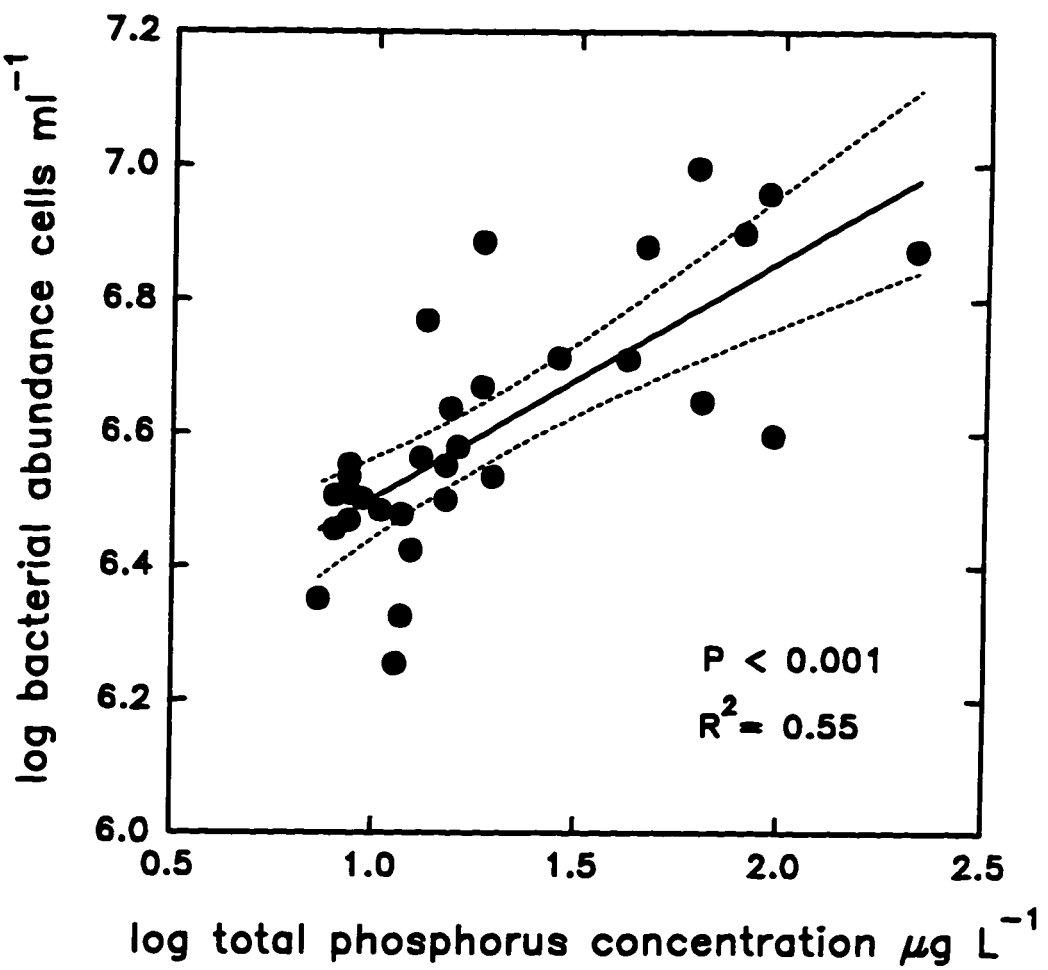

7.2
7.0
6.8
6.6
6.4
6.2
6.0
0.5
1.0
1.5
2.0
2.5
log bacterial abundance cells ml^{-1}
log total phosphorus concentration μg L^{-1}
P < 0.001
R^2= 0.55

Figure 5.2. Significant relationship between Chl *a* concentration and heterotrophic bacterial abundance for rivers sampled during July 1994 (log bacterial abundance = 6.31 + 0.43 log Chl *a*). Dashed lines represent 95% confidence intervals.

Figure 5.2

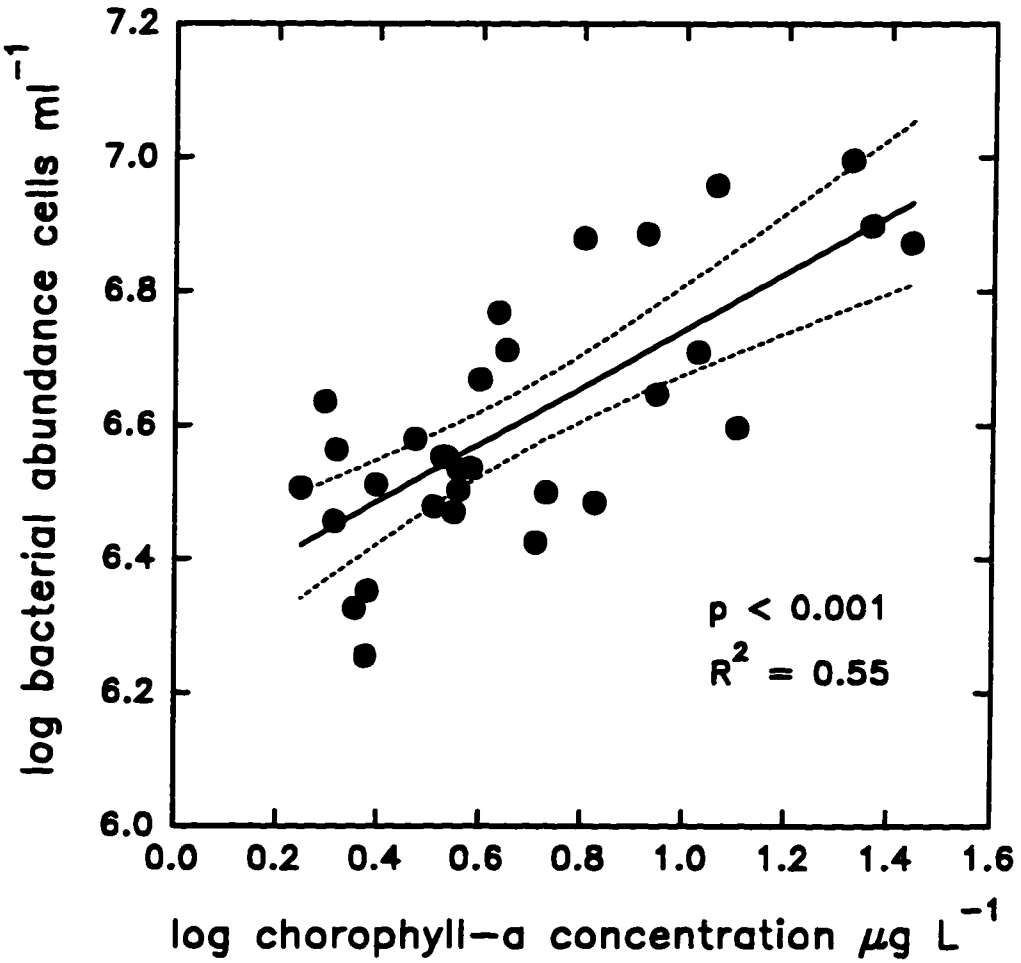

7.2
7.0
6.8
6.6
6.4
6.2
6.0
log bacterial abundance cells ml^{-1}
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
log chorophyll–a concentration μg L^{-1}
p < 0.001
R^2 = 0.55

Figure 5.3. Scatterplot demonstrating no relationship between DOC concentration and heterotrophic bacterial abundance for rivers sampled during July 1994.

Figure 5.3

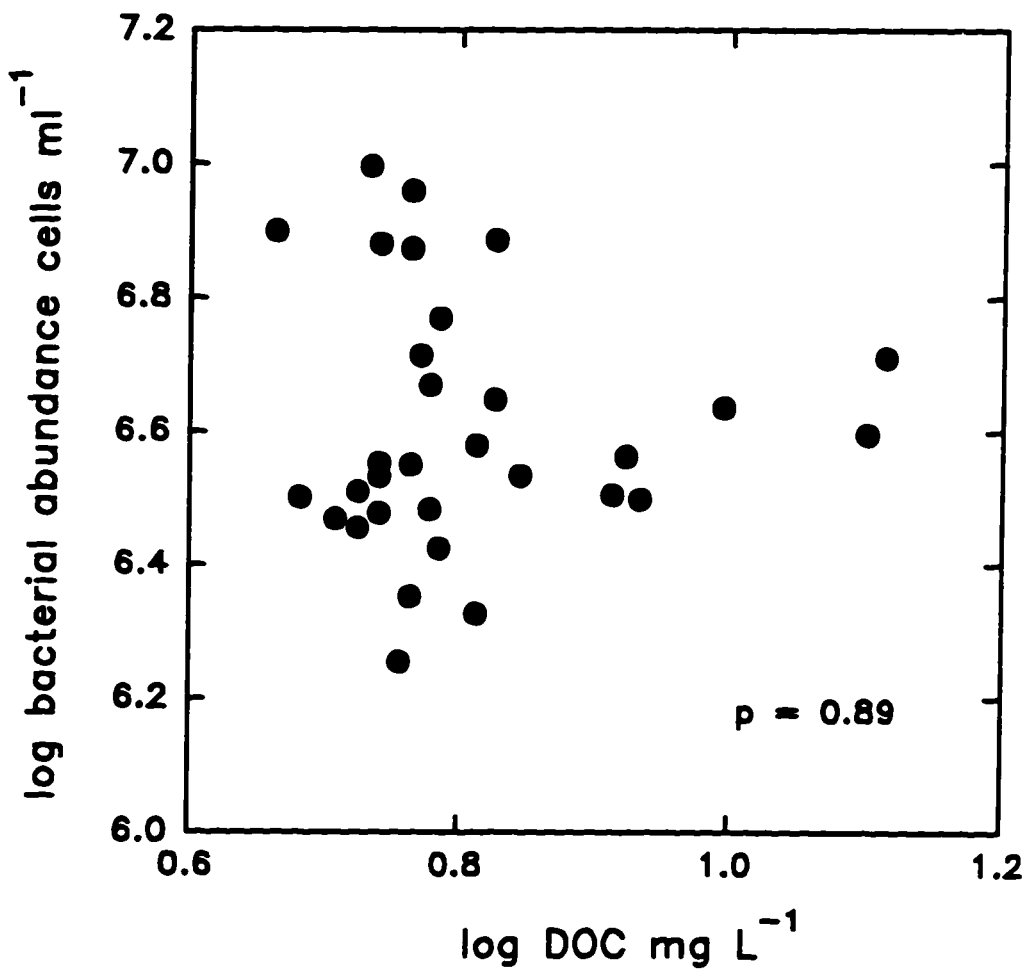

7.2
7.0
6.8
6.6
6.4
6.2
6.0
0.6
0.8
1.0
1.2
log bacterial abundance cells ml^{-1}
log DOC mg L^{-1}
p = 0.89

Figure 5.4. Scatterplot demonstrating no relationship between rotifer biomass and heterotrophic bacterial abundance for rivers sampled during July 1994.

Figure 5.4

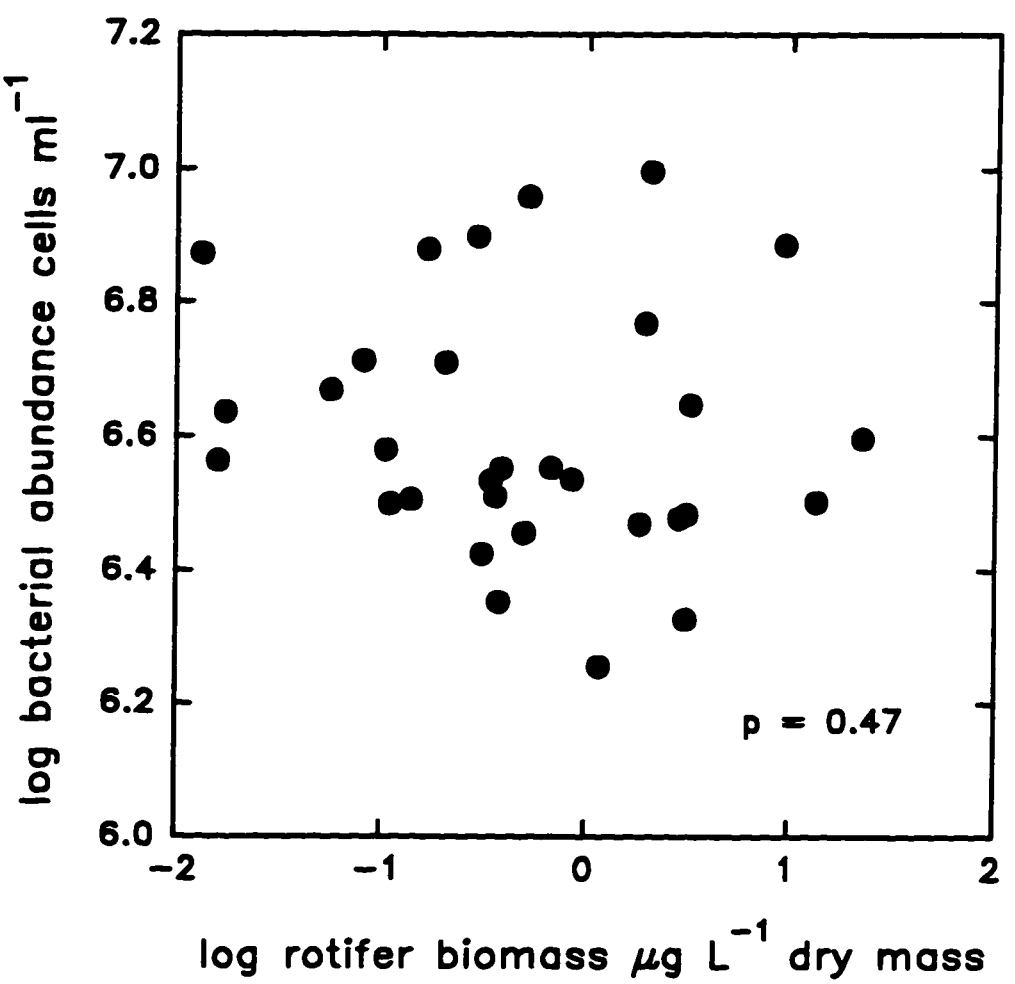

7.2
7.0
6.8
6.6
6.4
6.2
6.0
log bacterial abundance cells ml^{-1}
−2
−1
0
1
2
log rotifer biomass μg L^{-1} dry mass
p = 0.47

Figure 5.5. Significant relationship between heterotrophic bacterial abundance and heterotrophic flagellate abundance for rivers sampled during July 1994 (log flagellate abundance = -3.98 + 1.13 log bacterial abundance). Dashed lines represent 95% confidence intervals.

Figure 5.5

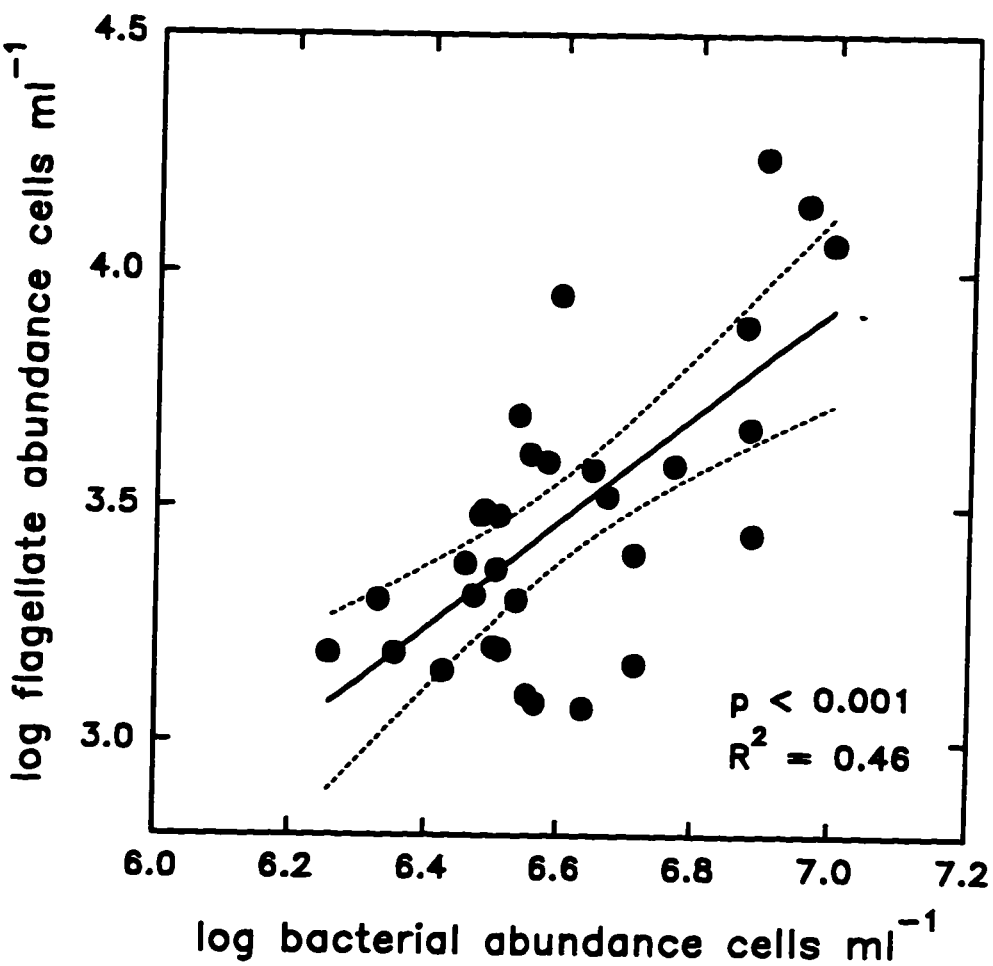

4.5
4.0
3.5
3.0
log flagellate abundance cells ml^{-1}
6.0
6.2
6.4
6.6
6.8
7.0
7.2
log bacterial abundance cells ml^{-1}
p < 0.001
R^2 = 0.46

Figure 5.6. Significant relationship between total phosphorus concentration and heterotrophic flagellate abundance for rivers sampled during July 1994 (log flagellate abundance = 2.73 + 0.58 log TP). Dashed lines represent 95% confidence intervals.

Figure 5.6

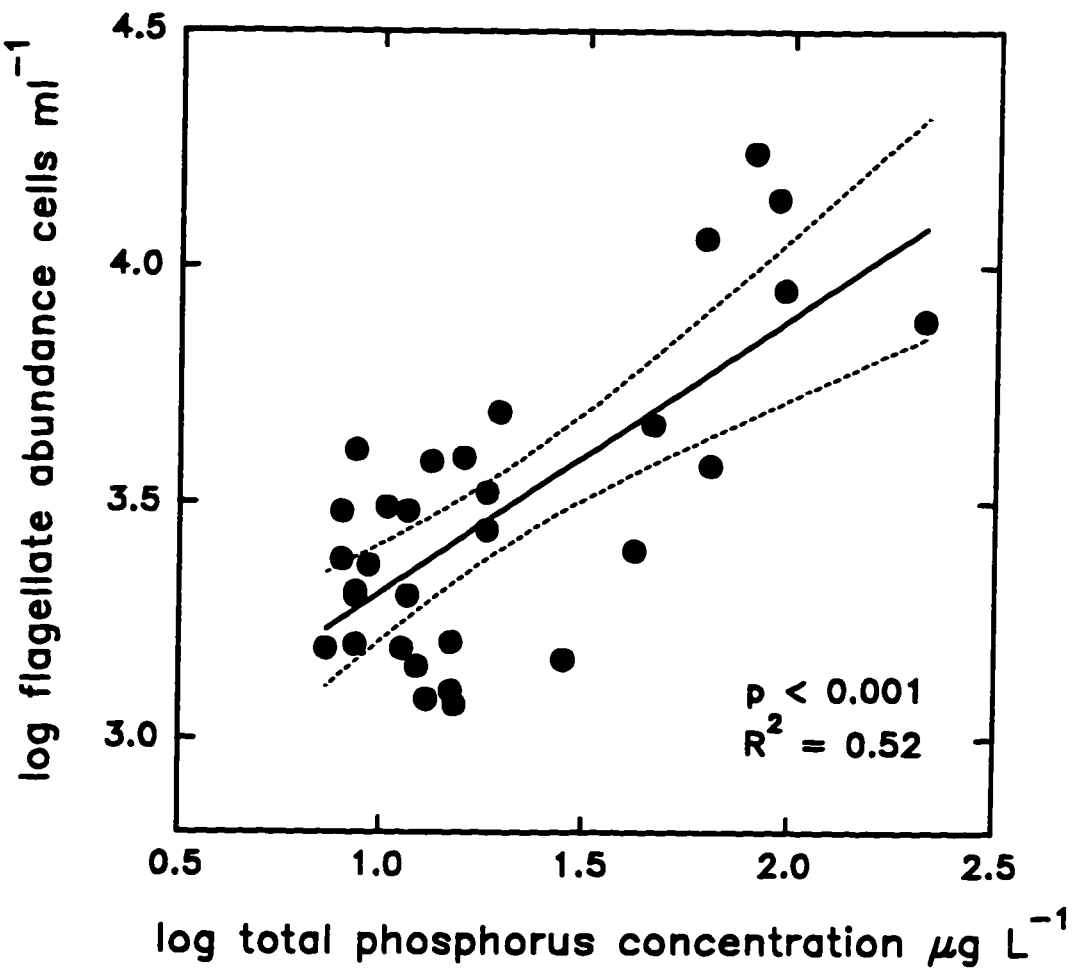
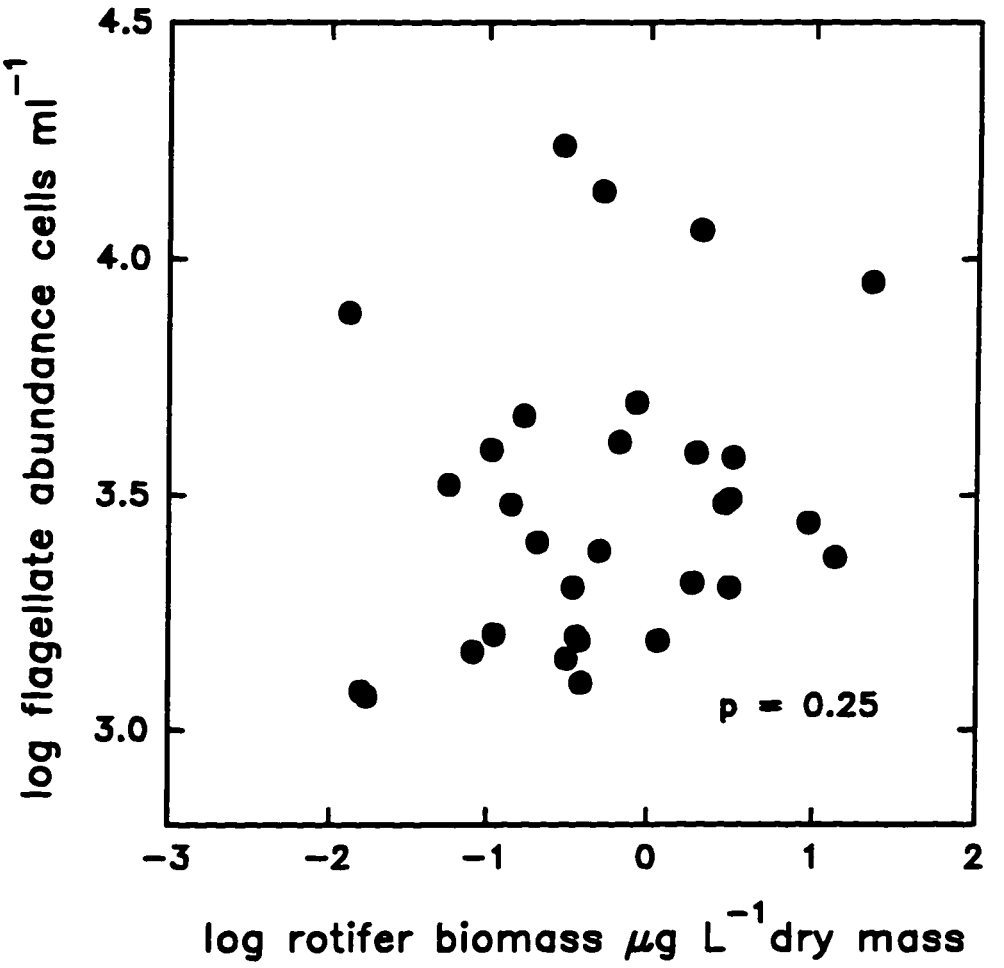

4.5
4.0
3.5
3.0
log flagellate abundance cells ml^{-1}
0.5
1.0
1.5
2.0
2.5
log total phosphorus concentration μg L^{-1}
p < 0.001
R^2 = 0.52

Figure 5.7. Scatterplot demonstrating no relationship between rotifer biomass and heterotrophic flagellate abundance for rivers sampled during July 1994.

Figure 5.7


4.5
4.0
3.5
3.0
log flagellate abundance cells ml^{-1}
p = 0.25
−3
−2
−1
0
1
2
log rotifer biomass μg L^{-1} dry mass

Chapter 6

Rivers Versus Lakes: Similarities and Differences

6.1 Introduction

This final chapter serves to summarize and unify major results by comparing what has been learned about plankton in temperate, lowland rivers to what is known about plankton in temperate, dimictic lakes. Such an approach must necessarily generalize about rivers and lakes and it should be understood that not all rivers or lakes conform to these generalizations. Tropical and arctic rivers and lakes, as well as steeply sloping mountain rivers and alpine lakes are likely exceptions. Though specific details are lost when such generalizations are made, the advantage is a more broad applicability of results.

Clearly, not all aspects of planktonic development in either rivers or lakes can be discussed in a single thesis, and some aspects still remain unclear. Therefore, this summary is not exhaustive, but instead focuses on results derived from the present research and relevant literature. For the following discussion the "typical" river is a north temperate, mid to large size, lowland river, as studied in previous chapters. Such rivers tend to be slow flowing and have gradients < 1% (river gradient being the change in elevation divided by river length). The "typical" lake is a north temperate, dimictic lake, similar to Rideau, Gatineau or Muskoka region lakes.

Prior to comparing and contrasting planktonic processes in temperate rivers and lakes, the hydrodynamic, morphological, and chemical characteristics that distinguish rivers from lakes will briefly be reviewed (Table 6.1). This background is required in order to better appreciate the differing conditions under which planktonic development and interactions occur. In a format similar to Ryder and Pesendorfer (1989), this chapter

was written not only as a review, but for heuristic purposes as well. In the final sections, potential management implications and suggestions for areas requiring further research are offered.

6.2 Rivers Versus Lakes: Hydrodynamic, Morphological and Chemical Characteristics

The question "What distinguishes rivers from lakes?" has been discussed at length in classical limnology (Margalef 1960). Soballe and Kimmel (1987) viewed the lotic-lentic distinction as arbitrary, instead suggesting that aquatic systems occupy positions along a continuum ordered by water residence time. Reynolds (1994) suggested that lakes are "special cases of flowing drainage systems in which hydraulic residence time is protracted". Nonetheless, intuition would suggest that the movement of water (flow), what force initiates that movement, and the effects of this movement on residence time, are the fundamental characteristics that separate rivers from lakes (Ryder and Pesendorfer 1989).

Therefore, from a hydrodynamic perspective, rivers can be characterized by the dominance of continuous, horizontal, downstream movement of water initiated by the force of gravity. As indicated in previous chapters, this movement of water results in rivers having relatively short water residence times. In contrast, the dominant water movement in lakes is vertical, circulatory and wind induced (though vertical gravitationally induced water movements occur during spring and fall turnover). Unlike rivers, the gravitationally induced, horizontal flow of water through a lake (i.e. inflow to

outflow) is much less significant than wind-driven circulation. Accordingly, lakes have relatively long water residence times (Table 6.1).

Morphological characteristics also distinguish rivers from lakes (Ryder and Pesendorfer 1989). Rivers tend to be long and linear with low width : shoreline length ratios and high watershed : surface area ratios. Lakes are generally short and oval with correspondingly high width : shoreline length ratios and low watershed : surface area ratios. In addition, the channel shape of rivers changes spatially. The channel generally widens and deepens in a downstream direction, though shallow and deep reaches are often interspersed (i.e. rapids and pools). In contrast, the basin morphometry of lakes is more stable (i.e. pan or cup shaped) and lakes tend to be deeper than rivers (Table 6.1) (Ryder and Pesendorfer 1989).

The movement of water, variable channel morphology, and shallow depths combine to prevent thermal stratification in rivers (Chapters 2 and 3). As a result, the vertical chemical profile of rivers tends to be homogenous and oxygen content is usually high (except in rivers receiving high loadings of nutrients or organic matter)(Ryder and Pesendorfer 1989). On the other hand, thermal stratification is a characteristic feature of temperate dimictic lakes and can result in vertical chemical stratification and more variable oxygen concentrations (Wetzel 1983) (Table 6.1).

Overall, nutrient concentrations (nitrogen and phosphorus) and total dissolved solids are higher in rivers than in lakes and vary horizontally and temporally, with a tendency to increase in a downstream direction (Moss *et al.* 1984, Garnier *et al.* 1995, Chapters 3 and 4). In lakes, nutrients and total dissolved solids vary temporally (e.g. high

concentrations during spring and fall turnover) (Wetzel 1983). In addition, a higher fraction of total phosphorus in rivers may be soluble reactive phosphorus (SRP). SRP concentration in rivers is often measurable (> 5.0 $\mu g\ L^{-1}$), whereas in surface waters of lakes during summer stratification, SRP concentration is usually below detection limits (Wetzel 1983). As a result, more total phosphorus may be "bioavailable" in rivers when compared to lakes. Rivers tend to be more turbid than lakes and a higher fraction of dissolved organic carbon in rivers may be of allochthonous, terrestrial origin (Chapter 5). The higher nutrient concentrations, increased turbidity and dominance of allochthonous dissolved organic carbon is due to the higher degree of contact between rivers and their watershed terrestrial sources in comparison to lakes (reflected in the watershed : surface area ratio mentioned above) (Table 6.1) (Moss *et al.* 1984, Sabater *et al.* 1993).

Clearly, there are numerous physical and chemical differences between rivers and lakes. Therefore, it seems reasonable to assume that planktonic development and interactions will also differ between the two ecosystems. As outlined in the following section, results of this thesis identify some of these differences in planktonic development, but also demonstrate important similarities between rivers and lakes.

6.3 Rivers Versus Lakes: Planktonic Biota

Phytoplankton can be abundant in eutrophic rivers (> 15 $\mu g\ L^{-1}$ of Chl *a*) and river phytoplankton biomass is most strongly related to nutrient concentrations (total phosphorus) (Chapters 2, 3 and 4). This is similar to north temperate lakes (Table 6.2). In summer, phytoplankton biomass in rivers is not related to water residence time possibly

due to the short generation time of phytoplankton (hours to days) (Chapter 4). Light does not appear to limit phytoplankton biomass in rivers due to shallow depths and extensive vertical mixing of the water column (Chapters 3 and 4). River phytoplankton also exhibits extensive longitudinal heterogeneity and, in general, biomass increases in a downstream direction due to both increasing nutrient concentrations and time for development (Chapters 2 and 3). The size structure of the phytoplankton community may also change longitudinally, with a gradual shift from small cells to larger cells with downstream travel (Yang *et al.* in press; Table 6.2).

Seasonally, it is speculated that a spring bloom of phytoplankton occurs in rivers once discharge conditions are favorable (Reynolds 1988). Through the summer and fall phytoplankton populations can maintain high densities due to continually high nutrient concentrations and low, stable discharges (Figure 2.2, 3.2). Only in late fall may river phytoplankton populations decrease due to increases in river discharge. In contrast, the spring bloom of phytoplankton in a typical mesotrophic lake is followed by an early summer clear water phase (often caused by sedimentation, zooplankton grazing and silica limitation of diatom growth). Throughout the remainder of the summer, phytoplankton in lakes slowly increases in density until the fall bloom which, like the spring bloom, is associated with increased nutrient concentrations during turnover (Wetzel 1983; Table 6.2).

Phytoplankton biomass is little affected by zooplankton grazing in rivers, but may be negatively impacted by benthic filtration. The lack of thermal stratification and shallow, well-mixed waters may allow for a high degree of contact between benthic filter

feeders and planktonic food particles (Chapter 3). In contrast, lake phytoplankton can be extensively grazed by zooplankton and the effect of benthic filtration will be lessened due to the presence of thermal stratification and greater depths (Table 6.2).

In general, zooplankton are sparse in rivers (usually < 20 $\mu g\ L^{-1}$ dry mass) and small taxa dominate the communities (e.g. rotifers, bosminids) (Chapter 4). In the downstream reaches of larger rivers, however, large taxa may increase in density (de Ruyter van Steveninck *et al.* 1992). In lakes, zooplankton are abundant (> 50 $\mu g\ L^{-1}$ dry mass) and both large (e.g. *Daphnia* sp.) and small taxa are present (Table 6.2). Due to longer generation times (days to weeks), zooplankton biomass in rivers is primarily related to water residence time rather than resources (Chl *a* or TP) (Chapter 4). In contrast, zooplankton in lakes is primarily related to resources such as Chl *a* or TP (Table 6.2). Zooplankton appear less tightly coupled to phytoplankton in rivers as there is no negative relationship between zooplankton and phytoplankton and less of a resource effect of phytoplankton on zooplankton (Chapters 3 and 4). In lakes, there is a tight coupling of phytoplankton and zooplankton (i.e. grazing and resource effects *sensu* McQueen *et al.* 1986). As with phytoplankton, zooplankton in shallow, well-mixed rivers may be negatively impacted by benthic feeders (Chapter 3) whereas in lakes this impact should be less significant, again due to thermal stratification and greater depths (Table 6.2).

Heterotrophic bacteria are abundant in both rivers and lakes (approximately 4.0 X 10^6 cells ml^{-1}) and bacteria are most strongly related to nutrient concentrations (TP) and Chl *a* in both system types (Chapter 5). In lakes, bacterial abundance can also be

positively related to dissolved organic carbon which is of a labile nature (algal exudates). In rivers, a bacteria-DOC relationship is lacking possibly due to the more refractory nature of river DOC, the majority of which may be of allochthonous, terrestrial origin (Chapter 5).

Heterotrophic flagellates are also abundant in both rivers and lakes (approximately 4.0 X 10^3 cells ml^{-1}) and are most strongly related to bacterial abundance and TP in both system types (Chapter 5). In lakes both heterotrophic bacterial and flagellate abundances can be negatively affected by zooplankton grazing, whereas in rivers zooplankton biomass is too sparse to affect microbial abundances (Chapter 5). Instead, benthic grazers may be significant consumers of microbial biomass in rivers (Meyer 1990). In lakes the microbial food web can supply energy to the classical food web via metazoan zooplankton grazing. In rivers the microbial food web may supply energy to support benthic rather than planktonic secondary production (Table 6.2).

6.4 Management Implications

Research focusing on river plankton has clear management implications. Abundances and processes of planktonic organisms at the base level of river food webs have effects on water quality parameters as well as higher trophic levels.

Results indicating which environmental factors may regulate planktonic development in rivers are important to organizations involved in the maintenance of a high level of river water quality (e.g. Regional Municipality of Ottawa-Carleton (RMOC), Rideau Valley Conservation Authority (RVCA)). Such organizations are

responsible for mitigating the effects of excessive algal or bacterial growth and must have information regarding possible regulation of planktonic development. For example, eutrophication and excessive algal development in the rivers Rhine and Meuse has led to decreased oxygen concentrations and associated negative effects on fish populations. Efforts are currently underway to "ecologically rehabilitate" the Rhine and Meuse by reducing agricultural runoff (i.e. reducing phosphorus input) in order to reduce phytoplankton development (Admiraal *et al.* 1993). Similarly, results of the present thesis can be linked to land-use and phosphorus export models developed by the RMOC and RVCA to predict changes in phytoplankton biomass which may occur as a result of changes in land-use. Results suggest that current efforts to reduce phosphorus inputs to the Rideau River should reduce phytoplankton densities. Furthermore, results support the contention that benthic filter feeders (specifically *D. polymorpha*) can have a large impact on phytoplankton densities. The potential use of *D. polymorpha* in water quality management has been suggested (Reeders and Bij de Vaate 1990), however, there are obvious concerns that the introduction of this exotic can change fundamental characteristics of aquatic ecosystems (e.g. shift from planktonic to benthic primary production and reductions in zooplankton and native bivalve abundance).

In addition to having relevance to water quality issues, research conducted on river plankton also has relevance to fisheries management. A river with high fish production is valued for recreational opportunities in western society. More importantly, the primary source of protein for people in many developing countries is fish produced in

rivers (e.g. Volta River, Amazon River) (Araujo-Lima *et al.* 1986, Gopal and Wetzel 1995).

Randall *et al.* (1995) concluded that rivers have higher fish production and biomass than lakes. Planktonic processes may be associated with this higher productivity. Higher nutrient concentrations (or bioavailable nutrient concentrations) may lead to increased phytoplankton and bacterioplankton productivity in rivers. This planktonic production may be a food source directly available to fish. Araujo-Lima *et al.* (1986) observed that a large fraction of fish biomass was derived directly from phytoplankton in the Amazon River. Alternatively, high autotrophic and heterotrophic plankton production may support high levels of benthic secondary production (Meyer 1990), which, in turn, may be a major food source for fishes. Therefore, either directly or indirectly, planktonic abundances and processes in rivers may have management implications for fisheries production.

6.5 Future Research and Final Word

This thesis has addressed certain fundamental questions concerning river plankton. As a result, a clearer picture of planktonic development and processes in rivers has emerged. However, many areas require further research in order to better elucidate the structure of river food webs.

The potential importance of planktonic-benthic coupling has been suggested. Benthic filter feeders may significantly feed on planktonic biota in large rivers and high levels of benthic production may be supported by high levels of planktonic production.

The planktonic-benthic couple may represent an important energy link in river food webs, though this possibility remains little studied.

An examination of the effect of river inflow on lake ecosystems is another area worthy of further research. The lotic to lentic transition zone has often been overlooked despite the possible importance of rivers in delivering nutrients and biota to lake ecosystems. Similarly, the processes that occur as lake water flows into rivers (i.e. lentic to lotic transition) remain understudied.

Littoral macrophytes, benthic algae and phytoplankton contribute to overall primary production in rivers and represent the energy source for higher trophic levels (e.g. aquatic insects, fish). It remains to be determined the relative contribution of each of these three primary producing communities to total river primary production. How primary production is partitioned in rivers could have a large influence on higher trophic levels and the overall structure of river food webs.

The effect of impoundment on river plankton development also remains little studied. When a dam is constructed on a river, conditions upstream become "more lentic" whereas conditions downstream remain lotic. Changes to planktonic food web structure may occur and these changes could have impacts on water quality as well as higher trophic levels. The ecological effects of dam construction have only recently received attention and potential changes to planktonic communities remain little known.

Finally, there is debate as to whether large rivers are autotrophic or heterotrophic systems. Due to large inputs of allochthonous organic matter, and often turbid conditions, rivers may be systems in which heterotrophic bacterial production contributes a

significant amount of energy to higher trophic levels. The extent of heterotrophic production in rivers and how this compares with primary production also requires further study.

In conclusion, there remain many opportunities for fruitful research in river ecology. Difficulties arise, however, because river ecosystems are distinct. Viewing rivers as either "very large streams" or "flowing lakes" appears too constrictive. The river ecologist must appreciate the distinctive nature of rivers and must be knowledgeable about various aspects of stream ecology, benthic ecology, plankton ecology, limnology, riparian ecology and hydrology. Only with such an holistic view can the integrity of river ecosystems be maintained or recaptured.

Table 6.1. Hydrodynamic, morphological and chemical characteristics of temperate rivers and lakes (following Ryder and Pesendorfer 1989).

Characteristic	Rivers	Lakes
dominant water movement	horizontal, downstream	vertical, circulatory
force initiating movement	gravity	wind induced
water residence time	short (days)	long (years)
shape	long, linear	short, oval
width : shoreline length	low	high
watershed : surface area	high	low
channel or basin shape	changes spatially	stable
mean depth	shallow	deep
thermal stratification	no	yes
vertical chemical profile	homogenous	stratified
oxygen content	high	variable
nutrient concentrations	high, increase downstream	low, temporally variable
turbidity	high	low
dissolved organic carbon	high, allochthonous	variable, autochthonous

Table 6.2. Characteristics of planktonic biota of temperate rivers and lakes.

Community	Rivers	Lakes
phytoplankton	- can be abundant in eutrophic, rivers (> 15 $\mu g\ L^{-1}$ Chl *a*) - related primarily to TP - downstream increases in biomass and cell size - seasonal changes in biomass due to changes in discharge conditions - little affected by zooplankton - may be greatly impacted by benthic filtration	- can be abundant in eutrophic lakes (> 15 $\mu g\ L^{-1}$ Chl *a*) - related primarily to TP - seasonal changes in biomass and cell size due to changes in nutrients and mixing regimes - can be extensively grazed by zooplankton (trophic couple) - lesser effect of benthic filtration due to increased depths, stratification
zooplankton	- sparse (< 20 $\mu g\ L^{-1}$ dry mass) - small taxa dominate (rotifers, bosminids) - large taxa rare - downstream increases in biomass - related primarily to water residence time rather than resources - no significant grazing effect on phytoplankton - may be greatly impacted by benthic filtration	- abundant in meso, eutrophic lakes (> 50 $\mu g\ L^{-1}$ dry mass) - both large and small taxa - related to resources (TP, Chl *a*) - significant grazing effect - lesser effect of benthic filtration due to increased depths, stratification

Table 6.2 continued.

Community	Rivers	Lakes
heterotrophic bacteria	- abundant (4.0×10^6 ml^{-1}) - related to nutrients, Chl *a* - not related to refractory DOC - not affected by zooplankton grazing - impact of benthic filtration may be significant	- abundant (4.0×10^6 ml^{-1}) - related to nutrients, Chl *a* - related to labile DOC - can be impacted by zooplankton grazing - impact of benthic filtration less significant due to depths, stratification
heterotrophic flagellates	- abundant (4.0×10^3 ml^{-1}) - related to bacteria and nutrients (TP) - not affected by zooplankton grazing - impact of benthic filtration may be significant	- abundant (4.0×10^3 ml^{-1}) - related to bacteria and nutrients (TP) - can be impacted by zooplankton grazing - impact of benthic filtration less significant due to depths, stratification

References

Admiraal, W., G. van der Velde, H. Smit and W.G. Cazemier. 1993. The rivers Rhine and Meuse in the Netherlands: present state and signs of ecological recovery. *Hydrobiologia*, **265**: 97-128.

Allen, J.D. 1995. *Stream ecology: structure and function of running waters*. Chapman Press, London, U.K.

Alpine, A.E. and J.E. Cloern. 1988. Phytoplankton growth rates in a light limited environment, San Francisco Bay. *Mar. Ecol. Prog. Ser.*, **44:** 167-173.

Araujo-Lima, C.A., B.R. Forsberg, R. Victoria and L. Martinelli. 1986. Energy sources for detritivorous fishes in the Amazon. *Science*, **234:** 1256-1258.

Azam, F., T. Fenchel, J.G. Field, J.S. Gray, L.A. Meyer-Reil and F. Thingstad. 1983. The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**: 257-263.

Baker, A.L. and K.K. Baker. 1979. Effects of temperature and current discharge on the concentration and photosynthetic activity of phytoplankton in the upper Mississippi River. *Freshwater Biol.*, **9:** 191-198.

Basu, B.K. and F.R. Pick. 1995. Longitudinal and seasonal development of planktonic chlorophyll *a* in the Rideau River, Ontario. *Can. J. Fish. Aquat. Sci.*, **52**: 804-815.

Basu, B.K. and F.R. Pick. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnol. Oceanogr.*, 41: 1572-1577.

Berninger, U.G., B.J. Finlay and P. Kuuppo-Leinikki. 1991. Protozoan control of bacterial abundances in freshwater. *Limnol. Oceanogr.*, **36**: 139-147.

Bird, D.F. and J. Kalff. 1984. Empirical relationships between bacterial abundance and chlorphyll concentration in fresh and marine waters. *Can. J. Fish. Aquat. Sci.*, **41**: 1015-1023.

Bothar, A. and K.T. Kiss. 1990. Phytoplankton and zooplankton relationships in the eutrophicated River Danube. *Hydrobiologia*, **191**: 165-171.

Bottrell, H.H., A. Duncan, Z.M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larson and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.*, **24**: 419-456.

Bunt, C.M., H.J. MacIsaac and W.G. Sprules. 1993. Pumping rates and projected filtering impacts of juvenile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Can. J. Fish. Aquat. Sci.*, **50**: 1017-1022.

Burnison, B.K. 1980. Modified dimethyl sulfoxide (DMSO) extraction for chlorophyll analysis of phytoplankton. *Can. J. Fish. Aquat. Sci.*, **37**: 729-733.

Canfield, D.E. Jr., 1983. Prediction of chlorophyll *a* concentrations in Florida lakes. The importance of phosphorus and nitrogen. *Water Resour. Bull.*, **19**: 255-262.

Canfield, D.E. Jr. and C.E. Watkins. 1984. Relationships between zooplankton abundance and chlorophyll *a* concentration in Florida lakes. *J. Freshwater Ecol.*, **2**: 335-344.

Capblancq, J. and H. Descamps. 1978. Dynamics of the phytoplankton in the River Lot. *Verh. Int. Ver. Theor. Angew. Limnol.*, **22**: 1479-1484.

Carlough, L.A. and J.L. Meyer. 1990. Rates of protozoan bactivory in three habitats of a southeastern blackwater river. *J. N. Am. Benthol. Soc.*, **9**: 45-53.

Chessman, B.C. 1985. Phytoplankton of the La Trobe River Victoria. *Aust. J. Mar. Freshw. Res.*, **36**: 115-122.

Cole, J.J., S. Findlay and M.L. Pace. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar. Ecol. Prog. Ser.*, **43**: 1-10.

Cole, J.J., N.F. Caraco and B.L. Peierls. 1992. Can phytoplankton maintain a positive carbon balance in a turbid freshwater, tidal estuary? *Limnol. Oceanogr.*, **37**: 1608-1617.

Currie, D.J. and J. Kalff. 1984. Can bacteria outcompete phytoplankton for phosphorus? A chemostat test. *Microb. Ecol.*, **10**: 205-216.

Currie, D.J. 1990. Large-scale variability and interactions among phytoplankton, bacterioplankton and phosphorus. *Limnol. Oceanogr.*, **35**: 1437-1455.

Davidson, T.K. 1990. *Rideau valley rural beaches program water quality study.* Rideau Valley Conservation Authority, Manotick, ONT, Canada.

Dauta, A. 1986. Modélisation du développement du phytoplancton dans une rivière canalisée eutrophe: le Lot (France). *Annls. Limnol.*, **22**: 119-132.

de Ruyter van Steveninck, E.D., B. van Zanten and W. Admiraal. 1990a. Phases in the development of riverine plankton: examples from the rivers Rhine and Meuse. *Hydrobiol. Bull.*, **24**: 47-55.

de Ruyter van Steveninck, E.D., B. van Zanten and W. Admiraal. 1990b. Changes in plankton communities in regulated reaches of the lower River Rhine. *Regul. Rivers Res. Manage.*, **5**: 67-75.

de Ruyter van Steveninck, E.D., W. Admiraal, L. Breebaart, G.M.J. Tubbing and B. van Zanten. 1992. Plankton in the River Rhine: structural and functional changes observed during downstream transport. *J. Plankton Res.*, **14:** 1351-1368.

Descy, J.P. 1987. Phytoplankton composition and dynamics in the River Meuse (Belgium). *Arch. Hydrobiol.*, **78**: 225-245.

Descy, J.P., P. Servais, J.S. Smitz, G. Billen and E. Everbecq. 1987. Phytoplankton biomass and production in the River Meuse (Belgium). *Water Res.*, **21:** 1557-1566.

Dillon, P.J. and F.H. Rigler. 1974. The phosphorus chlorophyll relationship in lakes. *Limnol. Oceanogr.*, **28**: 792-795.

Dolan, J.R. and C.L. Gallegos. 1991. Trophic coupling of rotifers, microflagellates, and bacteria during fall months in the Rhode River estuary. *Mar. Ecol. Prog. Ser.*, **77**: 147-156.

Dumont, H.J., I. Van de Velde and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, **19**: 75-97.

Edwards, R.T. and J.L. Meyer. 1986. Production and turnover of planktonic bacteria in two southeastern blackwater rivers. *Appl. Environ. Microbiol.*, **52:** 1317-1323.

Edwards, R.T. 1987. Sestonic bacteria as a food source for filtering invertebrates in two southeastern blackwater rivers. *Limnol. Oceanogr.*, **32:** 221-234.

Effler, S.W., C.M. Brooks, K. Whitehead, B. Wagner, S.M. Doerr, M. Perkins, C.A. Siegfried, L. Walrath and R.P. Canale. 1996. Impact of zebra mussel invasion on river water quality. *Water Environ. Res.*, **68**: 205-214.

Environment Canada. 1979. *Analytical methods manual*. Ottawa, ONT. Canada. Inland Waters Directorate, Water Quality Branch. 340 p.

Fenchel, T. 1986. The ecology of heterotrophic microflagellates. *Adv. Microb. Ecol.*, **9**: 57-97.

Ferrari, I., A. Farabegoli and R. Mazzoni. 1989. Abundance and diversity of planktonic rotifers in the Po River. *Hydrobiologia*, **186**: 201-208.

Findlay, S., M.L. Pace, D. Lints, J.J. Cole, N.F. Caraco, and B. Pierls. 1991. Weak coupling of bacterial and algal production in a heterotrophic ecosystem: The Hudson River estuary. *Limnol. Oceanogr.*, **36**: 268-278.

Fisher, S.W., D.C. Gossiaux, K.A. Bruner and P.F. Landrum. 1993. Investigations of the toxicokinetics of hydrophobic contaminants in the zebra mussel (*Dreissena polymorpha*). In Nalepa, T.F. and D.W. Schloesser. [eds.], *Zebra mussels: biology, impacts and control.* Lewis Publishers, Boca Raton, FLA, pp. 465-490.

Garnier, J., G. Billen and M. Coste. 1995. Seasonal succession of diatoms and Chlorophyceae in the drainage network of theSeine River: Observations and modeling. *Limnol. Oceanogr.*, **40**: 750-765.

Gasol, J.M. and D. Vaqué. 1993. Lack of coupling between heterotrophic nanoflagellates and bacteria: A general phenomenon across aquatic systems? *Limnol. Oceanogr.*, **38**: 657-665.

Goldman, J.C. and D.A. Caron. 1985. Experimental studies on an omnivorous microflagellate: implications for grazing and nutrient regeneration in the marine microbial food chain. *Deep Sea Res.*, **32**: 899-915.

Gopal, B. and R.G. Wetzel. 1995. *Limnology in developing countries*, Volume 1. International Scientific Publications, New Delhi, India.

Gosselain, V., J.P. Descy and E. Everbecq. 1994. The phytoplankton community of the River Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. *Hydrobiologia*, **289**: 179-191.

Greenberg, A.E. 1964. Plankton of the Sacramento River. *Ecology*, **45**: 40-49.

Haney, J.F. and D.J. Hall. 1975. Sugar coated *Daphnia*: A preservation technique for Cladocera. *Limnol. Oceanogr.*, **18**: 331-333.

Hanson, J.M. and R.H. Peters. 1984. Empirical predictions of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. Aquat. Sci.*, **41**: 439-445.

Holmes, N.T.H. and B.A. Whitton. 1981. Phytoplankton of four rivers, Tyne, Wear, Tees, Swale. *Hydrobiologia*, **80**: 111-127.

Hynes, H.B.N. 1972. *The ecology of running waters*. University of Toronto Press, Toronto, ONT.

Hynes, H.B.N. 1989. Introductory Address. *Can. Spec. Publ. Fish. Aquat. Sci.*, **106**: 5-10.

Jeffrey, S.W. and G.F. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*1 and *c*2 in higher plants, algae, and natural phytoplankton. *Biochem. Physiol. Planzen.*, **167**: 191-194.

Jones, F.H. 1984. The dynamics of suspended algal populations in the lower Wye catchment. *Water Res.*, **18**: 25-35.

Jones, R.I. and R.J. Barrington. 1985. A study of the suspended algae in the River Derwent, Derbyshire, UK. *Hydrobiologia*, **128:** 255-264.

Jorgenson, C.B. 1990. *Bivalve filter feeding: Hydrodynamics, bioenergenics, physiology, and ecology.* Olsen and Olsen, London, UK.

Kohler, J. 1993. Growth, production and losses of phytoplankton in the lowland River Spree. I. Population dynamics. *J. Plankton Res.*, **15**: 335-349.

Krogstad, T. and O. Lovstad. 1989. Erosion, phosphorus and phytoplankton response in rivers of south-eastern Norway. *Hydrobiologia*, **183:** 33-41.

Kryger, J. and H.U. Riisgard. 1988. Filtration rate capacities in 6 species of European freshwater bivalves. *Oecologia*, **77:** 34-38.

Lack, T.J. 1971. Quantitative studies on the phytoplankton of the Rivers Thames and Kennet at Reading. *Freshwater Biol.*, **1**: 213-224.

Lack, T.J., R.E. Youngman and R.W. Collingwood. 1978. Observations on a spring diatom bloom in the River Thames. *Verh. Int. Ver. Theor. Angew. Limnol.*, **20**: 1435-1439.

Leach, J.H. 1993. Impacts of zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In Nalepa, T.F. and D.W. Schloesser. [eds.], *Zebra mussels: biology, impacts and control.* Lewis Publishers, Boca Raton, FLA, pp. 381-397.

Lean, D.R.S. and E. White. 1983. Chemical and radiotracer measurement of phosphorus uptake by lake plankton. *Can. J. Fish. Aquat. Sci.*, **40:** 147-155.

Leopold, L.B., M.G. Wolman and J.P. Miller. 1964. *Fluvial processes in geomorphology.* W.H. Freeman. San Francisco. CA. U.S.A.

Lewis, W.M., Jr. 1988. Primary production in the Orinoco River. *Ecology,* **69:** 679-692.

MacIsaac, H.J., W.G. Sprules and J.H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics? *Can. J. Fish. Aquat. Sci.*, **48**: 2051-2060.

MacIsaac, H.J., W.G. Sprules, O.E. Johannsson and J.H. Leach. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia*, **92:** 30-39.

Mackie, G.L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, **219:** 251-268.

Margalef, R. 1960. Ideas for a synthetic approach to the ecology of running waters. *Int. Rev. Ges. Hydrobiol.*, **45**: 133-153.

Martel, A. 1995. Demography and growth of the exotic zebra mussel (*Dreissena polymorpha*) in the Rideau River (Ontario). *Can. J. Zool.*, **73:** 2244-2250.

Mazumder, A., D.R.S. Lean and W.D. Taylor. 1992. Dominance of small filter feeding zooplankton in the Lake Ontario foodweb. *J. Great Lakes Res.*, **18:** 456-466.

McCauley, E. and J. Kalff. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. *Can. J. Fish. Aquat. Sci.*, **38**: 458-463.

McQueen, D.J., J.R. Post and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.*, **43**: 1571-1581.

Meyer, J.L. 1990. A blackwater perspective on riverine ecosystems. *BioScience*, **40:** 643-651.

Moss, B., H. Balls, I. Booker, K. Manson and M. Timms. 1984. The River Bure, UK: patterns of change in chemistry and phytoplankton in a slow-flowing fertile river. *Verh. Int. Ver. Theor. Angew. Limnol.*, **22:** 1959-1964.

Moss, B., I. Booker, H. Balls and K. Manson. 1989. Phytoplankton distribution in a temperate floodplain lake and river system. I. Hydrology, nutrient sources and phytoplankton biomass. *J. Plankton Res.*, **11**: 813-838.

Murakami, T., C. Isaji, N. Kuroda, K. Yoshida and H. Haga. 1992. Potamoplanktonic diatoms in the Nagara River: flora, population dynamics and influence on water quality. *Jpn. J. Limnol.*, **53**: 1-12.

Nusch, E.A. 1978. Development of planktonic algae in the Ruhr River dependent on nutrient supply, waterflow, irradiance and temperature. *Verh. Int. Verin. Limnol.*, **20:** 1837-1843.

Oglesby, R.T., C.A. Carlson and J.A. McCann [eds.]. 1972. *River ecology and man.* Academic Press, New York, NY, U.S.A.

Pace, M.L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll *a* relationship. *Can. J. Fish. Aquat. Sci.*, **41**: 1089-1096.

Pace, M.L. and E. Funke. 1991. Regulation of planktonic microbialcommunities by nutrients and herbivores. *Ecology*, **72**: 904-914.

Pace, M.L., S.E.G. Findlay and D. Lints. 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. *Can. J. Fish. Aquat. Sci.*, **49**: 1060-1069.

Petticrew, E.L. and J. Kalff. 1992. Water flow and clay retention in submerged macrophyte beds. *Can. J. Fish. Aquat. Sci.*, **49**: 2483-2489.

Pick, F.R. and C. Berubé. 1992. Diel cycles in the frequency of dividing cells of freshwater picocyanobacteria. *J. Plankton Res.*, **14**: 1193-1198.

Pieterse, A.J., J.C. Roos, K.I. Roos and C. Pienaar. 1986. Preliminary observations on cross-channel and vertical heterogeneity in environmental and algological parameters in the Vaal River at Balkfontein, S.A. *Water S.A.*, (Pretoria). **12**: 173-184.

Pomeroy, L.R. and W.J. Wiebe. 1988. Energetics of microbial foodwebs. *Hydrobiologia*, **159**: 7-18.

Porter, K.G. and Y.S. Feig. 1980. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, **25**: 943-948.

Porter, K.G., E.B. Sherr, B.F. Sherr, M.L. Pace and R.W. Sanders. 1985. Protozoa in planktonic food webs. *J. Protozool.*, **32**: 409-415.

Pridmore, R.D., W.N. Vant and J.C. Rutherford. 1985. Chlorophyll-nutrient relationships in North Island lakes (New Zealand). *Hydrobiologia*, **121**: 181-189.

Quiros, R. 1990. Factors related to variance of residuals in chlorophyll-total phosphorus regressions in lakes and reservoirs of Argentina. *Hydrobiologia*, **200**: 343-355.

RMOC (Regional Municipality of Ottawa-Carleton). 1993. *Surface water quality technical report.* (available from RMOC Surface Water Quality Branch, R.O. Pickard Environmental Center, Gloucester, Ontario, Canada, K1J 8G8).

Randall, R.G., J.R.M. Kelso and C.K. Minns. 1995. Fish production in freshwaters: Are rivers more productive than lakes? *Can. J. Fish. Aquat. Sci.*, **52:** 631-643.

Reeders, H.H., A. Bij de Vaate, and F.J. Slim. 1989. The filtration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch lakes with reference to biological water quality management. *Freshwater Biol.*, 22: 133-141.

Reeders, H.H. and A. Bij de Vaate. 1990. Zebra mussels (*Dreissena polymorpha*): a new perspective for water quality management. *Hydrobiologia,* **200/201:** 437-450.

Reynolds, C.S. 1988. Potamoplankton: paradigms, paradoxes and prognoses. p. 285-311. In F.E. Round, [ed.] *Algae and the aquatic environment.* Biopress, Bristol U.K.

Reynolds, C.S. 1994. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia,* **289**: 9-21.

Riley, E.T. and E.E. Prepas. 1985. Comparison of the phosphorus-chlorophyll relationship in mixed and stratified lakes. *Can. J. Fish. Aquat. Sci.*, **42**: 831-835.

Rosemarin, A.S. 1975. Comparison of primary productivity per unit biomass between phytoplankton and periphyton in the Ottawa River near Ottawa, Canada. *Verh. Int. Ver. Theor. Angew. Limnol.*, **19**: 1584-1592.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculations of plankton rotifers. *Arch. Hydrobiol.*, **8**: 71-76.

Ryder, R.A. and J. Pesendorfer. 1989. Large rivers are more than flowing lakes: a comparative review. *Can. Spec. Publ. Fish. Aquat. Sci.*, **106**: 65-85.

Sabater, S. and I. Munoz. 1990. Successional dynamics of the phytoplankton in the lower part of the River Ebro. *J. Plankton Res.*, **12**: 573-592.

Sabater, F., J.L. Meyer and R.T. Edwards. 1993. Longitudinal patterns of dissolved organic carbon concentration and suspended bacterial density along a blackwater river. *Hydrobiologia*, **21**: 73-93.

Shaw, E. 1987. *Hydrology in practice*. Oxford Univ. Press, London, U.K.

Shiel, R.J., K.F. Walker and W.D. Williams. 1982. Plankton of the Lower Murray, South Australia. *Aust. J. Mar. Freshwater Res.*, **33**: 301-327.

Smith, V.H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical analysis. *Limnol. Oceanogr.*, **27**: 1101-1112.

Soballe, D.M. and R.W. Bachman. 1984. Influence of reservoir transit on riverine algal transport and abundance. *Can. J. Fish. Aquat. Sci.*, **41**: 1803-1813.

Soballe, D.M. and S.T. Threlkeld. 1985. Advection, phytoplankton biomass and nutrient transformations in a rapidly flushed impoundment. *Arch. Hydrobiol.*, **105**: 187-203.

Soballe, D.M. and B.L. Kimmel. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. *Ecology*, **68**: 1943-1954.

Sprung, M. and U. Rose. 1988. Influence of food size and food quantity on the feeding of the mussel *Dreissena polymorpha*. *Oecologia*, **77**: 526-532.

Stemberger, R.S. 1979. *A guide to rotifers of the Laurentian Great Lakes.* U.S. EPA report EPA-600/4-79-021.

Strahler, H.N. 1957. Quantitative analysis of watershed geomorphology. *Am. Geophys. Trans.*, **33**: 913-920.

Talling, J.F. and J. Rzoska. 1967. The development of plankton in relation to hydrological regime in the Blue Nile. *J. Ecol.*, **55**: 637-662.

Ten Winkel, E.H. and C. Davids. 1982. Food selection by *Dreissena polymorpha* (Mollusca: Bivalvia). *Freshwater Biol.*, **12**: 553-558.

Thorp, J.H. and A.P. Covich [eds.]. 1991. *Ecology and classification of North American freshwater invertebrates*. Academic Press Inc. San Diego, CA. U.S.A.

Thorp, J.H., A.R. Black, K.H. Haag and J.D. Wehr. 1994. Zooplankton assemblages in the Ohio River: seasonal, tributary and navigation dam effects. *Can. J. Fish. Aquat. Sci.*, **51**: 1634-1643.

Tranvik, L.J. 1989. Bacterioplankton growth, grazing mortality and quantitative relationship to primary production in a humic and a clearwater lake. *J. Plankton Res.*, **11**: 985-1000.

Tzaras, A. and F.R. Pick. 1994. The relationship between bacterial and heterotrophic flagellate abundance in oligotrophic to mesotrophic temperate lakes. *Mar. Microb. Food Webs*, **8**: 347-355.

Uehlinger, U. 1993. Primary production and respiration in the outlet of an eutrophic lake (River Glatt, Switzerland). *Arch. Hydrobiol.*, **128**: 39-55.

Van Nieuwenhuyse, E. and J.R. Jones. 1996. Phosphorus-chlorophyll relationship in temperate streams and its variation with stream catchment area. *Can. J. Fish. Aquat. Sci.*, **53**: 99-105.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.*, **37**: 370-377.

Vaqué, D., M.L. Pace, S. Findlay and D. Lints. 1992. Fate of bacterial production in a heterotrophic ecosystem: grazing by protists and metazoans in the Hudson Estuary. *Mar. Ecol. Prog. Ser.*, **89**: 155-163.

Water Survey of Canada. 1990. *Historical streamflow summary, Ontario*, Environment Canada, Ottawa, Ontario.

Water Survey of Canada. 1990. *Historical streamflow summary, Quebec.* Environment Canada, Ottawa, Ontario.

Wetzel, R.G. and B.A. Manny. 1977. Seasonal changes in particulate and dissolved organic carbon and nitrogen in a hardwater stream. *Arch. Hydrobiol.*, **80**: 20-30.

Wetzel, R.G. 1983. *Limnology*, second edition. Saunders Publishing, Toronto, ONT.

Wilson, A.S. and D.J. Currie. Fish stocking in 33 Ontario lakes: unleashing the trophic trickle. submitted to *Ecol. Monogr.*, June 1996.

Yang, J.R., B.K. Basu, P. Hamilton and F.R. Pick. The development of a true riverine phytoplankton assemblage along a lake-fed, lowland river. *Archiv. Hydrobiol.*, in press.

Zacharius, O. 1898. Das potamoplankton. *Zool. Anz.*, **21**: 41-48.

Zar, J.H. 1984. Multiple comparisons. In *Biostatistical Analysis*. J.H. Zar [ed.]. Prentice-Hall, Englewood Cliffs, N.J., U.S.A.