## NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

## AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

# Heterotrophy in lake plankton

by

Paul A. del Giorgio

Department of Biology
McGill University

A thesis presented to the Faculty of Graduate Studies and Research, McGill University, in partial fulfillment of the requirements for the degree of Doctor in Philosophy

December 1993

ISBN 0-315-94608-3

Canada

# Abstract

The overall aim of this thesis was to determine the relative importance of heterotrophy and autotrophy in lake plankton. Empirical analyses using extensive surveys of literature data revealed three specific patterns in metabolism and biomass structure in freshwater plankton. First, the ratio of phytoplankton production to plankton respiration (P/R ratio) tends to be low in unproductive lakes (<1), and increases along gradients of enrichment. Second, the contribution of planktonic heterotrophs (bacteria and zooplankton) to community respiration is highest in oligotrophic lakes. Third, planktonic heterotrophs dominate community biomass in oligotrophic lakes, whereas phytoplankton increasingly dominate plankton biomass along gradients of enrichment. These three distinct patterns were then tested simultaneously in a set of lakes that span a wide trophic gradient. Results indicated that the plankton of oligotrophic and mesotrophic lakes were characterized by P/R ratios well below unity, and a high contribution of heterotrophs to both community respiration and biomass. These trends are completely the opposite in the most productive lakes. The plankton communities of oligotrophic temperate lakes are predominantly heterotrophic and extensively utilize external inputs of carbon, and therefore only the plankton of eutrophic lakes conformed to the classical phytoplankton-based food web. In most lakes, excess heterotrophic activity could be supported by inputs of organic matter from the drainage basin. Excess plankton respiration, fueled by allochthonous organic carbon, could represent an important source of $CO_2$ to lakes.

# Résumé

Le but général de cette présente thèse était de déterminer l'importance relative de l'hététrophie et de l'autotrophie chez le plancton limnétique. Des analyses empiriques basées sur des revues étendues des données publiées ont révélé l'existence de trois patrons majeurs de variation du métabolisme et de la struture de la biomasse du plancton en eaux douces. Premièrement, le rapport entre la production du phytoplancton et la respiration du plancton (le rapport P/R) tend à être plus faible dans les lacs improductifs (<1), et augmente en fonction d'un gradient d'enrichissement. En second lieu, la contribution des organismes hétérotrophes (bactéries et zooplancton) à la respiration de la communauté est plus forte dans les lacs oligotrophes. Troïsièmement, les organismes hétérotrophes planctoniques dominent la biomasse de la communauté dans les lacs oligotrophes. Par contre, le phytoplancton domine de plus en plus la biomasse planctonique en fontion de gradients d'enrichissement. Ces trois patrons distincts ont été testés simultanément dans le contexte d'une série de lacs variant en fonction d'un gradient trophique. Les résultats indiquent que le plancton des lacs oligotrophes et mésotrophes est caractérisé par des rapports P/R bien en-dessous de l'unité et par une forte contribution des organismes hétérotrophes à la respiration et la biomasse de la communauté. Ces tendances sont complètement inversées dans les lacs très productifs. Les communautés planctoniques des lacs tempérés oligotrophes sont principalement hétérotrophes et utilisent en grande partie les apports de carbone externes. Conséquemment, seul le plancton des lacs eutrophes se conforme à la théorie classique de la chaîne alimentaire basée sur le phytoplancton. Dans la plupart des lacs, l'activité

excédentaire des organismes hétérotrophes pourrait être supportée par des apports en matière organique provenant du bassin de drainage. La respiration planctonique excédentaire, supportée par le carbon organique allochtone, pourrait représenter une importante source de $CO_2$ pour les lacs.

# Table of contents

# List of Tables

*Chapter 4.*

# List of Figures

*Chapter 3.*



*Chapter 4.*

# Preface

*Remarks on style and authorship*

The Faculty of Graduate Studies requires that the following text be cited in full:

*"The candidate has the option, subject to the approval of their Department, of including as part of their thesis the text, or duplicated published text, of an original paper or papers. Manuscript-style theses must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation. Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (e.g., in appendices) to allow clear and precise judgment to be made of the importance and originality of the research reported. The thesis should be more than a mere collection of manuscripts published or unpublished. It must include a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts which provide logical bridges between different manuscripts are usually desirable in the interests of cohesion.*

*It is acceptable for theses to include, as chapters, authentic copies of papers already published, provided these are duplicated clearly and bound as an integral part of the thesis. In such instances, connecting texts are mandatory and supplementary explanatory material is always necessary. Photographs or other materials which do not duplicate well must be included in their original form.*

*While inclusion of manuscripts co-authored by the candidate and others is acceptable, the candidate is required to make an explicit statement on who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims at the Ph.D. Oral*

*Defense. Since the task of the Examiners is made more difficult in these cases, it is the candidate's interest to make the responsibilities of authors perfectly clear."*

The results of this thesis are presented in 5 chapters, portions of which have been submitted to peer-reviewed journals. My supervisor, Dr. R. H. Peters, provided the funds and logistic support necessary to carry out this research, and also extensive discussion and criticism, and therefore appears as co-author of several manuscripts. An earlier version of Chapter 1 was published in the Canadian Journal of Fisheries and Aquatic Sciences (vol. 50: 282- 289), co-authored by R. H. Peters. Portions of Chapter 2 have been submitted to The American Naturalist, co-authored by G. M. Gasol, who provided the data on plankton biomass for several Québec lakes, and also discussion and ideas on the biomass distribution in freshwater plankton communities. Parts of Chapter 3 and 4 appear in the Journal of Plankton Research (vol. 14: 1773-1741). The remainder of Chapter 4 has been submitted for publication in Limnology and Oceanography, co-authored by R. H. Peters. Chapter 5, co-authored by R. H. Peters, is written in a synthetic and condensed format, adhering to the style requirements of the journal Science, where it was submitted for publication. The format of the manuscript was not modified to be included as a chapter of this thesis, because it conveys the necessary information in a brief and effective way.

# Contributions to original knowledge

## General contributions

1) This thesis is the first quantification of the change in planktonic P/R ratios along gradients of nutrients and of dissolved organic carbon in lakes. The patterns found indicate that plankton communities function as heterotrophic systems in a much wider variety of lakes than was previously recognized (Chapters 1 and 4). Community metabolism in oligotrophic temperate lakes is shown to be dominated by the respiration of heterotrophs (bacteria and zooplankton), whereas phytoplankton dominate planktonic respiration in eutrophic lakes (Chapters 1 and 3).

2) This thesis is also the first report of a systematic shift in the allocation of biomass into heterotrophs and autotrophs along gradients of enrichment in lakes. The plankton of oligotrophic lakes is characterized by a dominance of heterotrophic biomass (bacteria and zooplankton), whereas in highly productive lakes, phytoplankton dominate community biomass (Chapters 2 and 5).

3) This is the first study to simultaneously quantify patterns in plankton community biomass and metabolism across gradients of enrichment and of dissolved organic carbon in lakes. The plankton of unproductive lakes are characterized by low P/R ratios, and a high contribution of heterotrophs to both community biomass and respiration. The opposite trends characterize the most productive lakes. Thus, it is shown that in most lakes, plankton communities do not conform to the classical phytoplankton-based food webs (Chapter 5).

## Specific contributions

*Chapter 1*

1) This chapter represents the first large-scale empirical analysis of plankton respiration across lakes. An extensive literature data set shows that plankton respiration is strongly correlated to measures of lake trophy, such as chlorophyll concentration. In addition, rates of plankton respiration are shown to increase less than rates of phytoplankton production along gradients of enrichment in lakes. As a result, P/R ratios are not constant across lakes, but increase along gradients of enrichment. Oligotrophic and mesotrophic lakes appear to be characterized by P/R ratios that are well below unity, and only the most productive lakes have P/R ratios above 1.

2) Plankton community respiration along gradients of enrichment was reconstructed from the predicted biomass and size of planktonic organisms, using published empirical and allometric equations. The results of this calculations indicate that bacteria and zooplankton dominate community respiration in most oligotrophic lakes, and that the contribution of phytoplankton increases with lake trophy.

*Chapter 2*

1) An extensive literature data set, coupled with measurements taken in Québec lakes, were used to show that the proportions of heterotrophs (bacteria and zooplankton) and autotrophs (phytoplankton) vary systematically across lakes. This study is the first to show that ratio of total heterotrophic to total autotrophic biomass (H/A ratio) is not constant, but rather declines steeply along gradients of enrichment in lakes.

2) This study also shows that the biomass of heterotrophs remains approximately constant along a gradient of food resources, comprised not only by phytoplankton, but also detrital carbon in the dissolved organic pool.

*Chapter 3*

1) This investigation is the first large-scale empirical study of the relationship between ETS (electron transport system) activity and oxygen consumption in freshwater plankton. The ratio of respiration to ETS activity is not constant across lakes, and it varies systematically with lake trophy and dissolved organic carbon concentration.

2) This is the first study that has linked the variation in the R:ETS ratio across lakes to changes in the contribution of heterotrophs and autotrophs to community respiration. Thus, it is shown that plankton metabolism in oligotrophic lakes, and in lakes with high concentrations of DOC, is dominated by the respiration of heterotrophs (bacteria and zooplankton).

*Chapter 4*

1) This represents the first comparative field study to compare simultaneously phytoplankton production, plankton respiration and planktonic P/R ratios in lakes. P/R ratios were found to be related to chlorophyll and total phosphorus concentration, and also to dissolved organic carbon. The results indicate that the plankton of oligotrophic and mesotrophic lakes are energetically not self-sufficient and are shown to utilize substantial amounts of external organic carbon.

2) This is also the first comparative study to simultaneously relate lake and drainage basin morphometry to phytoplankton production, plankton respiration and community P/R ratios.

*Chapter 5*

1) This final chapter shows that previously unrelated patterns in biomass allocation (H/A ratio), contribution of heterotrophs and autotrophs to respiration (R:ETS ratio) and metabolism (P/R ratio), are consistent within the same set of lakes. The overall trend that emerges is the dominance of heterotrophs on plankton community metabolism and biomass in oligotrophic temperate lakes, fueled by external sources of organic carbon. This represents the first quantification of the overall degree of heterotrophy in lake plankton communities along gradients of enrichment.

2) The results from this large-scale comparative analysis provide the strongest evidence available to date in support of the hypothesis that $CO_2$ supersaturation in temperate oligotrophic lakes may originate from planktonic respiration of terrestrially-derived organic matter.

# ACKNOWLEDGEMENTS

I wish to thank Rob Peters for providing the financial, logistic, and intellectual support that I needed to complete this thesis. I am grateful for his advice, his trust in my work, and his generosity. Above all, I appreciate the freedom to learn, to decide, and to create, that I always enjoyed under his supervision. I thank the other three members of my thesis committee, Dr. Jaap Kalff, Dr. Dolors Planas, and Dr. John Downing, for their constructive criticism and encouragement.

Eric Melina, Sandra Clinton, Gregg Scarborough and particularly Worth Everett, were invaluable field and laboratory assistants. The success of this research owes much to their competent and effective work during three consecutive field seasons. Sara Griesbach and Gary Bowen have managed to keep our laboratory functioning is spite of the odds, and their help in daily needs during four years is greatly appreciated. Robert Lamarche was always helpful with advice on computing problems, and Tony Briza designed and constructed various field and laboratory gear. Dr. Dolors Planas (UQAM) and Dr. John Downing (Université de Montreal) allowed me to use equipment and facilities in their respective institutions, which greatly contributed to this research. Gilbert Cabana kindly translated the abstract to french.

During my thesis I have greatly benefited from discussions with colleagues inside and outside of McGill. Joe Rasmussen has always provided insightful ideas, and often solutions, to every kind of problem that I have brought up to him. I have learned much, and broadened my ideas, from

discussions with Josep Gasol, Mark Schallenberg, Helene Cyr, Robert France, Mark Chandler, Gilbert Cabana and Steven Baines. I am also grateful for having been a member of the Groupe de Récherche Inter-universitaire en Limnologie (GRIL), which has been an ideal forum to exchange ideas and opinions on science, and to expand my perception of limnological problems. As a graduate student at McGill, I have been fortunate to have the friendship of many colleagues. Special thanks to Josep Gasol, Mark Chandler, Iain Cuthbert and André Cimbleris for the good times.

Financial support for my project was provided by an National Science, Engineering and Research Council of Canada (NSERC) grant to R. H. Peters, an Fonds pour la Formation de Chercheurs at l'Aide a la Recherche (FCAR) team grant to J. Kalff, R. H. Peters and J. Rasmussen, and Vineberg Family Fellowship to myself. Additional funds from the Clemens-Rigler Travel Fund, the Department of Biology Graduate Committee, and the American Society of Limnology and Oceanography allowed me to present portions of this research at national and international meetings. I gratefully acknowledge this support.

Finally, I wish to thank my wife, Paula, for her love and happiness, her strength and intelligence. My love for her, and my gratitude, are much more than could ever be expressed in words. I dedicate this thesis to her.

# GENERAL INTRODUCTION

The perception of lakes as microcosms (Forbes 1887) is deeply ingrained in limnological theory and practice. This perception reduced lakes, and the communities living there, to almost self-contained systems, and is a conveniently simplified version of the more complex surrounding terrestrial ecosystems. This notion of lakes as almost closed systems later evolved into the concept that lakes function as living organisms (Hutchinson 1941) which can be studied in relative isolation. This concept has been widely accepted in spite of early comparative studies (Birge and Juday 1927) which often linked lake function to characteristics of the drainage basin. For example, Birge and Juday distinguished, among other categories, autotrophic lakes, which derive their organic matter from internal sources, and allotrophic lakes, which derive a large portion of the organic matter from the drainage basin (Birge and Juday 1927). "Colored" lakes were generally regarded as allotrophic because of the high concentrations of dissolved organic carbon (DOC) in the water, whereas "clear-water" lakes were considered essentially autotrophic systems.

Early in limnology, lakes with high concentrations of DOC and high water color had been recognized as a distinct category. The term "dystrophic" (Naumann 1922) reflects this early perception that brown-water lakes differ substantially from clear-water lakes, and thus had to be placed outside the established production series from oligotrophy to eutrophy (Thienemann 1926). For this reason, the notion that dystrophic lakes could function as heterotrophic systems, proposed by Birge and Juday (1927), found some acceptance among limnologists, but did not seriously challenge the concept of self-sufficiency of most lakes. Hutchinson (1967) pointed out that the "term dystrophic suggests a more pathological condition than perhaps exists", but for many

decades brown-water lakes remained somewhat of an oddity, often outside mainstream limnology (Jones 1992).

Although lakes were still treated essentially as autotrophic systems for most practical purposes, there was increasing consensus among limnologists that lakes should not be studied in isolation because of the importance of the interactions with the drainage basin. These ideas culminated in the nutrient loading models in the late sixties and seventies (Vollenweider 1975), and models for organic carbon loading from the drainage basin (Rasmussen et al. 1989). Whole-lake carbon budgets revealed that, to some extent, all lakes are heterotrophic, and utilize allochthonous inputs of organic carbon (Odum and Prentki 1978; Wetzel and Richey 1978). Under this perspective, humic lakes represented extreme cases of heterotrophy in lakes. The dichotomy between colored and clear lakes never disappeared, however, and clear-water lakes are still often perceived as predominantly autotrophic.

The development of concepts for freshwater plankton has paralleled that for lakes. As in lakes, the perception of plankton communities evolved from the notion of self-contained systems, to the present-day consensus that most freshwater plankton communities utilize varying amounts of external organic supplements (Jones 1992). In lakes, the understanding of plankton function involves an arbitrary dichotomy between clear and colored lakes. It is now widely recognized that the plankton of humic lakes is predominantly heterotrophic, deriving much of its organic carbon from sources other than phytoplankton photosynthesis (Hessen et al. 1990). The traditional phytoplankton-based food web is still thought to operate in most other systems, and thus the measurement of phytoplankton photosynthesis or production remains a central objective of contemporary limnology. The rationale behind the innumerable published estimates of primary production in lakes is that plankton processes, such as

bacterial production, zooplankton grazing, community respiration or net sedimentation, should scale to phytoplankton production, since this is regarded as the major source of energy to the pelagial of most lakes.

Jones (1992) has summarized the current perceptions of plankton function across lakes. Using the evidence accumulated in the literature, he hypothesizes that plankton communities in oligotrophic lakes should generally be more heterotrophic than communities in highly productive lakes. He also hypothesizes that for any given productivity status, the plankton of colored lakes should be considerably more heterotrophic than the plankton of clear lakes. Implicit in Jones' qualitative description is the fact that heterotrophy in lake plankton is determined by both nutrient enrichment, and thus the potential for phytoplankton production, and dissolved organic carbon, which can fuel heterotrophic activity directly. There is now widespread consensus that dissolved organic carbon, derived mostly from terrestrial vegetation, is the major vector for energetic supplements to the plankton (Tranvik 1992).

The qualitative trends proposed by Jones (1992) provide a useful background for the question on the degree of heterotrophy in lake plankton. For the most part, however, these patterns have not been quantified in nature, and thus fundamental questions remain unanswered:

1) Is there a systematic shift from predominantly autotrophic plankton communities in clear-water lakes to predominantly heterotrophic communities in humic lakes?

2) If so, at what point along a gradient of dissolved organic carbon in lakes does the plankton become predominantly heterotrophic?

3) At what point along a gradient of increasing phytoplankton production does the plankton become predominantly autotrophic?

4) How do nutrient concentrations interact with DOC in lakes to shape the relative degree of heterotrophy in the plankton?
5) What Is the main determinant of heterotrophy in freshwater plankton: nutrient concentration, DOC concentration, or the interaction between the two?

To answer these questions, the traditional distinction between clear and colored lakes has to be substituted by an approach that relates plankton metabolism and structure to gradients of both dissolved organic carbon and nutrient concentration. In my thesis I have taken this approach, with the overall objective of examining changes in the degree of heterotrophy in plankton communities across lakes. In this context, heterotrophy refers to the utilization by the plankton of energy sources other than phytoplankton production, such as organic carbon derived from littoral and terrestrial vegetation. These energetic subsidies affect many aspects of plankton community metabolism and structure, including community respiration relative to primary production, the respiration of planktonic heterotrophs relative to the respiration of phytoplankton, the production of bacteria and zooplankton relative to phytoplankton production, and the distribution of biomass into planktonic autotrophs and heterotrophs. Any of these characteristics may be considered as an index of heterotrophy in the plankton. When combined, they should provide a more quantitative statement of how plankton communities are structured around both internal and external energy sources.

For this investigation, I chose to study three indices of plankton heterotrophy: First, the balance between phytoplankton production and plankton respiration (P/R ratio), which is a primary index of heterotrophy for any ecosystem. Second, the contribution of heterotrophs and autotrophs to community respiration, which is an indication of patterns in carbon flow within communities. Third, the distribution of

biomass into heterotrophic (bacteria and zooplankton) and autotrophic components, which is influenced by both internal and external sources of organic carbon. This thesis describes general patterns between these indices and both nutrient and dissolved organic carbon concentrations, and quantifies the amount of organic carbon in excess of phytoplankton production that plankton communities utilize in different lakes.

In the first chapter (del Giorgio and Peters 1993), I present the results of an extensive literature search on rates of phytoplankton production and plankton respiration in lakes. Both processes appear strongly correlated to measures of trophy, such as chlorophyll concentration and total phosphorus, but their change along trophic gradients is markedly different. Planktonic P/R ratios calculated from these data tend to be well below unity in the most unproductive lakes, and increase along gradients of enrichment, approaching or exceeding unity in the most productive lakes. This pattern agrees with previous findings by Ahrens and Peters (1992) for a limited set of lakes in Québec, and suggests a generalized imbalance between phytoplankton photosynthesis and community respiration in oligotrophic lakes. A reconstruction of plankton community respiration along trophic gradients, using published empirical and allometric equations, indicated that in unproductive lakes, which are characterized by low community P/R ratios, bacteria and zooplankton should dominate community respiration. The plankton of oligotrophic lakes thus appears to be heavily dependent on external carbon inputs, which fuel an elevated activity of heterotrophs relative to phytoplankton.

This initial evidence suggested highly heterotrophic plankton communities in unproductive lakes, and communities dominated by the production and respiration of phytoplankton in eutrophic systems. I then hypothesized that there should be a

coherent shift in the distribution of biomass into autotrophs and heterotrophs, paralleling the changes in metabolism described above. In Chapter 2, I test this hypothesis using an extensive literature survey of data on the total biomass of autotrophs and heterotrophs for a wide variety of lakes worldwide (del Giorgio and Gasol submitted). The results of this study indicate, for the first time, a strong declining trend in the ratio of total heterotrophic to total autotrophic biomass along gradients of enrichment in lakes.

These studies involving literature data suggested strong patterns in biomass and metabolism along nutrient gradients, and a systematic shift in plankton heterotrophy across lakes. There are several disadvantages, however, in such literature surveys. First, sampling and analytical techniques varied among studies, and it was almost impossible to correct for this heterogeneity. Secondly, the data for phytoplankton production, plankton respiration and biomass did not originate from the same lakes, so the degree to which patterns in metabolism and biomass are coherent was uncertain. Third, few papers from which data were extracted reported DOC or water color, a surrogate measure of DOC (Cuthbert and del Giorgio 1992), so patterns in biomass and metabolism could only be quantified along gradients of enrichment.

In Chapters 3, 4 and 5 I present the results of my field work, where I tested the patterns in planktonic metabolism and biomass distribution simultaneously in a set of 20 southern Québec lakes. The lakes chosen for this study span a wide trophic range, and also a wide range in dissolved organic carbon concentration, and were thus appropriate to examine the changes in plankton heterotrophy along gradients of enrichment and of DOC.

Chapter 3 (del Giorgio 1992) is the first large-scale comparison between planktonic oxygen consumption and ETS (electron transport system) activity in lakes. The objectives of this investigation were twofold. First, it was an attempt to validate ETS as a reliable method for estimating freshwater plankton respiration. Second, the relationship between ETS and oxygen consumption was used an index of the relative contribution of autotrophs and heterotrophs (bacteria and zooplankton) to community respiration. Results indicate that the ratio of respiration (as oxygen consumption) to ETS activity (R:ETS ratio) is not constant across lakes, and an empirical equation is provided to convert from activity to *in situ* oxygen consumption. The relationship between respiration and ETS activity further suggests that the contribution of heterotrophs to community respiration is high in oligotrophic lakes, peaks in colored lakes, and declines with trophy. Phytoplankton appear to dominate community respiration in the most productive lakes, in agreement with the pattern proposed in Chapter 1.

Chapter 4 (del Giorgio and Peters submitted), is the first large-scale comparative study of planktonic P/R ratios in lakes. The measured trends in planktonic P/R ratios along the growing season agreed well with both the qualitative predictions by Jones (1992) and the quantitative patterns proposed in Chapter 1. Planktonic P/R ratios were a function of both nutrient concentration and DOC. P/R ratios tended to be low in all unproductive lakes, regardless of the water color, but for any given level of chlorophyll or total phosphorus, colored lakes tended to have lower P/R ratios than clear-water lakes. P/R ratios only approached or exceeded unity in the most eutrophic lakes that I studied. Plankton respiration in excess of phytoplankton production ranged from 30 to 86 mg C $m^{-3}$ $d^{-1}$, and this imbalance could be explained by allochthonous inputs of organic carbon in most lakes.

In Chapter 5 (del Giorgio and Peters submitted), I present the results of a study of the biomass distribution into autotrophs and heterotrophs for this same set of 20 southern Québec lakes. The measured pattern agrees well with that empirically derived in Chapter 2: the ratio of total heterotrophic biomass to total autotrophic biomass (H/A ratio) strongly declines along gradients of enrichment in lakes. The plankton of oligotrophic lakes is dominated by the biomass of heterotrophs (bacteria, micro- and macrozooplankton), whereas in the more eutrophic lakes, phytoplankton overwhelmingly dominate community biomass. DOC does not influence total heterotrophic biomass in these lakes, but there are strong qualitative shifts in the composition of the total heterotrophic biomass along gradients of DOC or water color.

Chapter 5 also serves as a summary and conclusion of my field results concerning plankton metabolism and biomass, because I have superimposed the pattern in biomass distribution, with the patterns in planktonic R:ETS and P/R ratios that were described in Chapters 3 and 4. I show that these three indices of heterotrophy in the plankton are coherent, and conclude that plankton communities of oligotrophic temperate lakes are predominantly heterotrophic and are dominated by the biomass and activity of planktonic heterotrophs. As lakes become more productive, phytoplankton overwhelmingly dominate community biomass and metabolism. These broad patterns suggest that pelagial communities of most oligotrophic lakes, whether clear or colored, are not energetically self-sufficient and extensively utilize external sources of carbon, presumably of terrestrial origin.

## REFERENCES

Ahrens, M. and R. H. Peters. 1991. Plankton community respiration: relationships with size distribution and lake trophy. Hydrobiologia 224: 77-87.

Birge, E. A., and C. Juday. 1927. The organic content of the water of small lakes. Proc. Amer. Phil. Soc. 66: 357-372.

Cuthbert, I. D. and P. A. del Giorgio. 1992. Toward a standard method of measuring color in freshwater. Limnol. Oceanogr. 37: 1319-1326.

del Giorgio, P. A. 1992.The relationship between ETS (electron transport system) activity and oxygen consumption in lake plankton: a cross-system calibration. J. Plankton Res. 14: 1723-1741.

del Giorgio, P. A. and J. M. Gasol. Biomass allocation in freshwater plankton communities. Submitted to The American Naturalist.

del Giorgio, P. A. and R. H. Peters. 1993. The balance between phytoplankton production and plankton respiration in lakes. Can J. Fish. Aquat. Sci. 50: 282-289.

del Giorgio, P. A. and R. H. Peters. Patterns in planktonic P/R ratios in lakes: influence of lake trophy and dissolved organic carbon. Submitted to Limnology and Oceanography.

del Giorgio, P. A. and R. H. Peters. Heterotrophic dominance in the plankton of unproductive temperate lakes. Submitted to Science.

Forbes, S. A. 1987. The lake as a microcosm. Bull. Sci. Assoc. Peoria, Illinois, 1987: 77-87.

Hessen, D. O., T. Andersen and A. Lyche. 1990. Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. Limnol. Oceanogr. 35: 84-99.

Hutchinson, G. E. 1941. The mechanisms of intermediary metabolism in stratified lakes. Ecol. Monogr. 11: 21-60.

Hutchinson, G. E. 1967. A treatise in limnology. Vol. 2. Wiley, New York. 1010 pp.

Jones, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73-91.

Naumann, E. 1921. Die Sestonfärburg des Süsswassers. Arch. Hydrobiol. 13: 647-692.

Odum, W. E. and R. T. Prentki. 1978. Analysis of five North American lake ecosystems IV. Allochthonous organic inputs. Verh. int. Ver. Limnol. 20: 574-580.

Rasmussen, J. B., L. Godbout, and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. Limnol. Oceanogr. 34: 409-434.

Thienemann, A. 1926. Der Nahrungskreislauf im Wasser. Verh. Dstch. Zool. Ges. 2: 29-79.

Tranvik, K. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

Vollenweider, R. A. 1975. Input-output models with special reference to the phosphorus loading concept in limnology. Schweiz. Z. Hydrol. 37: 53-83.

Wetzel, R. G. and J. E. Richey. 1978. Analysis of five North American lake ecosystems VII. Control mechanisms and regulation. Verh. int. Ver. Limnol. 20: 605-608.

Chapter 1

# THE BALANCE BETWEEN PHYTOPLANKTON PRODUCTION AND PLANKTON RESPIRATION IN LAKES

## ABSTRACT

We analyzed published rates of algal photosynthesis and plankton community respiration to test the hypothesis that the ratio of planktonic primary production to community respiration (P/R) varies systematically with lake trophy. Regression analyses show that algal production and plankton respiration are closely related to chlorophyll concentrations for lakes spanning a wide trophic range. More surprisingly, plankton respiration exceeds algal photosynthesis in oligotrophic lakes, and P/R rises above unity only when chlorophyll concentrations are above 17 mg $m^{-3}$. A simple allometric model based on the predicted biomasses of the different planktonic components yields rates of community respiration which are in good agreement with measured values. Moreover, the model suggests that in oligotrophic lakes, microbial respiration may greatly exceed the current estimates based on bacterial production data, and that heterotrophs contribute proportionately more to total plankton metabolism than they do in eutrophic lakes. Because such high respiration rates require external energy subsidies, these results challenge the view that pelagial communities of most lakes are even approximately self-supporting.

## INTRODUCTION

The concept that either lakes or plankton communities can be considered isolated microcosms has little support in modern limnology. The importance of allochthonous inputs of organic matter to lake metabolism and function has been described by many authors (Wetzel and Richey 1978; Odum and Prentki 1978; Likens and Bormann 1979; Wetzel 1983; 1990). Various components of the plankton have been shown to utilize both dissolved organic carbon from the watershed, and that leached from littoral macrophytes (Findlay et al. 1986; Salonen and Hammar 1986; Benner et al. 1988, Tranvik 1992). But in spite of the growing evidence that external inputs of carbon may fuel a considerable fraction of pelagial metabolism, phytoplankton are often considered the driving force behind pelagic function, and plankton processes are still commonly scaled to phytoplankton carbon fixation (Odum and Prentki 1978).

This seeming inconsistency between acknowledging the role of external carbon, yet giving a central place to primary production is possible because the relative contributions of external inputs of carbon to plankton community metabolism have been quantified only for a limited number and range of lakes. The impact of carbon subsidies is most evident and has been well documented for colored lakes with high concentrations of humic substances (Salonen and Hammar 1986; Johansson 1983; Kankaala 1988), and for shallow lakes or littoral areas with extensive macrophyte development (Wetzel 1990). However, virtually all pelagial communities receive external organic inputs and no broad pattern has yet emerged on the relative importance of these inputs across a wide range of lakes. Odum and Prentki (1978) hypothesized that the dominance of heterotrophic or autotrophic processes in a lake is controlled more by the magnitude of autochthonous production than by allochthonous inputs. If this hypothesis is extended to the plankton community, it implies that the

relative importance of external carbon inputs to overall plankton metabolism should decline as phytoplankton production increases, along the trophic gradient of lakes.

The literature offers some support for the hypothesis that the impact of energetic subsidies is greater in the plankton of oligotrophic lakes. High rates of secondary production relative to primary production (Scavia and Laird 1988; McCauley and Kalff 1981), and high ratios of heterotrophic to autotrophic biomass (Currie 1991) have been reported for oligotrophic lakes. There are also reports of low ratios of phytoplankton production to community respiration (P/R ratios), often well below unity, in oligotrophic plankton (Hessen et al. 1990; Sarvala et al. 1981; Devol 1979; Wissmar et al. 1977). High relative values of heterotrophic biomass and production may be interpreted as the result of organic matter cycling within the community (Straye: 1988) or high turnover of the algae (Harris 1984), but low P/R ratios directly reflect consumption of carbon in excess of algal production. Planktonic P/R ratios thus quantify the dependency of that community on external inputs of carbon (Odum 1957).

In this paper, we compare literature data on plankton respiration and primary production to determine whether planktonic P/R ratios change consistently with lake trophic status as measured by chlorophyll concentration, and thus to examine the effectiveness of scaling or standardizing plankton processes to phytoplankton production. Secondly, we reconstruct plankton community respiration along a trophic gradient using published empirical equations that relate biomass of different components of the plankton to total phosphorus, and allometric equations that relate metabolic rate to body size. This reconstruction provides a check on the P/R patterns and allows an exploration of the changes in the metabolic contribution of different planktonic components that are likely to occur along a trophic gradient.

## MATERIALS AND METHODS

**Primary Production:** Published measurements of daily volumetric primary production and chlorophyll concentration for 118 lakes worldwide were extracted from 15 studies (Table 1). Points represent annual or seasonal averages for single lakes, either given by the authors or calculated from data in tables or graphs. Points for different years for the same lake are treated independently. The purpose of this paper is to compare these production data with estimates of plankton respiration, which are generally averages over the mixed layer or, in very shallow lakes, over the entire depth. Volumetric rates of primary production, however, are generally averaged over the euphotic zone, and this may bias the comparison with the respiration rates, particularly at high chlorophyll concentrations. The data were thus divided into three groups: data calculated as average volumetric rates for the mixed layer, data averaged for the euphotic zone, and unspecified data. When only areal estimates were provided by the authors, these rates were divided by the depth of the euphotic zone. The three data sub-sets were then analyzed individually and the results compared to the full data set.

**Plankton Respiration:** Volumetric rates of plankton respiration and chlorophyll concentration for 36 lakes worldwide were extracted from 23 studies (Table 1). Only studies that actually measured oxygen consumption or $CO_2$ production were considered. For example, studies that measured electron transport system (ETS) activity were not included because of uncertainties in the ratio of respiration to ETS for complex plankton communities. Points are annual or growing season means for individual lakes, given by the authors or calculated from tables or graphs. Generally the data are integrated values for the epilimnion or in case of very shallow lakes or ponds, the entire depth, and are the results of incubations ranging from 3 to 24 h.

Oxygen consumption was transformed to carbon units using a RQ of 1 (0.375 mg $O_2$ / mg C).

**Data Analyses:** Data were log-transformed to attain normality and homoscedasticity and analyzed by linear regression with the SYSTAT statistical package (Wilkinson 1987). The data set is available from the authors or from the Repository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario K1A 0S2. The complete data sets for phytoplankton production and plankton respiration appear in Appendix 1 and 2, respectively, of this thesis.

**Allometric Model:** Predicted biomasses and respiration rates of five planktonic components (bacteria, nano phytoplankton, net phytoplankton, micro- and macrozooplankton) were calculated to provide an independent check on the credibility of the respiration measurements and to determine the contributions of major functional groupings to plankton respiration. First, we simulated a gradient of TP from 1 to 100 mg $m^{-3}$, and estimated the biomasses of the five planktonic components mentioned above along this trophic gradient, from published empirical equations; these equations utilize TP as an independent variable to predict the biomass of each component and were standardized to the same units (mg WW $l^{-1}$, Table 2); a mean individual size was assigned to each planktonic component (Table 2); specific respiration rates for each of the components were estimated from assumed body sizes and appropriate published allometric equations (Table 2); thus, for any given TP level, the respiration rates for each group were calculated as the products of the predicted biomass at that TP concentration and size specific respiration rates. Since all the literature data on production and respiration are expressed as a function of chlorophyll concentration, we transformed our simulated TP gradient into a chlorophyll (CH) gradient using the equation logCH = 1.45 x logTP - 1.14 (Dillon and Rigler 1974). We assumed that only

Table 1. Sources for data on phytoplankton production and plankton community respiration.

| Primary production | Plankton respiration |
|---|---|
| Stockner and Shortreed 1985 | Jones 1977 |
| Belay and Wood 1984 | Kravtsova et al. 1988 |
| Beaver and Crisman 1991 | Talling et al. 1973 |
| Bayne et al. 1990 | Chenard 1980 |
| Tolstoy 1988 | Hunding 1979 |
| Jackson and Hecky 1980 | Caron 1976 |
| Carmouze et al. 1983 | Northcote et al. 1989 |
| Malueg et al. 1972 | Barica 1975 |
| Beuchamp and Kerekes 1986 | Fontaine and Carter Ewel 1981 |
| Lafond et al. 1990 | Serruya and Serruya 1972 |
| Kifle and Belay 1990 | Grobbelaar and Soeder 1985 |
| Dubinsky et al. 1984 | Mitchell and Burns 1979 |
| Adams et al. 1990 | Ahrens and Peters 1991 |
| Heyman 1983 | Gibson 1975 |
| Ruggiu and Mosello 1984 | Jakson 1969 |
| | Ganf 1974 |
| | Spurr 1975 |
| | CSIR 1985 |
| | Markager and Sand-Jensen 1989 |
| | Pick 1984 |
| | Salonen et al. 1983 |
| | Alimov and Winberg 1972 |
| | Kamp-Nielsen 1981 |

Table 2. Summary of plankton respiration model. For the five planktonic components an equivalent spherical diameter (ESD) was assumed. The biomass of each component was calculated with empirical equations that relate biomass (B, standardized to mg wet weight.$m^{-3}$) to total phosphorus (TP in mg.$m^{-3}$). The specific respiration rates for each component were calculated with allometric equations and the assumed body size. Component respiration rates were calculated multiplying the predicted biomass by the specific respiration rates.

| Component | ESD | Predicted Biomass | Specific Respiration |
|---|---|---|---|
| Bacteria [1,4] | 0.56 | $B = 13.8\ TP^{0.66}$ | $R = 2.71\ M^{-0.17}$ |
| Nanoplankton (NANO) [2,4] | 5 | $B = 190\ TP^{0.41}$ | (mg $O_2$.g $ww^{-1}.d^{-1}$) |
| Netplankton (NET) [2,4] | 25 | $B = 18.6\ TP^{1.32}$ | standarized at 20°C |
| Microzooplankton (MICRO) [3,4] | 120 | $B = 170\ TP^{0.71}$ | |
| Macrozooplankton (MACRO) [3,5] | 450 | $B = 200\ TP^{0.65}$ | $R = 15\ M^{-0.31}$ (pg C.pg $C^{-1}.d^{-1}$) |

Biomass equations from 1, 2 and 3. Specific respiration equations from 4 and 5.
1) Bird and Kalff 1984; 2) Watson and McCauley 1988; 3) Pace 1984; 4) Robinson et al. 1983; 5) Ikeda and Motoda 1978

70% of the predicted bacterial biomass was metabolically active (Newell et al. 1988). Community respiration is the sum of the component rates. Units were standardized assuming 1 $\mu m^3$ = 1 pg wet weight; wet weight : dry weight of 10:1 for zooplankton. Macrozooplankton respiration was calculated by assuming 1 pg wet weight = 0.07 pg C and $O_2$ flux was converted to C flux by assuming a RQ of 1.

## RESULTS AND DISCUSSION

**Plankton Respiration *vs* Chlorophyll**: Volumetric rates of plankton respiration (R in mg $C.m^{-3}.\ d^{-1}$) are strongly positively correlated with chlorophyll (Ch in $mg.m^{-3}$) in a set of lakes spanning a wide trophic range (0.3-5000 $mg.m^{-3}$)(Fig. 1):

$$R = 45\ Ch^{0.65} \quad (r^2 = 0.91, n = 41, S_{xy} = 0.218)\ (Eq.1)$$

Measurements of lake plankton respiration are scarce, relative to the abundance of primary and secondary production data, and there are even fewer comparative studies of plankton respiration across lakes with which to validate our results. Ahrens and Peters (1991) reported a strong relationship between plankton respiration rate and chlorophyll and total phosphorus concentration for a set of 12 lakes, all from southern Quebec, and spanning a rather limited range of TP. The present analysis includes these data, but also greatly expands the trophic and geographical range of lakes. The resulting patterns remain unchanged. Thus, the strong relationship between plankton respiration and TP or chlorophyll reported by Ahrens and Peters (1991) does not seem to be constrained to similar lakes within the same region. Welch et al. (1976) measured winter respiration in 16 Ontario lakes and reported a very weak relationship between volumetric rates and chlorophyll, but the lakes in their study span a very narrow trophic range and winter respiration includes sediment respiration. Welch (1974) reported metabolic rates of 9 arctic lakes but did not include TP or chlorophyll

data. Since the literature could not provide an independent data set with which we could compare our results, we calculated the rates of community respiration (mg C. $m^{-3}.d^{-1}$) along a gradient of chlorophyll ($mg.m^{-3}$) from the predicted biomass of different components of the plankton (Table 2) and obtained the equation:

$$R = 59\ Ch^{0.56} \quad \text{(Eq.2)}$$

The confidence intervals around equation 2 are extremely wide, due to the propagation of the error of the empirical relationships used to construct the model. Nevertheless, the exponent (slope) of this equation agrees very well with equation (1) derived from literature data for respiration (Fig. 3a). This result also agrees with the findings of Ahrens and Peters (1991) that allometric equations derived in the laboratory can be extrapolated to natural populations. Community respiration thus seems consistent with trends in planktonic biomass along a broad trophic range, and equations 1 and 2 indicate essentially the same pattern: plankton respiration increases more slowly than chlorophyll concentration in lakes.

**Primary Production *vs* Chlorophyll:** There is a strong positive relationship between volumetric rates of phytoplankton production (P in mg C. $m^{-3}.d^{-1}$) and chlorophyll (Ch in $mg.m^{-3}$) in a global data set (Fig. 2):

$$P = 10.3\ Ch^{1.19} \quad (r^2 = 0.75,\ n = 163,\ S_{xy} = 0.380) \quad \text{(Eq.3)}$$

This data set includes lakes from temperate, subtropical and equatorial regions with chlorophyll concentrations ranging from 0.2 to over 100 $mg.m^{-3}$. The parameters of our production equation are not significantly different ($P < 0.01$) from those based on an independent data set (Smith 1979) of 58 northern temperate lakes (Fig. 3a). The

Figure 1. Volumetric rates of plankton respiration as a function of the chlorophyll concentration. Points represent annual or seasonal euphotic zone or epilimnetic means for 36 lakes. The plot show the line of best fit and the 95% confidence intervals for the predicted values.

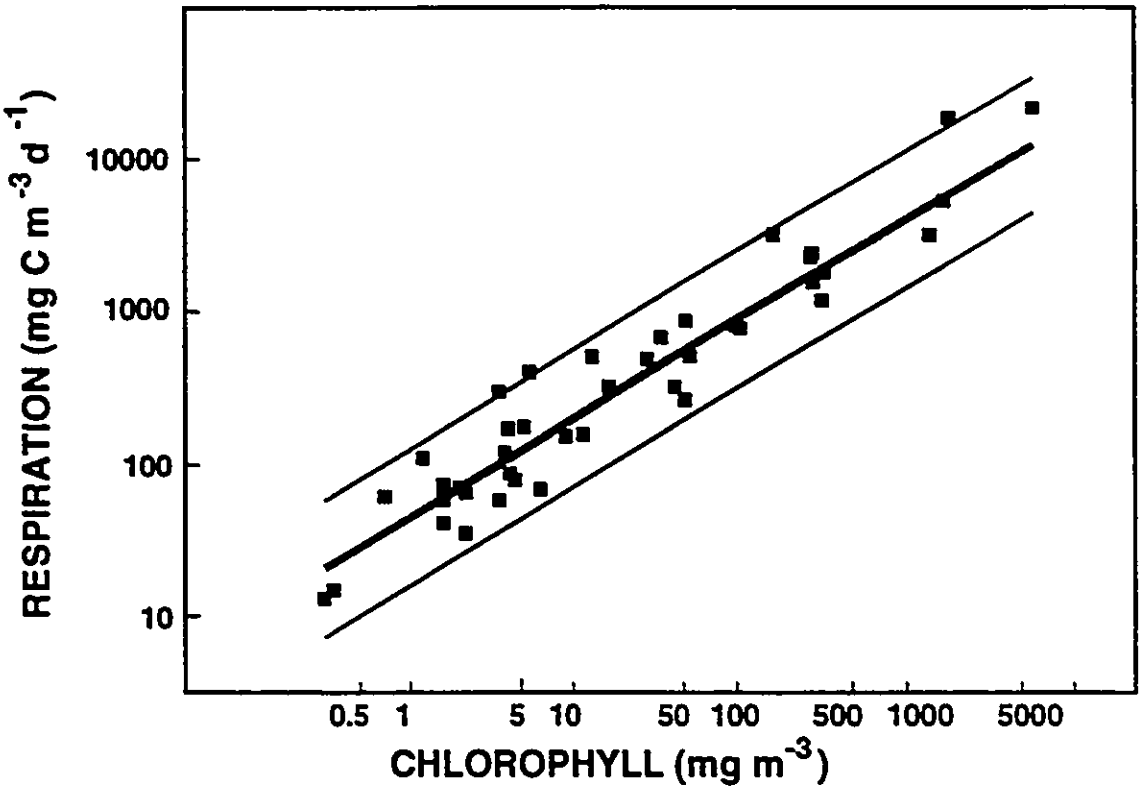
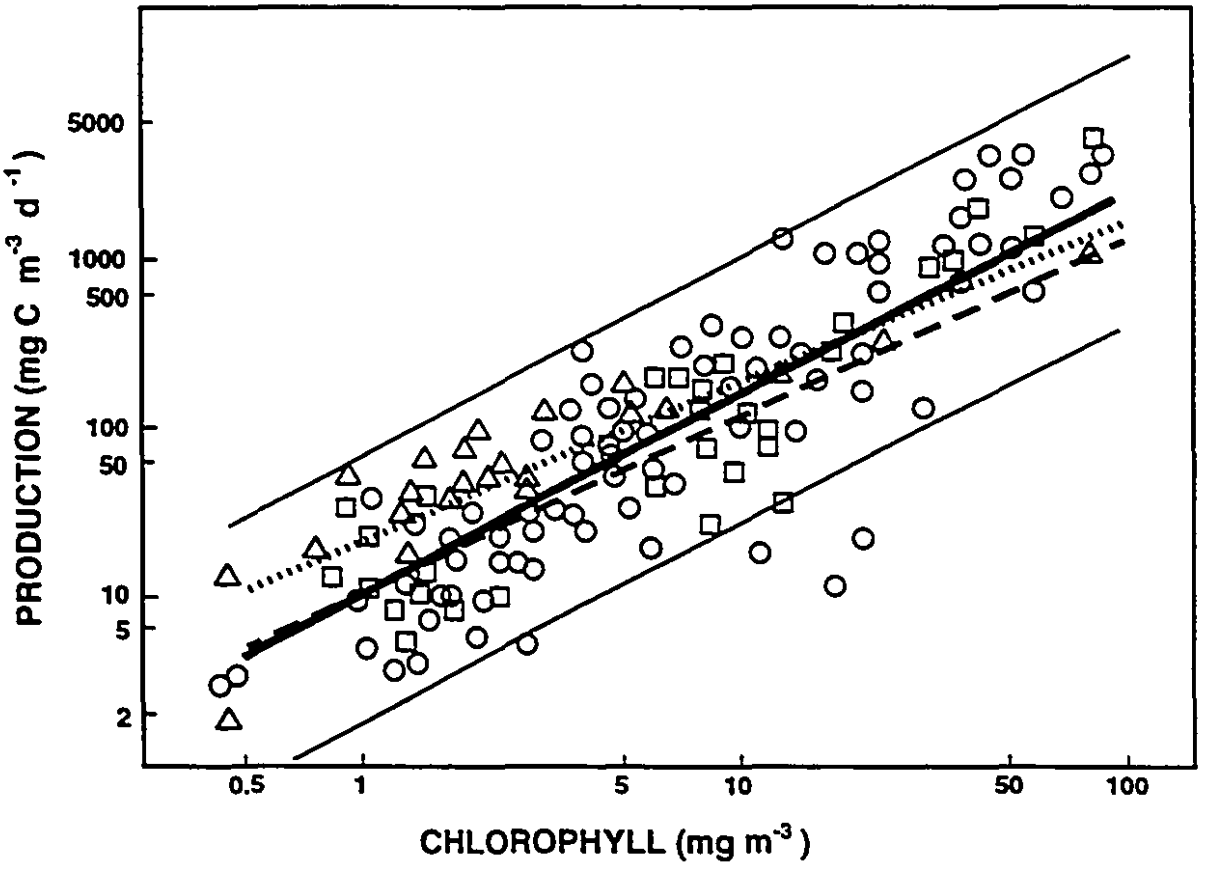

RESPIRATION (mg C m$^{-3}$ d$^{-1}$)
10000
1000
100
10
0.5
1
5
10
50
100
500
1000
5000
CHLOROPHYLL (mg m$^{-3}$)

Figure 2. Volumetric rates of phytoplankton production as a function of the chlorophyll concentration. Points represent seasonal euphotic or epilimnetic means for 118 lakes worldwide. The plot shows the line of best fit and the 95% confidence intervals for the predicted values (full lines) for the complete data set. Triangles are rates integrated over the mixed layer, and the dotted line is the best fit line to these data. Squares represent rates integrated over the euphotic zone, and the dashed line is the best fit line for this sub-set. Circles indicate data for which the integration depth was not specified.


PRODUCTION (mg C m$^{-3}$ d$^{-1}$)
5000
1000
500
100
50
10
5
2
0.5
1
5
10
50
100
CHLOROPHYLL (mg m$^{-3}$)

similarity of the two equations suggests that the relation between volumetric phytoplankton production and chlorophyll is robust over a wide variety of freshwater ecosystems with the range of 0.3-120 mg chlorophyll.$m^{-3}$. Available data (del Giorgio, unpublished) suggest that primary production rises more slowly above 150-200 mg .$m^{-3}$ where the relationship is not linear, so the regression should not be extrapolated to even more eutrophic sites.

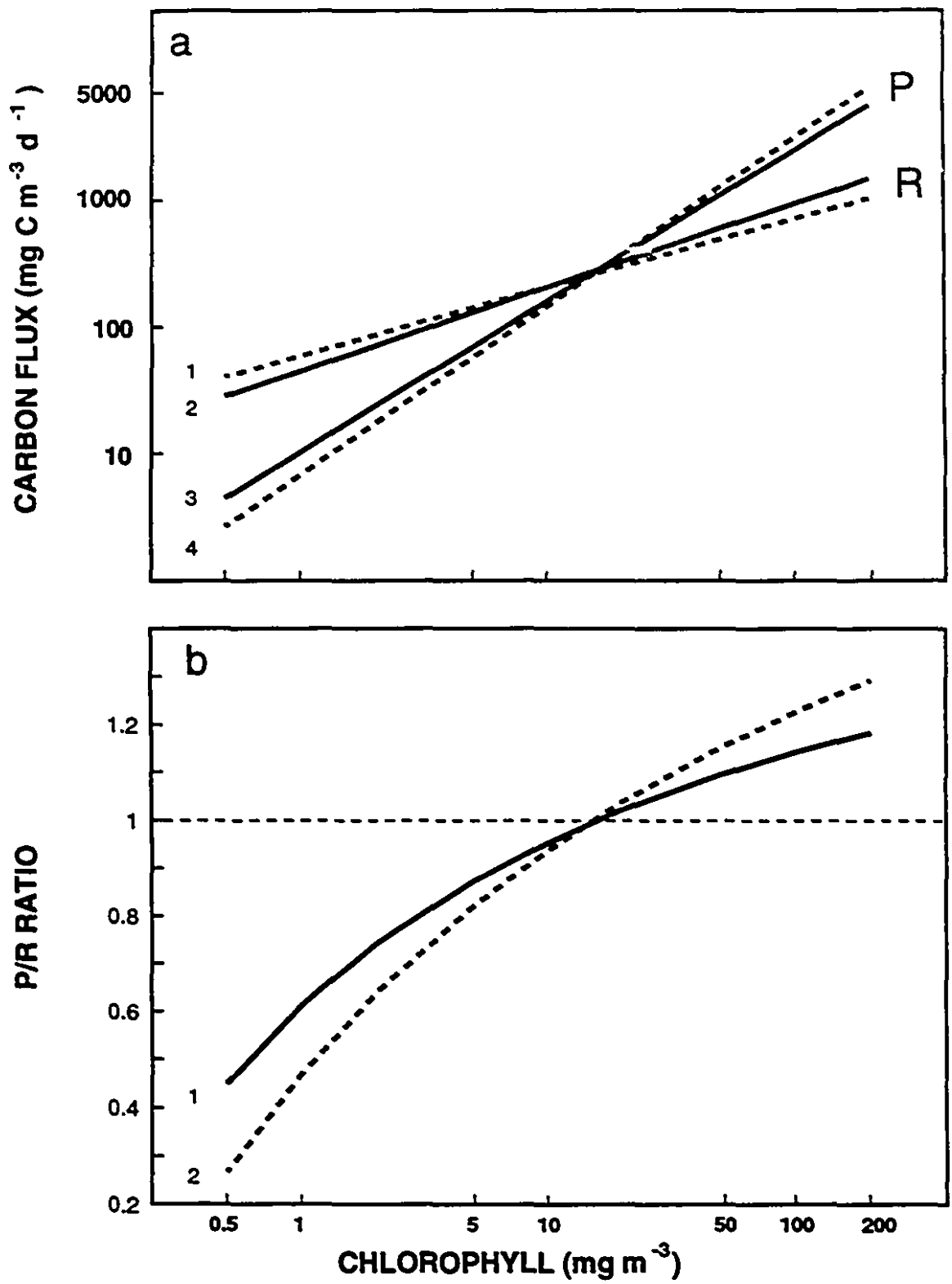
As chlorophyll concentrations increase, the depth of the euphotic zone decreases (Bannister 1974). In eutrophic lakes, the euphotic zone may comprise only a small portion of the mixed layer, so that rates of photosynthesis integrated over the euphotic zone are likely to overestimate mean volumetric rates of the mixed layer. Conversely, the euphotic zone may extend well below the epilimnion in clear oligotrophic lakes. This may result in a bias when comparing production with plankton respiration averaged over the epilimnion or the entire depth in shallow lakes. Our analysis aggregates rates integrated over the euphotic zone, the mixed layer, and data for which the depth of integration was unspecified. To assess any systematic differences in the various estimates of volumetric primary production we separated the analysis of rates integrated over the euphotic zone from those integrated over the epilimnion. Data for which the integration depth was not specified were not included in either. Figure 2 shows the regression lines for the sub-sets of euphotic and mixed layer estimates, together with the general model. The slopes of the regression models for the rates integrated over the euphotic zone or the epilimnion are not significantly different ($P < 0.05$) from each other or from the slope for the mixed data set. The intercept for the epilimnetic data is significantly different ($P < 0.05$) from the intercepts of the other two models, which are not significantly different ($P < 0.05$) from each other. Thus, the model using the aggregated data would seem to slightly underestimate volumetric rates of primary production for the mixed layer of oligotrophic lakes, and

overestimate the rates in eutrophic waters (Fig. 2), as could be expected. The magnitude of these differences is small, however, compared to the variability of the data and equation 2, derived from the aggregated data, may be used for practical purposes.

**The P/R Ratio:** The high intercept of equation 1, relative to equation 3, shows that in oligotrophy plankton respiration (Eq. 1) is high relative to phytoplankton production (Eq. 3), but the lower slope of equation 1 shows that respiration increases less rapidly with chlorophyll than does phytoplankton production (Fig. 3a). As a result, P/R is low in less rich lakes, and rises above unity only when chlorophyll concentrations are above 17-20 $mg.m^{-3}$, that is, for eutrophic lakes (Fig. 3b). The conclusions of the analysis are strengthened when Model II regression (Ricker 1973) is applied. The slope for the respiration equation remains almost unchanged, due to the very high $r^2$ of Eq.1, whereas the slope of the production model (Eq.3) further increases (Model II slope = 1.37). Combination of the equation for calculated plankton respiration (Eq.2) with the production equation based on Smith's data yields essentially the same pattern, even though the data sets in Figure 3a-b are independent. If only the rates of production calculated for the mixed layer (Fig. 2) were used, the pattern would be the same, but the point where the P/R ratios rise above unity would be lowered to around 10 $mg.m^{-3}$ chlorophyll.

Methodological problems may affect these patterns. The standard $^{14}C$ method may underestimate rates of carbon assimilation, particularly in very unproductive waters (Laws et al. 1987). In addition, many studies have not taken into account the organic carbon excreted (EOC) by the algae and there is evidence that EOC is relatively more important, up to 40-50% of the total carbon assimilated, in the phytoplankton of oligotrophic areas (Baines and Pace 1991). Also, the chlorophyll-production equations

Figure 3. (a) Equations describing planktonic primary production and respiration vs chlorophyll concentration: Line 1, planktonic respiration as the summed respiration of different components of the plankton (Eq. 2). Line 2, total plankton respiration line derived from literature data (Eq. 1). Line 3 represents phytoplankton production derived from literature data (Eq.3). Line 4 is phytoplankton production proposed by Smith (1979). (Fig. 3b) P/R ratios of the plankton estimated from 1) phytoplankton production (Eq. 3) and plankton respiration (Eq. 1) derived from literature data and 2) primary production taken from Smith (1979) and plankton respiration calculated from biomass (Eq. 2).


a
5000
1000
100
10
CARBON FLUX (mg C m-3 d-1)
P
R
1
2
3
4
b
1.2
1
0.8
0.6
0.4
0.2
P/R RATIO
1
2
0.5
1
5
10
50
100
200
CHLOROPHYLL (mg m-3)

tend to underestimate rates in very oligotrophic sites. All of these errors would decrease estimates of primary production in oligotrophic lakes, but it is presently impractical to correct for these potential sources of error, because they are not well quantified. On the other hand, there are reasons to suspect that plankton respiration may also be underestimated. Long incubations may reduce estimated respiration (Williams 1981), and respiration in the aphotic zone is not included so errors in underestimating P may be offset by other errors that underestimate R. The use of a constant RQ of 1 to convert oxygen uptake data to carbon adds further uncertainty to the comparison between the production and respiration data. The respiratory quotient of natural populations varies with the type and physiological condition of the organisms and the substrates that are consumed. We have chosen an RQ of 1 because the value lies approximately halfway within the range of reported values (0.8-1.2) for natural plankton communities. We repeated the analysis using constant quotients of 0.8 or 1.2, which resulted in slightly different intercepts of the respiration vs chlorophyll equation expressed in carbon units, but in no major change in the patterns shown. However, if planktonic RQs change in a systematic manner, and are positively related to TP, the respiration relationship in Figures 1 and 3a would have a lower intercept and a steeper slope. This pattern would again reduce the discrepancy between respiration and production. Nevertheless, available figures suggest that the combined effects of various methodological problems are not large enough to override the trends in Figure 2, although they could certainly shift the point of intersection of the P and R lines. The value of 17-20 $mg.m^{-3}$ chlorophyll is therefore only indicative.

The inclusion of hypolimnetic oxygen consumption would lower the P/R ratios even further. Cornett and Rigler (1979) found that areal hypolimnetic oxygen deficits were affected by lake morphometry and increased with hypolimnetic depth. Since eutrophic lakes tend to be shallower, considering the oxygen consumed in the whole water

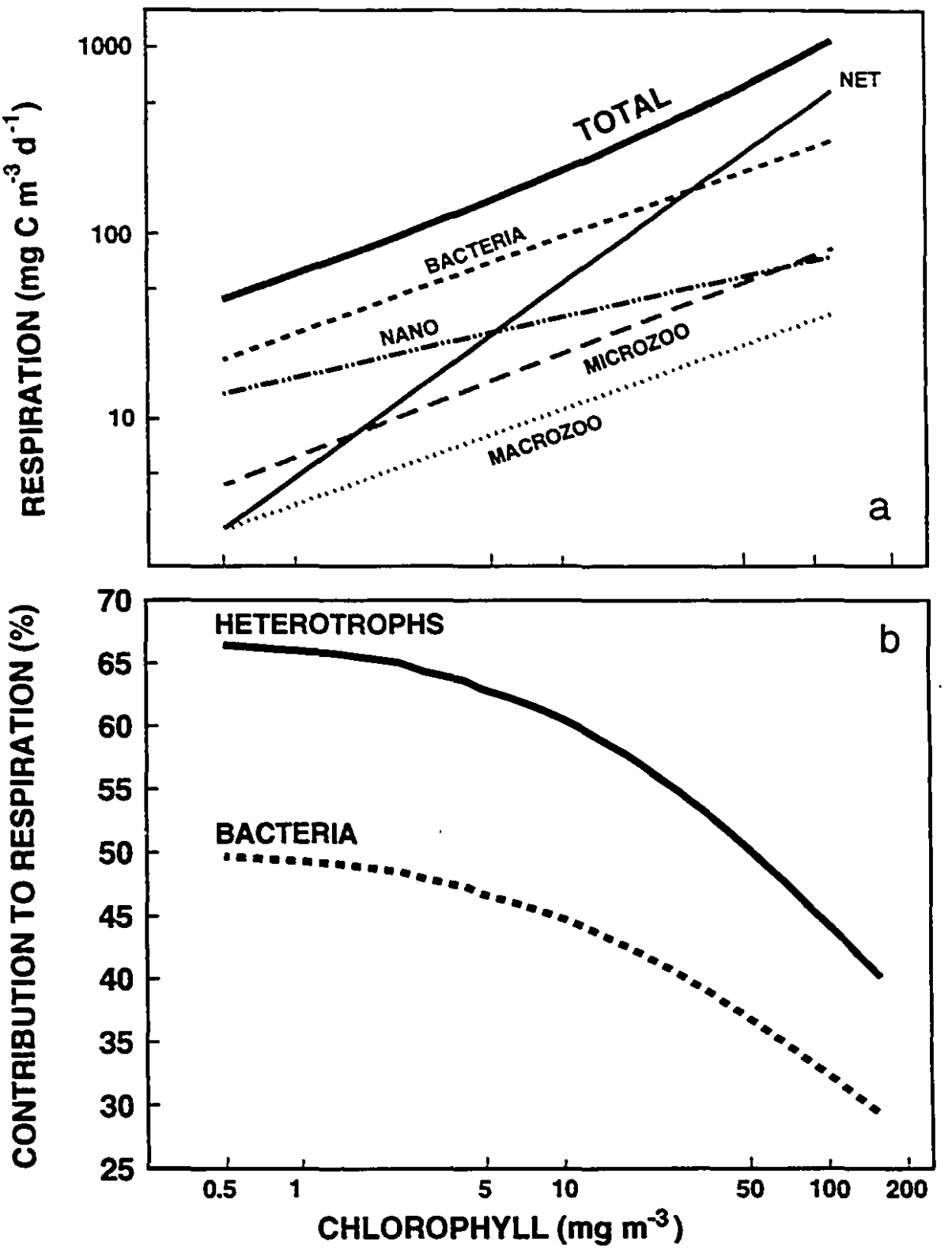
column would depress ratios more in oligotrophic lakes. In eutrophic lakes respiration may shift from the water column to the sediments (Charlton 1980), so that benthic metabolism represents a major portion of the carbon flow. Sediment oxygen consumption, however, varies little (Graneli 1978; Charlton 1980; Cornett 1982). Therefore, the inclusion of aerobic sediment respiration is unlikely to alter patterns in P/R. Anaerobic carbon pathways may play a major role in the metabolism of more productive lakes; however, they could not be included in our present analysis.

Figure 3 suggests that the plankton communities in many oligotrophic to mesotrophic lakes consume more organic carbon than the phytoplankton produce. The origin of the carbon supplements to the plankton will vary with the watershed and lake morphometry. In shallower lakes, the littoral macrophytes and periphyton will probably be major sources of additional organic matter (Wetzel 1990), whereas deep oligotrophic lakes, often with steeper slopes will be more influenced by material derived from the watershed. Many such lakes receive substantial amounts of allochthonous organic matter (Wissmar et al. 1977, Johansson 1983), as is reflected in varying degrees of color of the water (Rasmussen et al. 1989). Whatever its origin, the dissolved organic carbon (DOC) pool is likely to play a major role in supporting the consumption of carbon in excess of primary production (Tranvik 1992). Thus, it is conceivable that DOC levels interact with TP to further shape the P/R curves of the plankton along gradients of enrichment. Unfortunately, we could not test this hypothesis with the present data set because few of the papers from where the data were extracted reported either DOC, color, or even the size of the drainage basin, which can be used to estimate the DOC load. Thus, for a given TP level, we would expect the discrepancy between P and R to be greater in lakes where the DOC concentrations are high, but this hypothesis remains to be tested. Our results suggest that the changes in phytoplankton production are the main factor affecting the balance

between P and R in the plankton, and that the impact of the supplementary sources of carbon is greatest where phytoplankton production is low. We propose a simple explanation for this pattern: A portion of the DOC pool is derived from the phytoplankton, and has a short turn-over time. The bulk of the dissolved organic carbon, however, is derived from other sources, such as terrestrial runoff and macrophytes. These last fractions turn over more slowly, but nevertheless support a significant bacterial production (Tranvik 1988, 1992). Although the amount of DOC varies considerably across freshwater systems, most lakes fall within the 1.5 to 9 mg $l^{-1}$ range (Rasmussen et al. 1989). Thus, the bacterial activity supported by the DOC pool is unlikely to vary by more than a factor of 6. Lakes, however, commonly vary in TP, chlorophyll concentration and primary production by three orders of magnitude. Where phytoplankton production is extremely low, the baseline bacterial production supported by the DOC pool may equal or even exceed that supported by phytoplankton-derived carbon, even in clear-water lakes. Along a gradient of enrichment, however, the DOC pool and the bacterial activity associated with it does not increase nearly so much as primary production, and in eutrophy allochthonous DOC is much less important to the heterotrophic activity than carbon from phytoplankton.

**The Contribution of Planktonic Components to Community Respiration:** Respiration by net phytoplankton increases much more dramatically with trophy than does respiration by all the other components (Fig. 4a). As a result, heterotrophs contribute most to community respiration in oligotrophic lakes and less with increasing trophy (Fig. 4b). Overall, the sum of heterotroph respiration comprises over 65% of community respiration in oligotrophy but less than 40% in eutrophy. The contribution of bacteria alone similarly declines from over 50% to less than less than 30%. The calculated contribution of zooplankton (<20%) is in agreement with published reports

Figure 4. (a) Total respiration and respiration for individual components of the plankton community, calculated from the predicted biomasses, as functions of chlorophyll concentration. Abbreviations in Table 2. (b) The percent contribution of heterotrophs (bacteria + microzooplankton + macrozooplankton) to total plankton respiration, calculated from predicted biomass as functions of chlorophyll concentration.


1000
100
10
RESPIRATION (mg C m-3 d-1)
TOTAL
NET
BACTERIA
NANO
MICROZOO
MACROZOO
a
70
65
60
55
50
45
40
35
30
25
CONTRIBUTION TO RESPIRATION (%)
HETEROTROPHS
BACTERIA
b
0.5
1
5
10
50
100
200
CHLOROPHYLL (mg m-3)

of zooplankton respiration, which range from <10% to around 20% of community respiration (reviewed by Schwaerter et al. 1988). The highest value reported is 46% for oligotrophic Mirror Lake (Cole et al. 1989).

Our estimates of bacterial respiration are rather conservative. This is in part due to the assumption that only 70% of the predicted biomass of bacteria is metabolically active, and also to our decision to assign a rather high cell volume (0.09 $\mu m^3$), which results in a low specific respiration rate for the bacteria. Straskrabova (1979), Oleynik (1990) and Bell and Kuparinen (1984) report that bacterial respiration ranges from 30 to over 90% of total respiration for oligo- to mesotrophic waters; Schwaerter et al. 1988 report contributions of around 50% in two eutrophic lakes.

Bacteria seem less important in marine systems. There is ample evidence from marine studies, that the smaller size-classes (< 5 μm) may account for a large proportion of plankton community respiration, and that microheterotrophs may dominate the activity of these size-classes (Williams 1981; Hopkinson et al. 1989). However, based on measurements of bacterial production, it has been estimated that over 50% of primary production enters the microbial food web (Smith et al. 1986), and that bacterial production averages 20% of volumetric primary production across marine and freshwater systems (Cole et al. 1988). Based on these same calculations, Cole et al. (1988) have suggested that microbial respiration (bacteria plus protozoa) should not exceed 50% of net primary production. Given these limitations, Cole et al. (1988; 1989) also suggested that zooplankton respiration should equal or exceed bacterial respiration in lakes.

Our results for freshwater plankton indicate that bacterial respiration alone may equal and exceed phytoplankton production in oligotrophic lakes. There are several

explanations for the discrepancy between marine and freshwater systems. Most of the data for calculations of bacterial consumption and respiration are derived from marine plankton, where bacterial activity may depend more on primary production, especially in open waters where external inputs of carbon are small. Bacterial growth yields may be lower than the 40-50% generally assumed in carbon flow models (Smith et al. 1986), so marine calculations based on production rates may greatly underestimate bacterial respiration. Most importantly, the equation of bacterial production as a function of chlorophyll concentration of Cole et al. (1988) has a very low intercept. A more recent model (White et al. 1991) has a very similar slope, but the intercept is almost three times higher. As a result, this model yields rates of bacterial production that are three-fold higher than previous estimates for lakes with low chlorophyll concentrations. Bacterial respiration rates along a gradient of chlorophyll in lakes, recalculated from the bacterial production equation of White et al. (1991) and assuming a 20% growth yield, are in excellent agreement with our own estimates based on allometry. Moreover, both approaches indicate that bacterial respiration probably exceeds primary production in lakes with chlorophyll concentration below 4-5 $mg.m^{-3}$.

We surmise that a significant fraction of the excess respiration is most likely due to bacterial utilization of DOC from various external sources. The extent to which this repackaged organic matter is transferred to higher levels of the trophic web, and not dissipated at the base of the food web, has been a matter of contention (Ducklow 1991). Bacteria may exhibit very low growth yields when utilizing humic organic matter or detrital plant material (Linley and Newell 1984, Hessen 1992). If this is the case, only a small fraction of the total carbon taken up is actually converted into bacterial biomass, so that this allochthonous DOC may not have significant effects on the resources available to other planktonic organisms. However, empirical models

indicate that zooplankton biomass and production increase only slowly along gradients of TP or chlorophyll (McCauley and Kalff 1981; Pace 1986). As a result, zooplankton biomass and production, relative to phytoplankton, are highest in oligotrophic lakes, and decline abruptly with trophy. A number of processes have been invoked to explain this pattern: most concern the availability of algal carbon to consumers, such as the decrease in the proportion of edible algae with increasing trophy (Watson and McCauley 1988), a greater loss of algal carbon to sedimentation in eutrophic lakes (Hargrave 1973), or lower algal turnover rates toward eutrophy (Harris 1984). It is conceivable, however, that these patterns in zooplankton biomass and production reflect the larger relative importance of bacteria as food for zooplankton in oligotrophic lakes. Bacteria comprise a substantial portion of the biomass of oligotrophic plankton, and this contribution decreases with trophy. Zooplankton production may be high relative to phytoplankton biomass and production in oligotrophy, because zooplankton depend more on the bacteria. Such a process would elevate the intercepts and lower the slopes of the empirical models relating biomass and production of various components of the zooplankton to TP or chlorophyll.

## CONCLUSIONS

Planktonic P/R ratios are very low in unproductive lakes because a greater fraction of the total carbon flux in the planktonic food web flows through heterotrophs in oligotrophic systems, contributing to the respiration term of the ratio but not to the primary production term. Our results suggest that the dependence on carbon inputs external to the plankton is more pronounced in oligotrophic to mesotrophic lakes, in agreement with the hypothesis of Odum and Prentki (1978) that the magnitude of autotrophic production determines whether a system is auto- or heterotrophic. The concentrations of dissolved organic carbon, the main source of supplementary carbon

to the plankton, should interact with the levels of TP or chlorophyll to shape the planktonic P/R curves along trophic gradients, but this hypothesis should be further tested. It is noteworthy, however, that the data set used in this analysis comprised both colored and clear water lakes of varying trophy. Regardless of the humic content of the water, the plankton of oligotrophic lakes showed elevated rates of respiration relative to their counterparts in eutrophy. In addition, the trends presented in this analysis are approximate; there are problems inherent to the production estimates, the conversion from oxygen to carbon, and in the comparison of production and respiration data from entirely different sets of lakes. This calls for a cautious interpretation of the results, and for more rigorous tests of the patterns.

Current estimates place bacterial production by direct measurements as an average 20% of primary production. These estimates may have to be revised for oligotrophic lakes, because the magnitude of community respiration, and the likely contribution of bacteria to overall metabolism calculated in this paper are consistent only if rates of bacterial production are three-fold higher, or if bacterial growth yields approach zero. Whether this increased bacterial activity results in enhanced overall heterotrophic activity in the plankton is still a matter of contention. There is evidence, however, to suggest that zooplankton also show elevated biomass and production in relation to phytoplankton in oligotrophic lakes. Regardless of whether the external energy subsidies are dissipated at the bacterial level, or transmitted up the food web, scaling freshwater plankton processes to phytoplankton production seems inappropriate because it ignores much of the energy base of the community. This warning holds particularly in oligotrophic lakes.

## ACKNOWLEDGEMENTS

This research was supported by the Governments of Canada and of Quebec through NSERC and FCAR, respectively, and represents a contribution from the Limnology Research Centre, McGill University. We thank J. Gasol, and to three anonymous referees for their critical comments on the manuscript.

## REFERENCES

Adams, M.S., T.W. Meinke, and T.K. Kratz. 1990. Primary productivity of three Northern Wisconsin lakes, 1985-1987. Verh. int. Ver. Limnol. 24: 432-437.

Ahrens, M., and R.H. Peters. 1991. Plankton community respiration: relationships with size distribution and lake trophy. Hydrobiologia 224: 77-87.

Alimov, A.F., and G.G. Winberg. 1972. Biological productivity of two northern lakes. Verh. int. Ver. Limnol. 18: 65-70.

Baines, S.B., and M.L. Pace. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnol. Oceanogr. 36: 1078-1090.

Bannister, T.T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. 19: 1-12.

Barica, J. 1975. Collapses of algal blooms in prairie pothole lakes: their mechanism and ecological impact. Verh. int. Ver. Limnol. 19: 606-615.

Bayne, D.R., W.C. Seesock, C.E. Weber, and J.A. McGuire. 1990. Cultural eutrophication of West Point Lake - a 10-year study. Hydrobiologia 199: 143-156.

Beauchamp, S.T., and J. Kerekes. 1989. Effects of acidity and DOC on phytoplankton community structure and production in three acid lakes (Nova Scotia). Wat. Air Soil Poll. 46: 323-333.

Beaver, J.R., and T.L. Crisman. 1991. Importance of latitude and organic color on phytoplankton primary productivity in Florida lakes. Can. J. Fish. Aquat. Sci. 48: 1145 1150.

Belay, A., and R.B. Wood. 1984. Primary productivity in five Ethiopian Rift Valley lakes. Verh. int. Ver. Limnol. 22: 1187-1192.

Bell, R.T., and J. Kuparinen. 1984. Assessing phytoplankton and bacterioplankton during early spring in Lake Erken, Sweden. Appl. Environ. Microbiol. 48:1221-1230.

Benner, R., J. Lay, E. K'neesm and R.E. Hodson. 1988. Carbon conversion efficiency for bacterial growth on lignocellulose: implications for detritus-based food webs. Limnol. Oceanogr. 33: 1514-1526.

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

Carmouze, J.P., J.R. Durand, and C. Leveque (ED.) 1983. Lake Chad. Monographiae Biologicae 33. W. Junk, The Hague. 575 p.

Charlton, M.N. 1980. Hypolimnion oxygen consumption in lakes: discussion of productivity and morphometry effects. Can. J. Fish. Aquat. Sci. 37:1531-1539.

Chenard, P.G. 1980. Oxygen consumption in two subarctic lakes. M.Sc. Thesis, Univ. McGill, Montreal, Que. 133 p.

Caron, A.W. 1976. Benthic community metabolism and primary production of a culturally eutrophied high arctic lake. M.Sc. Thesis, Univ. McGill, Montreal, Que. 108 p.

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

----., N.F. Caraco, D.L. Strayer. 1989. A detailed organic carbon budget as an ecosystem-level calibration of bacterial respiration in an oligotrophic lake during midsummer. Limnol. Oceanogr. 34: 286-296.

Cornett, R.J. 1982. The prediction and interpretation of hypolimnetic oxygen deficits. Ph.D. thesis, McGill University.

----, and F.H.Rigler. 1979. Hypolimnetic oxygen deficits: their prediction and i interpretation. Science 205:580-581.

Currie, D.J. 1991. Large-scale variability and interactions among phytoplankton, bacterioplankton, and phosphorus. Limnol. Oceanogr. 35: 1437-1455.

CSIR. 1985. The limnology of Hartbeespoort Dam, p. 142-144. South African Nat. Sci. Programmes Rep. 10. Foundation for Research Development, Pretoria. 269 p.

Devol, A.H. 1979. Zooplankton respiration and its relation to plankton dynamics in two lakes of contrasting trophic state. Limnol. Oceanogr. 24:893-905.

Dillon, P. J., and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767-773.

Dubinsky, Z., T. Berman, and F. Schanz. 1984. Field experiments for in situ measurement of photosynthetic efficiency and quantum yield. J. Plankton Res. 6: 330-349.

Ducklow, H.W. 1991. The passage of carbon through microbial food webs: results from flow network models. Mar. Microb. Food Webs 5: 129-144.

Finlay, S., L. Carlough, M.T. Crocker, H.K. Gill, J.L. Meyer, and P.J. Phillip. 1986. Bacterial growth on macrophyte leachate and the fate of bacterial production. Limnol. Oceanogr. 31: 1335-1341.

Fontaine, T.D., and K. Carter Ewel. 1981. Metabolism of a Florida lake ecosystem. Limnol. Oceanogr. 26:754-763.

Ganf, G.G. 1974. Rate of oxygen uptake by the planktonic community of a shallow equatorial lake (Lake George, Uganda). Oecologia 15: 17-32.

Gibson, C.E. 1975. A field and laboratory study of oxygen uptake by planktonic blue-green algae. J. Ecol. 63: 867-880.

Graneli, W. 1978. Sediment oxygen uptake in South Swedish lakes. Oikos 30:7-16.

Grobbelaar, J.U., and C.J. Soeder. 1985. Respiration losses in planktonic green algae cultivated in raceway ponds. J. Plankton Res. 7: 497-506.

Hargrave, B.T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30: 1317-1326.

Harris, G.P. 1984. Phytoplankton productivity and growth measurements: past, present and future. J. Plankton Res. 6: 219-237.

Hessen, D.O. 1992. Dissolved organic carbon in a humic lake: effects on bacterial production and respiration. Hydrobiologia 229: 115-123.

----, T. Andersen, and A. Lyche. 1990. Carbon metabolism in a humic lake: Pool sizes and cycling through zooplankton. Limnol. Oceanogr. 35:84-99.

Heyman, U. 1983. Relations between production and biomass of phytoplankton in four Swedish lakes of different trophic status and humic content. Hydrobiologia 101: 89-104.

Hopkinson, C.S., B. Sherr, and W.J. Wiebe. 1989. Size fractioned metabolism of coastal microbial plankton. Mar. Ecol. Progr. Ser. 51: 155-166.

Hunding, C. 1979. The oxygen balance of Lake Myvatn, Iceland. Oikos 32: 139-150.

Ikeda, T., and S. Motoda. 1978. Zooplankton production in the Bering Sea calculated from 1956-1970 Oshoro Maru data. Mar. Sci. Comm. 4:329-346.

Jackson, D.F. 1969. Primary production studies in Onondaga Lake, N.Y. Verh. int. Ver. Limnol. 17: 86-94.

Jackson, T.A., and R.E. Hecky. 1980. Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37: 2300-2317.

Johansson, J.A. 1983. Seasonal development of bacterioplankton in two forest lakes in central Sweden. Hydrobiologia 101:71-88.

Jones, R.I. 1977. Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh). J. Ecol. 65: 561-577.

Kamp-Nielsen, L. 1981. Diurnal variation in phytoplankton oxygen metabolism. Verh. int. Ver. Limnol. 21: 431-437.

Kankaala, P. 1988. The relative importance of algae and bacteria as a food source for *Daphnia longispina* (Cladocera) in a polyhumic lake. Freshwat. Biol. 19: 285-

296.

Kifle, D., and A. Belay. 1990. Seasonal variation in phytoplankton primary production in relation to light and nutrients in Lake Awasa, Ethiopia. Hydrobiologia 196: 217-227.

Kravtsova, G.V., L.I. Vol'vich, and Y.A. Katretskiy. 1988. The role of various plankton components in the decomposition of organic matter. Hydrobiol. J. 28: 1-7.

Lafond, M., B. Pinel-Alloul, and P. Ross. 1990. Biomass and photosynthesis of size-fractioned phytoplankton in Canadian Shield lakes. Hydrobiologia 196: 25-38.

Laws, E. A., G. R. DiTullio, and D. G. Redalje. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogr. 32: 905-918.

Likens, G.E., and F.H. Bormann. 1979. The role of watershed and airshed in lake metabolism. Arch. Hydrobiol. 13: 195-211.

Linley, E.A.S., and R.C. Newell. 1984. Estimates of bacterial growth yields based on plant detritus. Bull. Mar. Sci. 35: 409-425.

Malueg, K.W., J.R.Tilstra, D.W. Schults, and C.F. Powers. 1972. Limnological observations on an ultra-oligotrophic lake in Oregon, USA. Verh. int. Ver. Limnol. 18: 292-302.

Markager, S., and K. Sand-Jensen. 1989. Patterns of night-time respiration in a dense phytoplankton community under a natural light regime. J. Ecol. 77: 49-61.

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

Mitchell, S.F., and C.W. Burns. 1979. Oxygen consumption in the epilimnia and hypolimnia of two eutrophic, warm- monomictic lakes. N. Z. Jour. Mar. Freshwat. Res. 13: 427-441.

Newell, S. Y., R. D. Fallon, B. F. Sherr, and E. B. Sherr. 1988. Mesoscale temporal variation in bacterial crop, percent active cells, productivity and output in a salt-

marsh tidal river. Verh. Internat. Ver. Limnol. 23: 1839-1845.

Northcote, T.G., P. Morales, D.A. Levy, and M.S. Greaven (eds.). 1989. Pollution in Lake Titicaca, Peru: training, research and management. Westwater Res. Centre, Univ. of British Columbia. 140 p.

Odum, H.T. 1957. Trophic structure and productivity in Silver Springs, Florida. Ecol. Monogr. 27:55-112.

Odum, W.E., and R.T. Prentki. 1978. Analysis of five North American lake ecosystems IV. Allochthonous carbon inputs. Verh. int. Ver. Limnol. 20:574-580.

Oleynik, G.N. 1990. Respiration rate of bacteria in the plankton subsystem of canals of the Ukraine. Hydrobiol. Bull. 12: 49-52.

Pace, M.L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. Limnol. Oceanogr. 31:45-55.

Pick, F.R. 1984. Photosynthesis and respiration of a metalimnetic chrysophyte population. Verh. int. Ver. Limnol. 22: 326-331.

Rasmussen, J.B., L. Godbout, and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. Limnol. Oceanogr. 34:1336-1343.

Robinson, W.R., R.H. Peters, and J. Zimmerman. 1983. The effects of body size and temperature on metabolic rate of organisms. Can. J. Zool. 61:281-288.

Ruggiu, D., and R. Mosello. 1984. Nutrient levels and phytoplankton characteristics in the deep southern alpine lakes. Verh. int. Ver. Limnol. 22: 1106-1112.

Salonen, K., and T. Hammar. 1986. On the importance of dis solved organic matter in the nutrition of zooplankton in some lake waters. Oecologia 68: 246-253.

----, K. Kononen, and L. Arvola. 1983. Respiration of plankton in two small, polyhumic lakes. Hydrobiologia 101:65-70.

Sarvala, K., and others. 1981. The ecosystem of lake Pääjärvi: secondary production and an ecological energy budget of the lake. Verh. int. Ver. Limnol. 21:454-459.

Scavia, D., and G.A. Laird. 1987. Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. 32:1017-1033.

Schwaerter, S., M. Søndergaard, B. Riemann, and L.M.J. Jensen. 1988. Respiration in eutrophic lakes: the contribution of bacterioplankton and bacterial growth yield. J. Plankton Res. 10:515-531.

Serruya, C., and S. Serruya. 1972. Oxygen content in Lake Kinneret: physical and biological consequences. Verh. int. Ver. Limnol. 18: 580-587.

Smith, R.E.H., W.G. Harrison, B. Irwin, and T. Platt. 1986. Metabolism and carbon exchange in microplankton of the Grand Banks (Newfoundland). Mar. Ecol. Progr. Ser. 34: 171-183.

Smith, V.H. 1979. Nutrient dependence of primary productivity in lakes. Limnol. Oceanogr. 24:1051-1064.

Spurr, B. 1975. Limnology of Bird Pond, Ross Island, Antarctica. N.Z. J. Mar. Freshwat. Res. 9: 547-562.

Stockner, J.S., and J.G. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia: empirical relationships between nutrient inputs and phytoplankton biomass and production. Can. J. Fish. Aquat. Sci. 42: 649-658.

Straskrabova, V. 1979. Oxygen methods for measuring the activity of water bacteria. Arch. Hydrobiol. 12: 3-10.

Strayer, D. 1988. On the limits of secondary production. Limnol. Oceanogr. 33:1217-1220.

Talling, J.F., R.B. Wood, M.V. Prosser, and R.M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshwat. Biol. 3: 53-76.

Tolstoy, A. 1988. Predicted and measured annual primary production of phytoplankton - examples from some Swedish lakes. Arch. Hydrobiol. 113: 381-404.

Tranvik, L. J. 1988. Availability of dissolved organic carbon for planktonic bacteria in

oligotrophic lakes of different humic content. Microb. Ecol. 16: 311-322.

----. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

Watson, S., and E. McCauley. 1988. Contrasting patterns of net- and nanoplankton production and biomass among lakes. Can. J. Fish. Aquat. Sci. 45:915-920.

Welch, H.E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. 19: 65-73.

----, P.J. Dillon, and A. Sreedharan. 1976. Factors affec ting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809-1815.

Wetzel, R.G. 1983. Limnology, Saunders.

----. 1990. Detritus, macrophytes and nutrient cycling in lakes, p. 233-252. In R. de Bernardi, G. Giussani, and L. Barbanti (eds.) Scientific perspectives in theoretical and applied limnology. Mem. ist. Ital. Idrobiol. 47.

----, and J.E. Richey. 1978. Analysis of five North American lake ecosystems VII. Control mechanisms and regulation. Verh. int. Ver. Limnol. 20:605-608.

White, P.A., J. Kalff, J.B. Rasmussen, and J.M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb. Ecol. 21: 99-118.

Wilkinson, L. 1987. SYSTAT: the system for statistics. SYSTAT Inc., Evanston.

Williams, P.J.leB. 1981. Microbial contribution to overall marine plankton metabolism: direct measurements of respiration. Oceanol. Acta 4:359-364.

Wissmar, R.C, J.E. Richey, and D.E.J. Spyridakis. 1977. The importance of allochthonous particulate carbon pathways in a subalpine lake. J. Fish. Res. Board Can. 34:1410-1418.

Chapter 2

# BIOMASS ALLOCATION IN FRESHWATER PLANKTON COMMUNITIES

## ABSTRACT

Both resource control of heterotrophic biomass and heterotrophic regulation of plant populations imply that heterotrophic biomass should constitute an increasingly smaller proportion of total system biomass as the turnover time of autotrophs increases. Although this trend is widely accepted, it has seldom been tested, perhaps because comparable data for many ecosystems are hard to collect. The plankton are an exception to this difficulty. Because the biomasses of both autotrophs and heterotrophs can be estimated with relative ease, and because workers use similar techniques, data are available from a wide range of lakes. Both literature data, representing a wide geographic range, and data from a localized set of lakes show that the ratio of heterotrophic to autotrophic biomass (H/A ratio) is well above unity where autotrophic biomass is low, and declines where autotrophic biomass is high. A similar pattern is found in marine and terrestrial systems. In terrestrial systems, this pattern has been explained by changes in the turnover time of the autotrophic biomass, but in lakes energetic subsidies from the littoral and the watershed are likely needed to support the relatively high heterotrophic biomass of many oligotrophic systems.

## INTRODUCTION

One of the oldest and most important paradigms in ecology suggests that biomass is usually distributed as a pyramid (Elton 1927), where a broad autotrophic base supports successively smaller strata of heterotrophs (Odum 1971; Wetzel 1983), although inverted biomass pyramids may occur where the autotrophic base has a high rate of turnover (Odum 1971). Despite its popularity, only a few authors have described biomass allocation into autotrophic and heterotrophic components across ecosystems (e.g. Whittaker and Likens 1973; O'Neill 1976; O'Neill and DeAngelis 1981), and no general model has been quantified. Interest in the relative contributions of autotrophs and heterotrophs to overall biomass has been revived by the increasing consensus that heterotrophs play an important role in regulating plant populations and biomass in ecosystems (O'Neill 1976; Carpenter and Kitchell 1988; McNaughton et al. 1989; Cyr and Pace 1993).

There are currently two major models that attempt to describe the relationships among biomasses of different trophic levels. The more traditional prey-dependent theory assumes that the rate of consumption of prey by predator depends only on prey density, and sets the basis for trophic interactions and top-down control within food webs (Oksanen et al. 1981; Fretwell 1987). Ratio-dependent theory, on the other hand, asserts that consumption of prey depends on the ratio of predator to prey (Arditi et al. 1991; Berryman 1992). Prey- and ratio-dependent models suggest very different patterns of biomass along gradients of primary productivity. In ratio-dependent models, all trophic levels increase proportionately, whereas in prey-dependent models the responses vary depending on the trophic level and the number of levels (Ginzburg and Akçakaya 1992). Empirical evidence often contradicts the predictions of prey-dependent models (Oksanen et al. 1981; Fretwell 1987), because in a wide variety of terrestrial and aquatic systems both resource and consumer biomass continuously

increase along gradients of productivity (McNaughton et al. 1989; Ginzburg and Akçakaya 1992; Cyr and Pace 1993). This evidence has been synthesized by Hunter and Price (1992), who conclude that trophic interactions occur within a basic template set by bottom-up forces or resource control, and this view is consistent with models that postulate density or ratio-dependent interactions among trophic components (Arditi et al. 1991). Ratio-dependent models integrate the effects of enrichment and biological control (Arditi et al. 1991; Berryman 1992) and are supported by extensive empirical data (McCauley et al. 1988; Power 1992; Ginzburg and Akçakaya 1992; Hunter and Price 1992).

Whereas field data often show that the biomasses of all trophic levels tend to increase with increasing productivity (Power 1992), as predicted by ratio-dependent theory, there is evidence that the response varies quantitatively across systems (Ginzburg and Akçakaya 1992). Thus, the relative proportions of primary producers and consumers, or of total autotrophic and heterotrophic biomasses, often vary among systems, and do not always increase at the same rate along productivity gradients in different systems. These departures from a constant ratio may be interpreted as the consequence of trophic interactions within food webs (Ginzburg and Akçakaya 1992). It is still not clear, however, whether the ratio of producer to consumer biomass varies in a systematic manner along productivity gradients or among terrestrial and aquatic systems. The situation is then analogous to the lack of a general model to describe the variations in shape of the biomass pyramid across systems. A problem that has impeded this kind of broad-scale comparison is the difficulty in quantifying the biomass of discrete trophic levels, especially given the widespread occurrence of omnivory in most ecosystems (Peters 1977). A very simple, yet more objective approach to this problem is to use the total biomass of autotrophs or primary producers and the total biomass of heterotrophs that depend on them, regardless of their position in the food

web, as a first approach to quantify broad patterns in the ratios of producer and consumer biomass along gradients of productivity.

There is evidence for broad-scale patterns in biomass allocation into autotrophic and heterotrophic compartments. O'Neill and DeAngelis (1981) hypothesized that the ratio of total heterotrophic to autotrophic biomass (H/A ratio) should be highest in the systems with the most rapid turnover of the autotrophic base, because increased regulation is needed where the potential for exhausting limiting nutrient resources is greatest. This view is consistent with resource control of heterotrophs (McCauley et al. 1988), because autotrophic populations that have high specific production rates are able to support higher relative heterotrophic biomass. Both approaches suggest that, given the rapid turnover of phytoplankton, planktonic communities should exhibit higher H/A ratios than most terrestrial systems. Within planktonic communities, higher autotrophic turnover rates have traditionally been associated with low phytoplankton biomass (Harris 1984; Holligan et al. 1984), so in both freshwater and marine systems, a declining trend in H/A ratios should occur along gradients of producer biomass and enrichment.

In this paper, we use the total biomasses of auto- and heterotrophic freshwater plankton to test the hypothesis that the H/A ratio declines systematically along gradients of increasing autotrophic biomass. We use both data extracted from the literature, representing a wide geographic range, and actual measurements of planktonic biomass from a localized set of lakes in southern Québec. We then question whether changes in the relative contribution of autotrophs and heterotrophs are related to changes in resource availability along trophic gradients (bottom-up), or the result of trophic interactions within food webs (top-down). Plankton communities are particularly well suited to explore these questions: the biomass of both autotrophs

and heterotrophs can be estimated with relative ease, and researchers use similar methods, so there is a wealth of published data on a wide variety of lakes that can be compared. In addition, freshwater planktonic communities are relatively well defined spatially and temporally, minimizing some of the major obstacles in comparing food webs, as outlined by Power (1992). One problem in dealing with freshwater pelagic food webs, however, is defining the resource base of the community. In lakes, external organic carbon subsidies often constitute a substantial component of the energy base of the plankton (Jones 1992; del Giorgio and Peters 1993), and an analysis of bottom-up control and trophic interactions that ignores this component would be incomplete. We therefore attempt to incorporate the entire resource base of the plankton by analyzing the biomass distribution into planktonic autotrophs and heterotrophs along gradients of both nutrient enrichment and of external carbon inputs to lakes. Finally, we compare trends in freshwater pelagic communities with marine and terrestrial ecosystems to establish the generality of this pattern.

## Materials and Methods

**Plankton biomass, field data:** Plankton biomass and related parameters were sampled along the growing season in 18 southern Québec lakes, selected to span 1.5 orders of magnitude in total phosphorus (TP) and chlorophyll a (CHL); these lakes vary three-fold in dissolved organic carbon concentration (DOC). The morphometry of the lakes is also varied: mean depth ranges from 4 to 80 m, and surface area from 0.8 to 90 $km^2$. The lakes were sampled monthly from May to September 1990. After determining the thermal profile, a diaphragm pump was used to collect water from the entire epilimnion and the upper half of the metalimnion. In the laboratory, chlorophyll (CHL) concentration was measured spectrophotometrically in ethanol extracts of samples collected on Gelman AE glass fiber filters following Bergmann and Peters

(1980); total phosphorus (TP) was measured using the ascorbic acid method following persulphate digestion (Griesbach and Peters 1991); dissolved organic carbon (DOC) was measured from filtered (0.45 µm membrane) and acidified water samples using a Dorhman Carbon Analyzer; color (COL) is reported as absorbance of the filtered lake water (0.45 µm membrane), read in a 10 cm cell at a wavelength of 440 nm (Cuthbert and del Giorgio 1992).

The total numbers of bacteria, microzooplankton (nanoflagellates, ciliates, rotifers) and macrozooplankton (crustacean zooplankton and larger ciliates), together with their size, were determined for each sample. Conversion factors given by Bjørnsen (1986) for bacteria, Børsheim and Bratbak (1987) for flagellates, Gates et al. (1982) for ciliates, and McCauley (1984) for zooplankton were used to transform these densities to biomass estimates. Total heterotrophic biomass is the sum of the biomasses of these components. Details of sampling, counting and biomass calculation for bacteria, micro- and macrozooplankton are given in appendices 4, 5, and 6, respectively. Phytoplankton biomass was not measured directly, but rather calculated from the measured chlorophyll a concentration, using a conversion factor of 40 mg C per mg CHL. This value represents the midrange of carbon to chlorophyll ratios repor ted for natural phytoplankton communities (Banse 1977; Tolstoy 1977; Welschmeyer and Lorenzen 1984; White et al. 1988). The potential bias in the calculation of biomass from chlorophyll was assessed by independently calculating phytoplankton biomass (in mg ww $l^{-1}$) from total phosphorus, using the empirical equation that Watson and McCauley (1988) developed for this same set of Québec lakes. The two approaches were compared in the sampled lakes, where the appropriate data were available.

Table 1. Literature data used to construct the ratio of total heterotrophic to total autotrophic biomass (H/A ratio). Phyto (phytoplankton biomass), Bac (bacterial biomass) and Zoo (zooplankton biomass).Total heterotrophic biomass is the sum of zooplankton and bacteria.

| Lake | Phyto | Bac | Zoo | Units | H/A | Reference |
|---|---|---|---|---|---|---|
| Frederiksborg Slotsø | 3921.0 | 276.0 | 149.0$ | µgC $l^{-1}$ | 0.11 | Christtoffersen et al. 1990 |
| | 2027.0 | 255.0 | 1927.0$ | µgC $l^{-1}$ | 1.08 | " |
| Nøsjøvatn | 1230.0 | 74.0 | 139.0$ | µgC $l^{-1}$ | 0.17 | Vadstein et al. 1989 |
| Ontario | 2132.0 | 281.0 | 432.0$ | µg ww $l^{-1}$ | 0.33 | Lean et al. 1987 |
| | 1151.0 | 193.0 | 360.0$ | µg ww $l^{-1}$ | 0.48 | |
| Alligator | 67.0* | 59.2 | 55.2 | µgC $l^{-1}$ | 1.71 | Shortreed & Stockner 1986 |
| Big Kalzas | 26.0* | 29.7 | 18.0 | µgC $l^{-1}$ | 1.80 | " |
| Claire | 22.0* | 49.0 | 43.2 | µgC $l^{-1}$ | 4.19 | " |
| Coghlan | 19.0* | 35.4 | 26.0 | µgC $l^{-1}$ | 3.23 | " |
| Ethel | 135.0* | 30.0 | 19.6 | µgC $l^{-1}$ | 0.37 | " |
| Fox | 30.0* | 43.6 | 45.6 | µgC $l^{-1}$ | 2.97 | " |
| Jojo | 27.0* | 65.9 | 35.2 | µgC $l^{-1}$ | 1.94 | " |
| Quiet | 28.0* | 41.0 | 43.4 | µgC $l^{-1}$ | 2.69 | " |
| Sekulmun | 22.0* | 31.7 | 28.8 | µgC $l^{-1}$ | 2.75 | " |
| Snafu | 66.0* | 66.2 | 108.4 | µgC $l^{-1}$ | 2.65 | " |
| Twin | 37.0* | 55.2 | 22.4 | µgC $l^{-1}$ | 2.10 | " |
| Wellesley | 78.0* | 69.6 | 80.8 | µgC $l^{-1}$ | 1.93 | " |
| Wolf | 55.0* | 33.4 | 20.8 | µgC $l^{-1}$ | 0.99 | " |
| "Oligotrophic lake" | 1.0* | 0.2 | 0.7 | gC $m^{-2}$ | 0.95 | Riemann et al. 1986 |
| "Eutrophic lake" | 15.0* | 1.0 | 1.9 | gC $m^{-2}$ | 0.19 | " |

Continuation Table 1

| | | | | | | |
|---|---|---|---|---|---|---|
| Barrow Pond | 11.0 | 37.0 | 33.0 | mgC $m^{-2}$ | 6.36 | Hobbie 1984 |
| Hjålmaren | 7.7 | 2.7 | 1.7 | mg ww $l^{-1}$ | 0.57 | Willén 1984 |
| | 8.2 | 1.6 | 1.2 | mg ww $l^{-1}$ | 0.34 | " |
| | 2.8 | 1.0 | 1.6 | mg ww $l^{-1}$ | 0.92 | " |
| | 1.7 | 0.8 | 1.6 | mg ww $l^{-1}$ | 1.44 | " |
| Biwa | 5.6 | 0.5 | 0.8 | gC $m^{-2}$ | 0.23 | Mori et al. 1984 |
| Yunoko | 8.7 | 0.3 | 0.2 | gC $m^{-2}$ | 0.06 | " |
| Suwa | 13.3 | 0.5 | 1.0 | gC $m^{-2}$ | 0.11 | " |
| Kojima | 9.6 | 0.5 | 0.6 | gC $m^{-2}$ | 0.12 | " |
| Krivoîe | 1.2 | 2.4 | 1.8 | kcal $m^{-2}$ | 3.46 | Winberg 1972 |
| Krugloe | 0.3 | 0.7 | 1.1 | kcal $m^{-2}$ | 5.93 | " |
| Mirror | 375.0 | 80.0 | 20.0 | mgC $m^{-2}$ | 0.75 | Likens 1985 |
| Mendota | 1.8 | 0.2 | 3.5 | gC $m^{-2}$ | 2.06 | Brock 1985 |
| Bysjön | 10.3 | 2.4 | 11.5 | mg ww $l^{-1}$ | 1.36 | Coveney et al. 1977 |
| Constance | 1187.0* | 655.0 | 2187.0$ | mgC $m^{-2}$ | 2.39 | Geller et al. 1991 |
| Mossø | 784.0 | 126.0 | 4.5 | µgC $l^{-1}$ | 0.17 | Riemann et al. 1982 |
| | 1840.0 | 86.0 | 7.9 | µgC $l^{-1}$ | 0.05 | " |
| | 1400.0 | 125.0 | 16.4 | µgC $l^{-1}$ | 0.10 | " |
| Kjeisåsputten | 16.0 | 45.0 | 61.0 | µgC $l^{-1}$ | 6.63 | Hessen et al. 1990 |
| Quesenel# | 19.3* | 11.9 | 9.8 | µgC $l^{-1}$ | 1.13 | Stockner & Shortreed 1989 |
| Sproat# | 9.3* | 16.1 | 2.4 | µgC $l^{-1}$ | 2.00 | " |

When needed a conversion factor of $2.83 \times 10^{-8}$ µgC per bacteria was used

* Includes phototrophic picoplankton

$ Includes HNF and ciliates

# Phytoplankton biomass estimated from TP

Table 2. Summer average (geometric mean) values for the lakes sampled in southern Québec during 1990. Fitch Bay, Quinn Bay and South Bay are different basins of Lake Memphremagog. DOC: dissolved organic carbon. TP: total phosphorus. CHL: chlorophyll a. Algae 1: phytoplankton biomass calculated from chlorophyll. Algae 2: phytoplankton biomass calculated from total phosphorus. µZP: microzooplankton biomass, includes heterotrophic protists (flagellates and ciliates), rotifers and nauplii. MZP: macrozooplankton biomass (crustaceans). Ratio: ratio of total heterotrophic to total autotrophic biomass (H/A ratio) using Algae 1 biomass estimate.

| Lake | DOC | TP | CHL | Algae 1 | Algae 2 | Bacteria | µZP | MZP | Ratio |
|---|---|---|---|---|---|---|---|---|---|
| | mgC $l^{-1}$ | µg $l^{-1}$ | µg $l^{-1}$ | µgC $l^{-1}$ | µgC $l^{-1}$ | µgC $l^{-1}$ | µgC $l^{-1}$ | µgC $l^{-1}$ | |
| Aylmer | 5.61 | 10.82 | 2.26 | 90.40 | 134.59 | 12.87 | 12.41 | 5.69 | 0.34 |
| Bowker | 2.51 | 4.65 | 0.86 | 34.40 | 41.32 | 8.32 | 6.01 | 10.88 | 0.73 |
| Brome | 3.35 | 10.27 | 3.18 | 127.20 | 125.13 | 23.58 | 16.70 | 17.04 | 0.45 |
| Connelly | 4.52 | 7.72 | 2.81 | 112.40 | 83.88 | 9.53 | 15.50 | 12.11 | 0.33 |
| Coulombe | 7.00 | 10.44 | 3.67 | 146.80 | 128.03 | 12.82 | 20.84 | 14.66 | 0.33 |
| Croche | 4.52 | 4.56 | 1.87 | 72.00 | 40.21 | 7.80 | 23.84 | 14.87 | 0.64 |
| Cromwell | 7.53 | 9.77 | 5.16 | 206.40 | 116.74 | 8.35 | 21.66 | 13.62 | 0.21 |
| D'Argent | 5.04 | 9.89 | 3.25 | 130.00 | 118.72 | 18.72 | 17.68 | 14.62 | 0.39 |
| Fitch Bay | 3.80 | 9.80 | 3.41 | 136.40 | 117.21 | 12.75 | 31.06 | 17.36 | 0.45 |
| L'Achigan | 3.87 | 6.41 | 1.72 | 68.80 | 64.69 | 7.53 | 6.60 | 20.14 | 0.50 |
| Lovering | 5.50 | 7.93 | 2.18 | 87.20 | 87.15 | 8.93 | 13.71 | 9.38 | 0.37 |
| Magog | 4.00 | 16.51 | 5.45 | 218.00 | 243.25 | 21.26 | 31.80 | 37.40 | 0.41 |
| Nicolet | 2.93 | 4.04 | 1.16 | 46.40 | 33.88 | 7.63 | 5.86 | 5.00 | 0.40 |
| Quinn Bay | 3.74 | 10.60 | 3.94 | 157.60 | 130.81 | 9.74 | 31.73 | 7.16 | 0.31 |
| Silver | 2.73 | 6.94 | 2.33 | 93.60 | 72.36 | 12.82 | 9.25 | 6.17 | 0.30 |
| South Bay | 3.90 | 15.30 | 3.94 | 157.60 | 218.66 | 31.32 | 50.61 | 13.91 | 0.61 |
| Stukely | 3.76 | 5.50 | 0.96 | 38.40 | 52.22 | 8.25 | 4.68 | 14.60 | 0.72 |
| Waterloo | 5.11 | 33.17 | 13.15 | 526.00 | 645.95 | 37.82 | 33.99 | 65.74 | 0.26 |

**Literature data**: Overall 41 simultaneous estimates of bacterial, zooplankton and algal biomass were collected from the literature, representing one to several years for 34 lakes worldwide (table 1). Areal and volumetric biomass estimates were treated separately, to avoid interconversion errors. We tried to select studies that used comparable methods, but the data are inevitably heterogeneous. For example, algal picoplankton biomass was estimated in 21 lakes, heterotrophic protists were quantified in 7, and phototrophic sulphur bacteria biomass was estimated for 1 lake. When available, we accepted the conversion factors from biovolume to carbon employed by the different authors. When necessary, we converted from dry to wet weight using a factor of 0.1, and from dry weight to carbon using a factor of 0.4 (McCauley 1984).

**Data analyses**: Data were $\log_{10}$-transformed prior to all statistical analyses, to stabilize the variance and attain homoscedasticity. We used the linear regression module of the SYSTAT software (Wilkinson 1987) to describe relations but since there is measurement error in both the dependent in independent variables, the Model II regression slope (Ricker 1973) is provided as an estimate of the functional relationship. Slopes were compared to the null hypothesis of equality to 1 using t-tests. Some of the relationships that appear in this paper may involve spurious correlations (Prairie and Bird 1989), such as the relationship between the H/A (heterotrophic/autotrophic biomass) ratio and chlorophyll or plant biomass. To avoid misinterpretation, our conclusions are directly drawn from the relationship between the two components of the ratio. For example, the H/A ratio is said to decline with increasing algal biomass only when the slope of the relationships between total heterotrophic and autotrophic biomass is significantly less than 1. These relations are nevertheless presented as ratios, because they make the point of interest most clearly.

## RESULTS AND DISCUSSION

**The decline of H/A ratio with lake productivity**: The hypothesis that the H/A ratio of freshwater plankton communities declines with increasing algal biomass is fully supported by our data. For published data from 39 lakes (table 1), total heterotrophic biomass increased less rapidly than autotrophic biomass across the trophic gradient of lakes (fig. 1). Heterotrophic biomass rose as autotrophic biomass to the 0.4 power, for both volumetric (fig. 1A) and areal data (fig. 1B). Literature data can contain collinearities that might result in spurious relationships associated with differences in sampling, locality, sampling method, analytical techniques, etc. However, if the pattern in figure 1 reflects collinearity, the Québec data (table 2), which are largely free of these potential problems, should be different. Yet the same pattern in the H/A ratio was seen there (fig. 2): total heterotrophic biomass increased as autotrophic biomass to the 0.66 power, which is also significantly less than 1 (table 3), and not significantly different from the slopes of the literature data set ($p < 0.001$).

When literature and field data are combined, the H/A ratio decreased with increasing chlorophyll concentration, from 6.4 in unproductive lakes to 0.05 in extremely productive lakes (fig. 3). The Québec lakes represent a narrow portion of the entire spectrum of lakes in the data set, but followed the same trend. The ratio decreased from oligotrophic lake Bowker (H/A ratio = 0.73) to moderately eutrophic lakes Waterloo and Cromwell (H/A ratios = 0.26 and 0.21, respectively). For both Québec and literature lakes, heterotrophic biomass increased less rapidly along a gradient of enrichment than autotrophic biomass. Overall, this pattern translated into a continuum from a totally inverted pyramid in ultraoligotrophic lakes to a classical pyramid with a very broad base in eutrophic lakes; intermediate states of approximately equal hetero- and autotrophic biomass occurred in lakes with around 2-5 $\mu g\ CHL\ l^{-1}$.

Figure 1. Relationship between total autotrophic biomass and total heterotrophic biomass for the lakes in the literature that presented data in volumetric (A) or areal units (B). The parameters for the linear regressions are in table 3. Lines of equal biomass are presented.

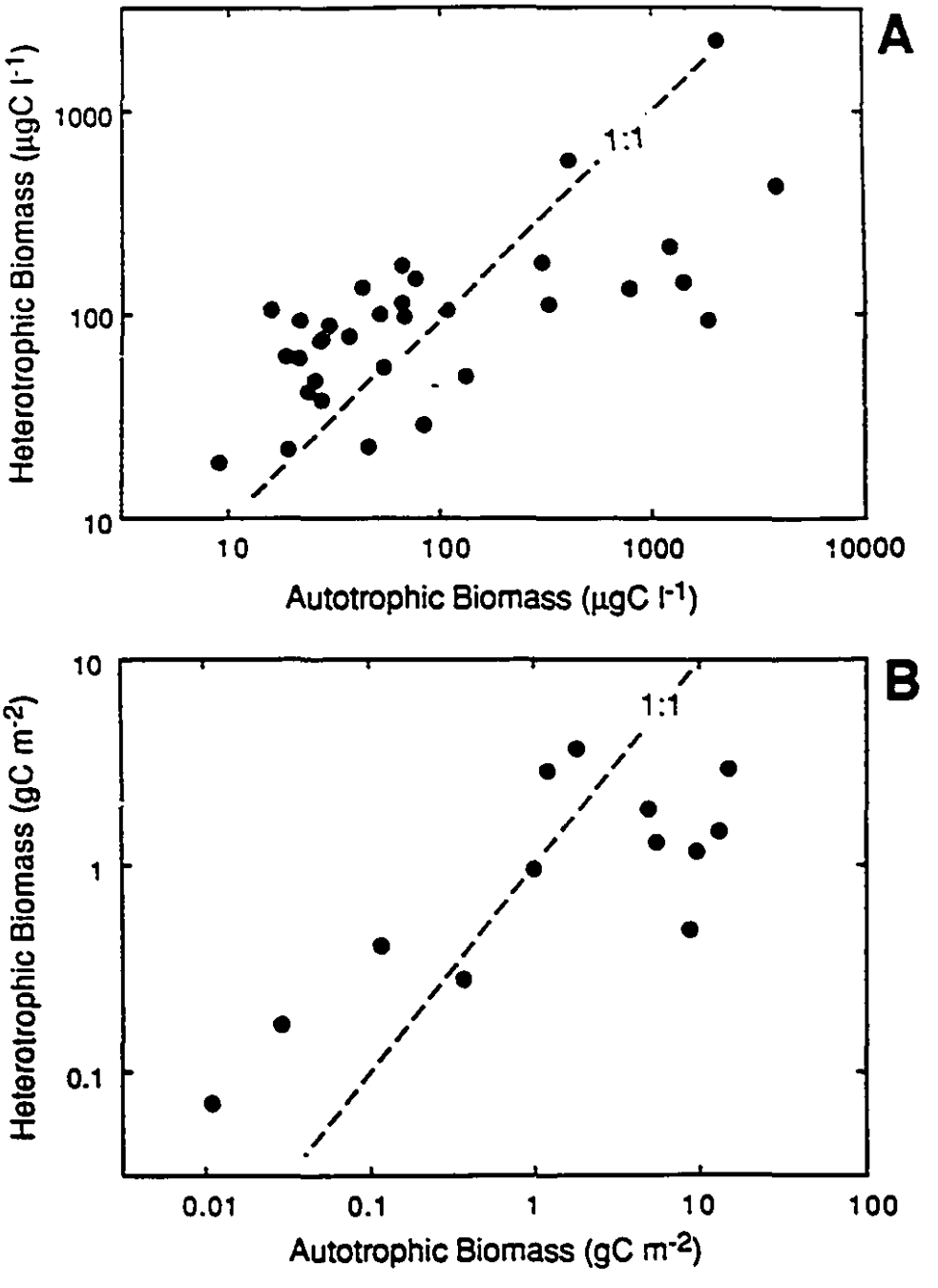
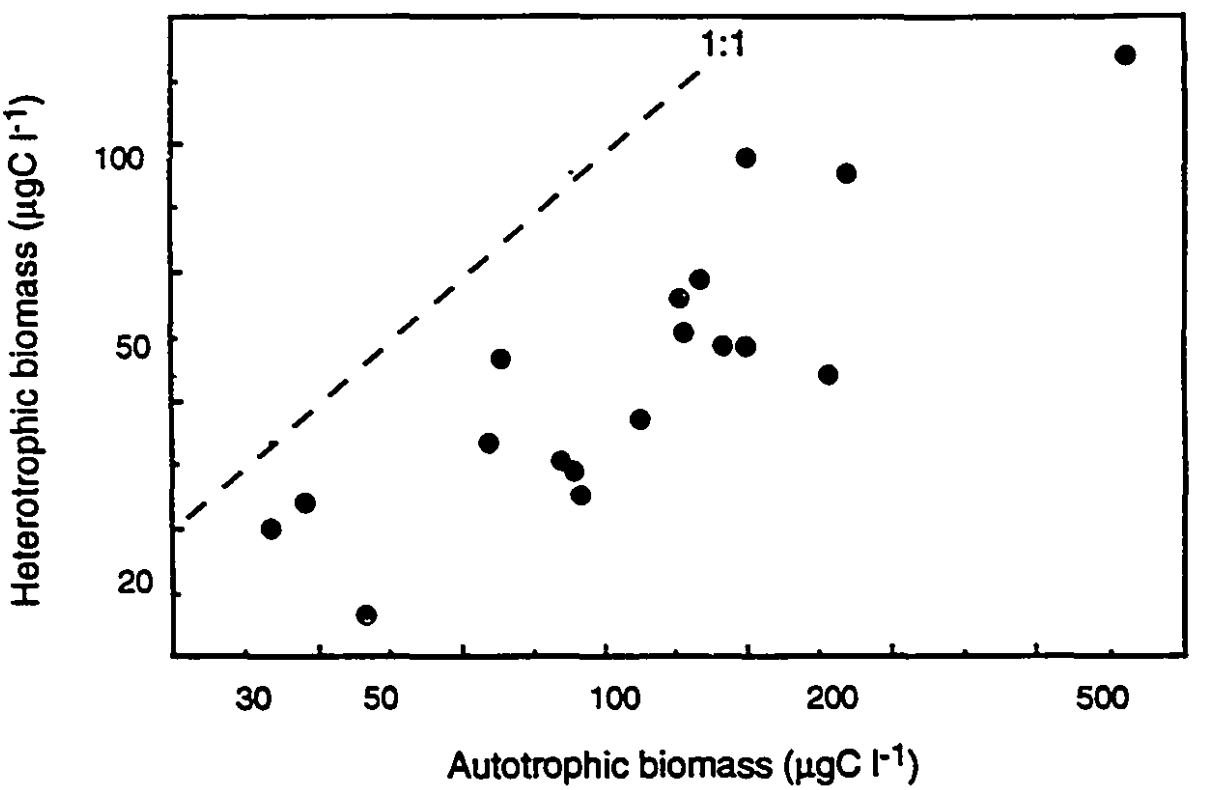

A
Heterotrophic Biomass (µgC l-1)
1000
100
10
1:1
10
100
1000
10000
Autotrophic Biomass (µgC l-1)
B
Heterotrophic Biomass (gC m-2)
10
1
0.1
1:1
0.01
0.1
1
10
100
Autotrophic Biomass (gC m-2)

Figure 2. Relationship between the geometric means of autotrophic biomass and total heterotrophic biomass for 18 lakes in southern Québec (data in table 2). The parameters for the linear regressions are in table 3. The line of equal biomass is shown.


1:1
100
50
20
Heterotrophic biomass (µgC l-1)
30
50
100
200
500
Autotrophic biomass (µgC l-1)

The Québec lakes tend to have lower H/A ratios than the literature lakes at comparable chlorophyll concentrations (fig. 3). It is less likely that this difference is due to an underestimation of the heterotrophic biomass in our field data, because all the major heterotrophic components were carefully considered. Our use of a fixed conversion factor from chlorophyll to carbon, however, may have resulted in an overestimation of the autotrophic biomass in certain lakes, and therefore, in an underestimation of the H/A ratio. A constant conversion factor assumes that the relationship between biomass and chlorophyll is constant among phytoplankton communities. Although chlorophyll to biomass ratios vary seasonally, with the physiological condition of the community, and among lakes (Tolstoy 1979; White et al. 1988), algal biomass and chlorophyll are correlated with a log-log slope of about 1 over a broad range of trophic states (Vörös and Padisàk 1991; OECD 1980, p. 163-167). Therefore, the use of a constant ratio may increase the error but probably does not systematically bias the analysis. Nevertheless, we assessed the possible bias of estimating phytoplankton biomass from chlorophyll by independently calculating autotrophic biomass for the Québec lakes from total phosphorus (table 2), using the empirical equation developed by Watson and McCauley (1988). This equation is particularly appropriate for our data because it was derived for almost exactly the same set of lakes sampled for the present study. The correspondence between total autotrophic biomass calculated from chlorophyll and from TP is good, and the log-log slope of the relationship is almost exactly 1 (fig. 4A). Although there is scatter around the two estimates of autotrophic biomass, there is no indication of a systematic bias in the calculation of algal biomass from chlorophyll. Therefore, almost identical trends between the H/A ratio and chlorophyll were obtained, whether algal biomass was estimated from chlorophyll or from TP (fig. 4B), suggesting that the patterns in H/A ratios along gradients of enrichment are robust, and not an artifact of the way autotrophic biomass was calculated.

Table 3. Linear regression statistics. All variables were $log_{10}$-transformed. The model II slope is provided as an estimate of the functional slope were there is error in the independent variable. BB: bacterial biomass. ZP: total zooplankton biomass. µZP: microzooplankton biomass. MZP: macrozooplankton biomass. CHL: chlorophyll a concentration (µg $l^{-1}$). HB: total heterotrophic biomass. AutoB: total autotrophic biomass. RATIO: ratio of heterotrophic to autotrophic biomass. All areal units in gC $m^{-2}$. All volumetric units in µgC $l^{-1}$. Data for Québec lakes are volumetric.

| | | | | | | | | Model II | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Data | Y | X | N | Y-int ± SE | Slope ± SE | P (b=1) | $r^2$ | slope | F ratio | P |
| Literature data | BB | AutoB | 13 | -0.59 ± 0.71 | 0.37 ± 0.07 | <0.000 | 0.71 | 0.44 | 27.11 | <0.000 |
| Areal | ZB | AutoB | 13 | -0.35 ± 0.12 | 0.41 ± 0.12 | <0.000 | 0.51 | 0.57 | 11.58 | 0.006 |
| | HB | AutoB | 13 | -0.12 ± 0.09 | 0.40 ± 0.09 | <0.000 | 0.62 | 0.51 | 18.16 | 0.001 |
| | ZB | BB | 13 | 0.20 ± 0.19 | 0.93 ± 0.27 | 0.400 | 0.52 | 1.29 | 12.00 | 0.005 |
| | HB | CHL | 13 | -0.32 ± 0.13 | 0.32 ± 0.10 | <0.000 | 0.47 | 0.46 | 10.01 | 0.009 |
| | RATIO | CHL | 13 | 0.17 ± 0.16 | -0.46 ± 0.12 | - | 0.55 | -0.62 | 13.66 | 0.003 |
| Literature data | BB | AutoB | 33 | 0.97 ± 0.12 | 0.36 ± 0.06 | <0.000 | 0.55 | 0.49 | 37.39 | <0.000 |
| Volumetric | ZB | AutoB | 33 | 0.97 ± 0.27 | 0.30 ± 0.13 | <0.000 | 0.15 | 0.77 | 5.56 | 0.025 |
| | HB | AutoB | 33 | 1.19 ± 0.16 | 0.40 ± 0.08 | <0.000 | 0.47 | 0.58 | 28.02 | <0.000 |
| | ZB | BB | 33 | 0.04 ± 0.40 | 0.91 ± 0.23 | 0.349 | 0.33 | 1.59 | 15.12 | <0.000 |
| | HB | CHL | 33 | 1.80 ± 0.07 | 031± 0.08 | <0.000 | 0.35 | 0.46 | 16.39 | <0.000 |
| | RATIO | CHL | 33 | 0.29 ± 0.08 | -0.50 ± 0.08 | - | 0.55 | -0.68 | 37.58 | <0.000 |
| Québec lakes | BB | AutoB | 18 | -0.02 ± 0.28 | 0.55 ± 0.13 | <0.000 | 0.51 | 0.71 | 16.65 | 0.001 |
| | µZB | AutoB | 18 | -0.56 ± 0.31 | 0.87 ± 0.15 | 0. 314 | 0.68 | 1.05 | 33.66 | <0.000 |
| | MZB | AutoB | 18 | -0.03 ± 0.39 | 0.57 ± 0.19 | <0.000 | 0.36 | -0.95 | 8.933 | 0.009 |

Continuation Table 3

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | HB | AutoB | 18 | 0.30 ± 0.20 | 0.66 ± 0.10 | <0.000 | 0.74 | 0.77 | 45.01 | <0.000 |
| | ZB | BB | 18 | 0.64 ± 0.23 | 0.77 ± 0.20 | 0.077 | 0.48 | 1.11 | 14.73 | 0.001 |
| | HB | CHL | 18 | 1.36 ± 0.05 | 0.66 ± 0.10 | <0.000 | 0.74 | 0.77 | 44.99 | <0.000 |
| | RATIO | CHL | 18 | -0.24± 0.05 | -0.34 ± 0.10 | - | 0.42 | -0.52 | 11.66 | 0.004 |
| Literature data (all) | RATIO | CHL | 46 | 0.26 ± 0.07 | -0.48 ± 0.07 | - | 0.55 | -0.65 | 54.35 | <0.000 |
| Literature + Quebec | RATIO | CHL | 64 | 0.12 ± 0.06 | -0.48 ± 0.07 | - | 0.46 | -0.71 | 52.02 | <0.000 |

**P (b = 1) Probability of the $H_0$ slope = 1 (t-test)**

Table 4. Slopes of the empirical equations compiled from the literature, relating biomass and production of planktonic components (Y) to indices of trophy (X)(CHL: chlorophyll a, TP: total phosphorus). All variables were log-transformed. CB: cyanobacterial biomass. PB: phytoplankton biomass. NANO: nanoplankton biomass. NET: net plankton biomass. PP: primary production. NANOP: nanoplankton primary production. NETP: net plankton primary production. BD: bacterial density. BP: bacterial production. HNF: heterotrophic nanoflagellate biomass. CIL: ciliate biomass. MICROZOO: microzooplankton biomass. MACROZOO: macrozooplankton biomass. ZOO: zooplankton biomass. ZOOP: zooplankton production. FB: fish biomass. CPUE: catch per unit effort.

| Y | UNIT | X | UNIT | SLOPE | $r^2$ | REFERENCE |
|---|---|---|---|---|---|---|
| CHL | $\mu g\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.45 | 0.96 | Dillon and Rigler 1974 |
| CHL | $\mu g\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.14 | 0.79 | Smith and Shapiro 1981 |
| CHL | $\mu g\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.26 | 0.65 | Ostrofsky and Rigler 1987 |
| CHL | $\mu g\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.25 | 0.80 | Seip and Ibrekk 1988 |
| CHL | $\mu g\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.21 | 0.88 | Quirórs 1991 |
| CB | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 0.98 | 0.71 | Smith 1985 |
| CB | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 2.78 | 0.69 | Seip and Ibrekk 1988 |
| PB | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.40 | 0.88 | Watson and Kalff 1981 |
| NANO | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.31 | 0.93 | Watson and Kalff 1981 |
| NANO | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 0.57 | 0.43 | Watson and McCauley 1988 |
| NET | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.71 | 0.82 | Watson and Kalff 1981 |
| NET | $\mu g\ ww\ l^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.32 | 0.56 | Watson and McCauley 1988 |
| PP | $mgC\ m^{-3}\ d^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.02 | 0.94 | Smith 1979 |
| NANOP | $mgC\ m^{-3}\ d^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.14 | 0.95 | Watson and McCauley 1988 |
| NETP | $mgC\ m^{-3}\ d^{-1}$ | TP | $\mu g\ l^{-1}$ | 1.26 | 0.95 | Watson and McCauley 1988 |
| PP | $mgC\ m^{-3}\ d^{-1}$ | CHL | $\mu g\ l^{-1}$ | 1.36 | 0.81 | Smith 1979 |

Continuation Table 4

| | | | | | | |
|---|---|---|---|---|---|---|
| PP | mgC $m^{-3}$ $d^{-1}$ | CHL | µg $l^{-1}$ | 1.26 | 0.91 | del Giorgio and Peters 1993 |
| BD | mill $ml^{-1}$ | TP | µg $l^{-1}$ | 0.66 | 0.83 | Bird and Kalff 1984 |
| BD | mill $ml^{-1}$ | TP | µg $l^{-1}$ | 0.98 | 0.88 | Aizaki 1985 |
| BD | mill $ml^{-1}$ | TP | µg $l^{-1}$ | 0.41 | 0.56 | Currie 1990 |
| BD | mill $ml^{-1}$ | TP | µg $l^{-1}$ | 0.94 | 0.80 | J. M. Gasol unpublished |
| BD | mill $ml^{-1}$ | CHL | µg $l^{-1}$ | 0.76 | 0.90 | Bird and Kalff 1984 |
| BD | mill $ml^{-1}$ | CHL | µg $l^{-1}$ | 0.71 | 0.96 | Aizaki 1985 |
| BD | mill $ml^{-1}$ | CHL | µg $l^{-1}$ | 0.52 | 0.75 | Cole et al. 1988 |
| BD | mill $ml^{-1}$ | CHL | µg $l^{-1}$ | 0.29 | 0.45 | Currie 1990 |
| BD | mill $ml^{-1}$ | CHL | µg $l^{-1}$ | 0.58 | 0.47 | J. M. Gasol unpublished |
| BP | mgC $m^{-3}$ $d^{-1}$ | CHL | µg $l^{-1}$ | 0.62 | 0.62 | Cole et al. 1988 |
| BP | mgC $m^{-3}$ $d^{-1}$ | CHL | µg $l^{-1}$ | 0.49 | 0.20 | White et al. 1991 |
| HNF | µg ww $l^{-1}$ | TP | µg $l^{-1}$ | 0.66 | 0.50 | J. M. Gasol unpublished |
| CIL | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.79 | 0.54 | Beaver and Crisman 1989 |
| CIL | µg dw $l^{-1}$ | CHL | µg $l^{-1}$ | 0.68 | 0.67 | Beaver and Crisman 1988 |
| CIL | µg dw $l^{-1}$ | CHL | µg $l^{-1}$ | 0.49 | 0.79 | Pace 1986 |
| MICROZOO | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.57 | 0.72 | Pace 1986 |
| MACROZOO | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.65 | 0.86 | Pace 1986 |
| ZOO | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.91 | 0.72 | Hanson and Peters 1984 |
| ZOO | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.65 | 0.63 | Yan 1985 |
| ZOO | µg dw $l^{-1}$ | TP | µg $l^{-1}$ | 0.64 | 0.86 | Pace 1986 |
| ZOO | µg dw $l^{-1}$ | PB | µg ww $l^{-1}$ | 0.72 | 0.86 | McCauley and Kalff 1981 |
| ZOOP | mgC $m^{-2}$ $yr^{-1}$ | PP | mgC $m^{-2}$ $yr^{-1}$ | 0.81 | 0.91 | McCauley and Kalff 1981 |
| FB | kg $ha^{-1}$ | TP | µg $l^{-1}$ | 0.71 | 0.75 | Hanson and Leggett 1984 |
| CPUE | kg $net^{-1}$ std net $^{-1}$ | TP | µg $l^{-1}$ | 0.51 | 0.40 | Quirós 1990 |
| CPUE | kg $net^{-1}$ std net $^{-1}$ | CHL | µg $l^{-1}$ | 0.43 | 0.37 | Quirós 1990 |

Figure 3. The ratio of heterotrophic to autotrophic biomass (H/A Ratio) for the combined data as a function of chlorophyll concentration. The line of best fit is shown, and the parameters of the equation are in table 3.

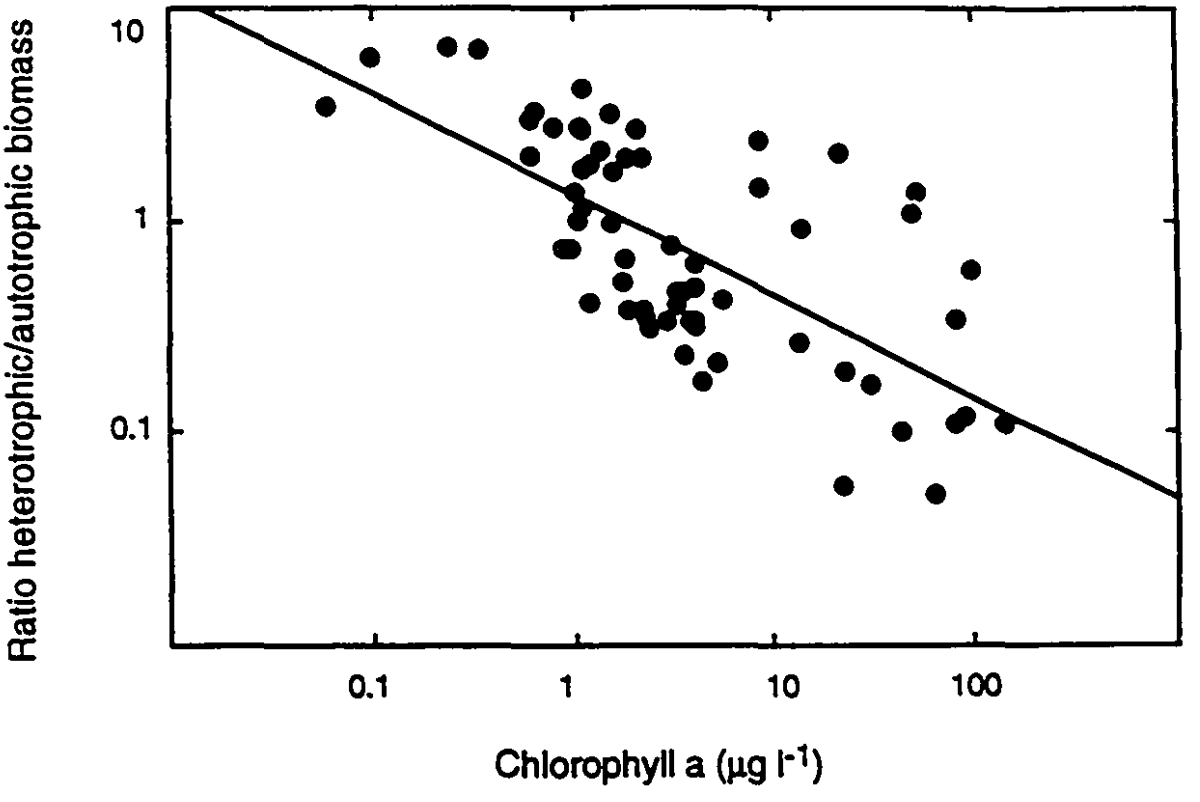
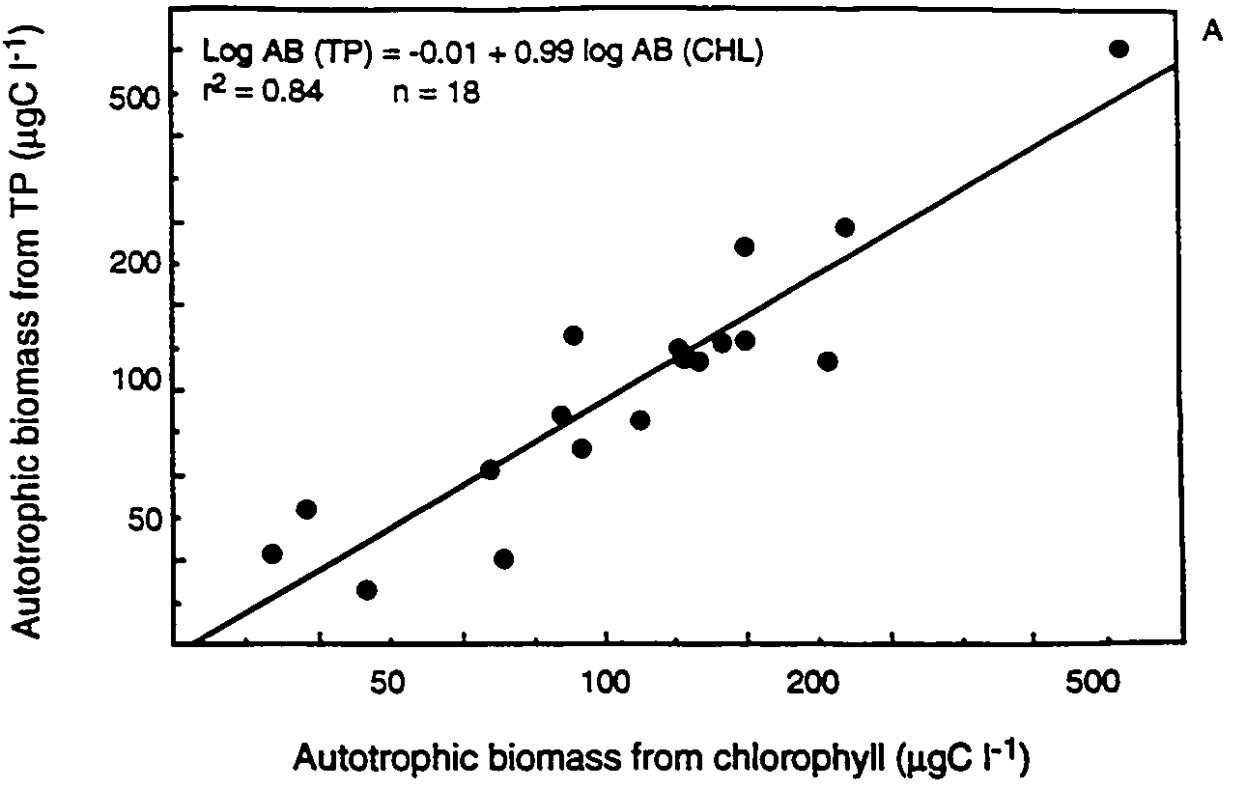
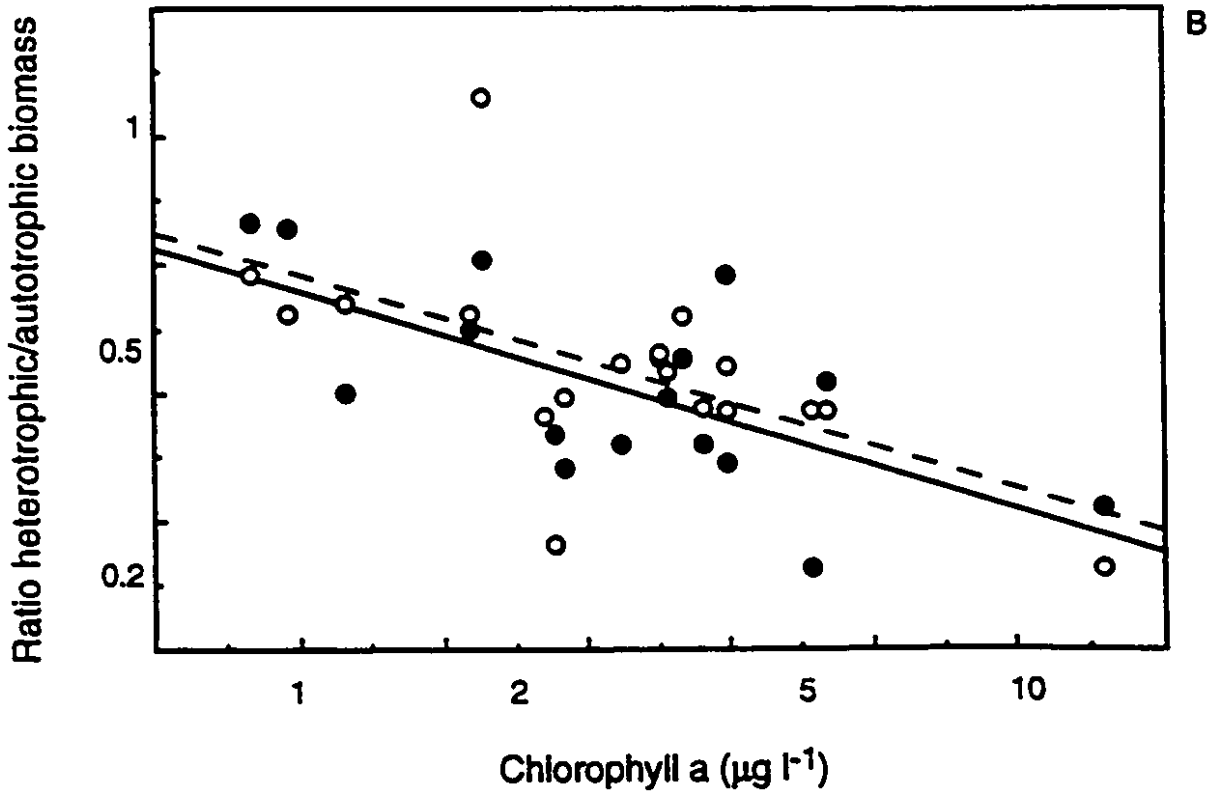

Ratio heterotrophic/autotrophic biomass
10
1
0.1
0.1
1
10
100
Chlorophyll a (µg l-1)

Figure 4. Relationship between autotrophic biomass calculated from chlorophyll a concentration, and autotrophic biomass calculated from TP using the equation by Watson and McCauley (1988) for the Québec lakes (fig. 4A). The ratio of total heterotrophic to total autotrophic biomass with mean summer chlorophyll a (CHL) for Québec lakes (fig 4B). Autotrophic biomass was calculated from chlorophyll (filled circles, dashed line. Log Ratio = -0.24 - 0.34 log CHL, $r^2 = 0.42$) or from TP (open circles, full line. Log Ratio = -0.22 - 0.33 log CHL, $r^2 = 0.36$).


A
Log AB (TP) = -0.01 + 0.99 log AB (CHL)
r² = 0.84 n = 18
Autotrophic biomass from TP (µgC l⁻¹)
500
200
100
50
50
100
200
500
Autotrophic biomass from chlorophyll (µgC l⁻¹)


B
Ratio heterotrophic/autotrophic biomass
1
0.5
0.2
1
2
5
10
Chlorophyll a (µg l⁻¹)

Our results are further supported by published empirical equations that relate the biomass of several planktonic components to chlorophyll or total phosphorus from the literature (table 4). The slopes of these equations, which are all based on log-transformed data, confirmed that the biomasses of individual heterotrophic components of the community increase more slowly than nutrient concentration or the autotrophic components along the same trophic gradients. In freshwater pelagic systems, the biomasses and production of heterotrophic components do not increase proportionally to the biomass and production of phytoplankton.

The disproportionately small increase in individual heterotrophic components of the plankton with autotrophic biomass along lake trophic gradients has been noted previously. Hillbricht-Ilkowska (1977) suggested that eutrophic lakes should have low ratios of herbivorous zooplankton to algal biomass; this prediction was empirically confirmed by Sprules and Knoechel (1984) in a set of 37 lakes in Ontario. McCauley and Kalff (1981) showed that the ratio of zooplankton to phytoplankton biomass decreases with increasing phytoplankton biomass in 17 southern Québec lakes, and this pattern has been repeatedly confirmed (Rognerud and Kjellberg 1984; Malthus and Mitchell 1990; Richman and Sager 1990). Bacterial density has also been shown to increase more slowly than chlorophyll concentration in lakes (Bird and Kalff 1984; Aizaki 1985; Currie 1990). Bird and Kalff (1984) argued that bacterial production might parallel the increase in algal biomass, but later comparative studies showed that bacterial production and density increase with lake trophy approximately at the same rate, but more slowly than chlorophyll concentrations (White et al. 1991).

**Influence of trophic interactions on plankton biomass distribution:** in the following section we compare the patterns in biomass allocation found in freshwater plankton communities with the predictions of prey-dependent and ratio-dependent

theories of community control. Prey- and ratio-dependent models suggest different patterns of biomass along gradients of primary productivity. In ratio-dependent models, all trophic levels increase proportionately, whereas in prey-dependent models the responses vary depending on the trophic level and the number of levels (Ginzburg and Akçakaya 1992). A key test for the strength of trophic interactions was proposed by Mittelbach et al. (1988), who suggested that in systems that are primarily controlled by predators, resource and consumer densities should be uncorrelated where productivity varies and the number of significant trophic levels remains fixed. The Québec data set may be appropriate to assess this hypothesis, because most of the lakes we sampled contain herbivorous and carnivorous zooplankton, and planktivorous and piscivorous fish. The number of trophic links thus may be relatively constant in these food webs, whereas productivity varies around 40-fold across these lakes (del Giorgio and Peters 1994). Since, as shown above, consumer and producer biomasses are positively correlated, the data do not support the hypothesis of predator control in these systems. It could be argued, however, that because there is no reference to the strength of these trophic links, in practice the number of effective trophic levels may vary (Power 1992). If this were the case, according to top-down theory we should expect either a pattern of stepwise increases in biomass (Oksanen et al. 1981), or major departures from the general trend in biomass allocation, corresponding to food webs predominantly regulated by predation control. None of these effects were observed, either in the narrow trophic span of the Québec lakes, or in the much wider range of data from the literature, which encompasses a very heterogeneous set of lakes: consumer biomass increases continuously along gradients of increasing algal biomass and productivity in freshwater plankton communities. Moreover, both phytoplankton biomass and production increase continuously along gradients of nutrient enrichment, in the Québec lakes (del Giorgio and Peters 1994), and on a much wider trophic and geographic range (Smith 1979;

del Giorgio and Peters 1993), a pattern that counters the predictions of top-down control (Fretwell 1987).

The lumping together of bacteria, herbivorous and predacious plankton in this analysis may present some difficulties, particularly in comparisons with other ecosystems. Although bacteria and other decomposers often comprise the bulk of heterotrophic biomass in many terrestrial ecosystems (Heal and McLean 1975; Swift et al. 1979), these organisms have seldom been considered in formulations of predator-prey interactions and community control. In freshwater pelagic systems, bacteria cannot be ignored because these organisms are an integral part of planktonic food webs and many consumers graze on both bacteria and phytoplankton indiscriminately (Sherr and Sherr 1988). An alternative way to view planktonic bacteria is not as consumers or decomposers but as producers of biomass. In higher plants, only some cells are photosynthetic, releasing dissolved organic matter into the phloem to be used by other non-photosynthetic cells, which function as heterotrophs. In strict analogy to higher plants, Flynn (1988) suggested that in aquatic systems bacteria should be considered as "primary producers" because they utilize dissolved organic carbon produced by photosynthetic cells, both aquatic and terrestrial, and convert this carbon into biomass which is then available to consumers. From this alternative stand-point, bacteria should be placed with planktonic autotrophs, because together with phytoplankton, they comprise the base of the food chain. Figure 5 shows the result of this analysis. Heterotrophic biomass, now the sum of micro- and macrozooplankton, is positively related to the sum of bacterial and phytoplankton carbon. The slope of this log-log relationship (0.75) is still rather low, but it is not significantly different from unity ($p < 0.05$), suggesting that planktonic primary and secondary consumers tend to approach an almost constant ratio in relation to their food supply, composed of both phytoplankton and bacteria. Whether bacteria are

Figure 5. The relationship between total zooplankton biomass and the sum of phytoplankton and bacterial biomass for the Québec lakes. The regression model and line of best fit are shown.

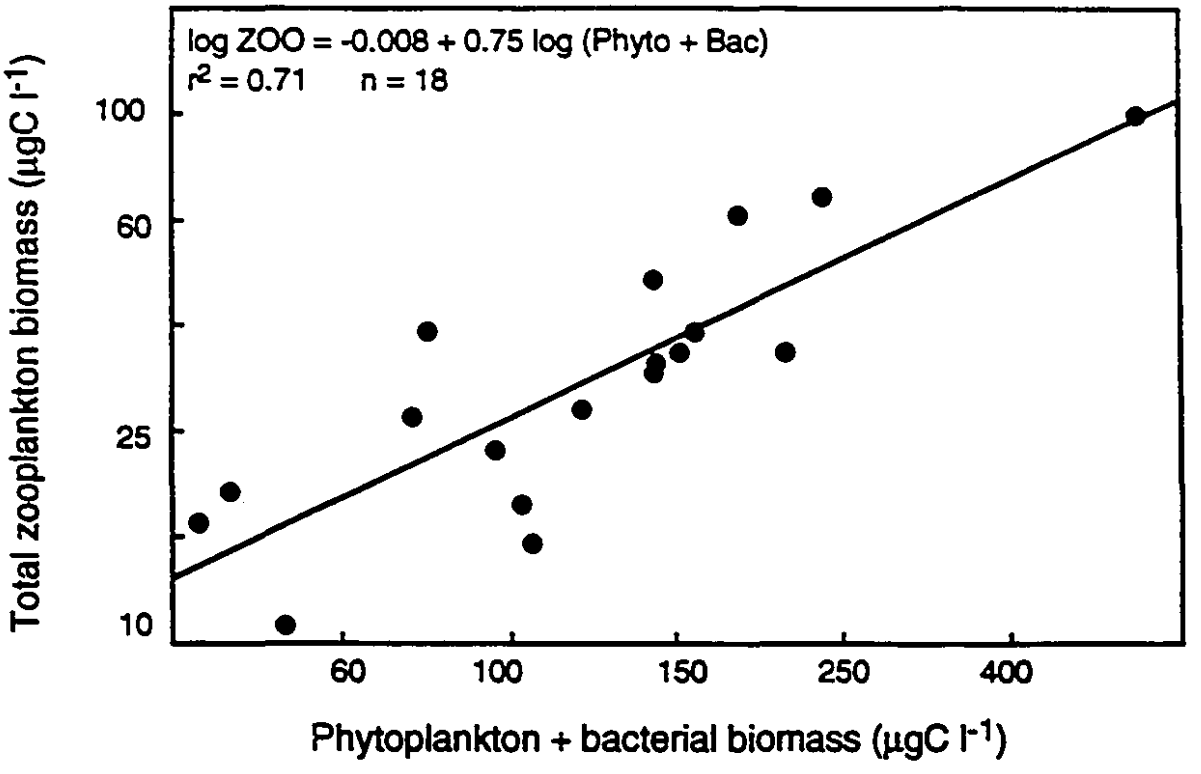
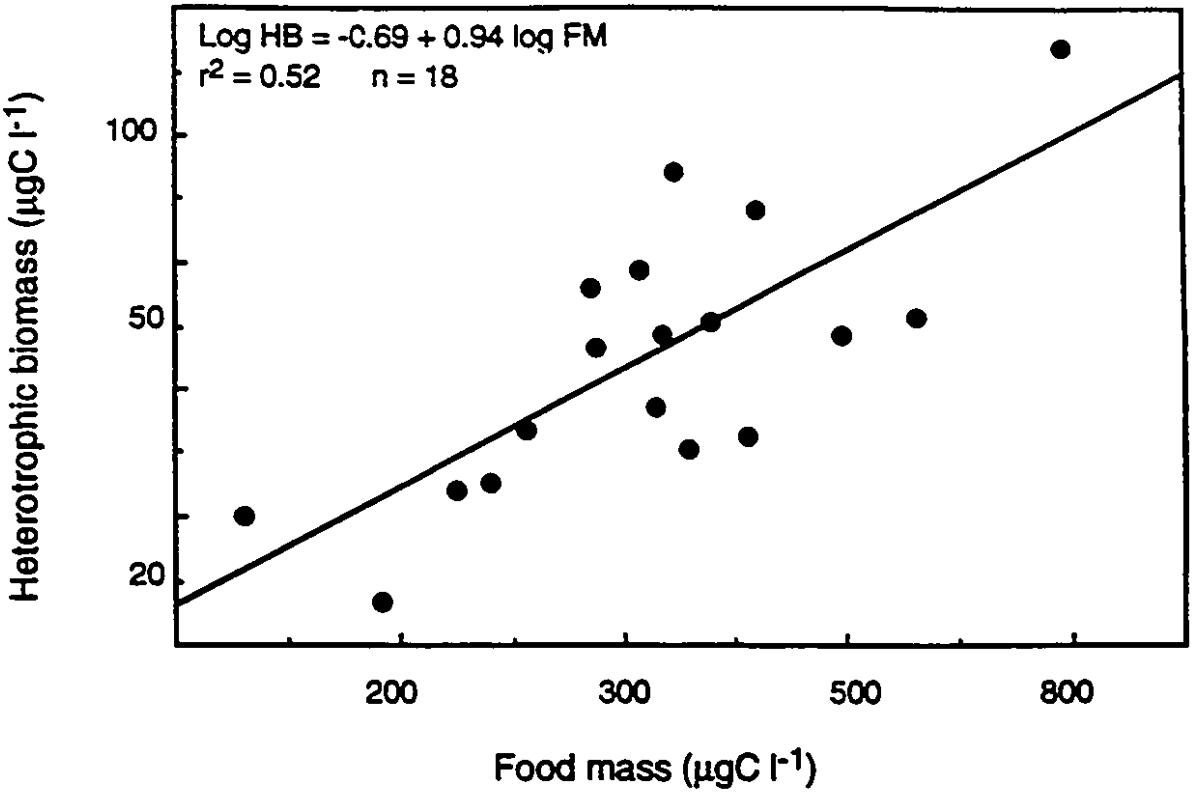

log ZOO = -0.008 + 0.75 log (Phyto + Bac)
r² = 0.71 n = 18
Total zooplankton biomass (µgC l⁻¹)
100
60
25
10
60
100
150
250
400
Phytoplankton + bacterial biomass (µgC l⁻¹)

Figure 6. The relationship between total heterotrophic biomass and total potential food base (F), calculated as the sum of phytoplankton biomass and the biologically labile fraction of the dissolved organic carbon (DOC) pool, for the 18 lakes sampled in southern Québec. The regression model and line of best fit are shown.


Log HB = -0.69 + 0.94 log FM
r2 = 0.52 n = 18
Heterotrophic biomass (µgC l-1)
100
50
20
200
300
500
800
Food mass (µgC l-1)

considered as consumers and included with the heterotrophic component, or as primary producers and included with the autotrophic component, the conclusions of the analysis are the same, because the biomass of planktonic heterotrophs generally increases with increasing food supply.

We surmise that the biomass allocation into autotrophic and heterotrophic compartments of the plankton along gradients of enrichment is not primarily determined by trophic interactions within the food webs that we chose to study. Rather, the patterns agree with the basic predictions of bottom-up control of community structure and ratio-dependent theory. There are two aspects of the models of planktonic biomass, however, that should be considered in more detail. First, our data, and also the empirical models collected from the literature (table 4) indicate that the slopes of the log-log relationships between autotrophic and heterotrophic biomass are generally well below 1, and therefore, the ratio of the two components varies systematically along gradients of enrichment in lakes. This trend applies to both total heterotrophic biomass, and the biomasses of individual heterotrophic components (tables 3 and 4). These slopes lie in between perfect ratio-dependency (slope of 1) and complete prey-dependent control (slope of 0), suggesting that there may be a trophic component in the patterns of biomass allocation in freshwater plankton (Ginzburg and Akçakaya 1992). Secondly, these same empirical relationships are often characterized by relatively high intercepts, (table 3), suggesting that in the absence of autotrophic biomass, there could still be measurable heterotrophic biomass. In the following sections we explore some of the bottom-up processes that may result in these low slopes and high intercepts.

**Resource control of planktonic biomass:** From the perspective of resource control, the high relative heterotrophic biomass found in most oligotrophic lakes could

be sustained by high algal turnover rates, by higher availability of primary production to heterotrophs or by utilization of external sources of carbon. One paradigm of phytoplankton ecology holds that turnover rates of algae are highest in oligotrophic systems, and decline along a gradient of increasing algal biomass (Odum 1971; Harris 1984). However, several authors have questioned the validity of this pattern for lakes (Westlake et al. 1980; Fee et al. 1987; McCauley et al. 1988). Comparative analyses indicate that phytoplankton production increases faster than chlorophyll concentrations (Smith 1979; Beaver and Crisman 1991; del Giorgio and Peters 1993). Since chlorophyll concentration is a measure of phytoplankton biomass, phytoplankton production per unit biomass must also increase with increasing algal biomass. Specific rates of production calculated on an areal basis should increase more slowly because light is limited to increasingly shallow strata at higher algal biomasses (Bannister 1974). Empirical models indicate that depth of the euphotic zone decreases as chlorophyll concentration to the -0.3 to -0.55 power (Canfield and Hodgson 1983), whereas volumetric rates of production increase as chlorophyll to the 1.2 to 1.6 power (Beaver and Crisman 1991, table 4). Thus, areal rates of production should increase roughly as the product of euphotic zone depth ($CHL^{-0.42}$) and volumetric production ($CHL^{1.4}$) along a gradient of increasing phytoplankton biomass. Since biomass (CHL $m^{-2}$) must increase at least as fast as the product of biomass ($CHL^{1}$) and euphotic zone depth ($CHL^{-0.42}$), specific production rates calculated on an areal basis are likely to increase as $[(CHL^{-0.42} \times CHL^{1.4} / CHL^{1} \times CHL^{-0.42})] = CHL^{0.4}$. In any case, rates of phytoplankton production per unit biomass, calculated from areal estimates, are unlikely to peak in oligotrophic lakes or to decrease along a gradient of enrichment.

Over a broad range of primary productivity in lakes, empirical evidence does not support the contention that the algal biomass of oligotrophic lakes turns over more

rapidly than the biomass of eutrophic lakes. The decline in H/A ratios in freshwater planktonic communities along gradients of increasing autotrophic biomass therefore may not be linked to a decrease in the turnover rate of the algal populations. There is evidence, however, that as algal biomass increases, the availability of this biomass to consumers may decrease (Watson and Kalff 1981; Malthus and Mitchell 1990) or that sedimentation losses may be relatively higher in shallower eutrophic lakes (Hargrave 1973). For these or other reasons, phytoplankton to zooplankton transfer may be more efficient in oligotrophic waters (Blackburn 1981; Sheldon et al. 1986). The fraction of total photosynthetically fixed carbon that is excreted by phytoplankton, an important source of energy for bacteria (Sundh and Bell 1992), also declines with trophy (Baines and Pace 1991). Higher transfer efficiencies may be coupled with lower turnover rates of heterotrophs, as Cho and Azam (1990) have suggested for oligotrophic marine plankton. The overall effects of these combined processes remain to be tested.

A third factor that may strongly influence the biomass distribution is dissolved organic carbon. Lake bacterioplankton utilize dissolved organic carbon (DOC): a portion is respired and the remainder is converted into biomass. This biomass is directly available to grazers, including mixotrophic algae, protozoans, ciliates, rotifers and larger crustacean zooplankton. A large fraction of the total heterotrophic biomass in planktonic communities is comprised by this detrital subsystem. Because planktonic grazers prey on both phytoplankton and smaller heterotrophs (Porter et al. 1988), these detrital carbon pathways are an integral part of pelagic food webs and cannot be treated separately (Sherr and Sherr 1988). Since the components of the detrital subsystems in pelagic food webs cannot be effectively excluded from the overall analysis, it is important to consider their sources of energy. The DOC pool in lakes is not only composed of products of algal excretion and lysis, but also of organic carbon leached from littoral macrophytes and from terrestrial vegetation within the drainage

basin (Wetzel 1992). Most lakes have a sizable pool of DOC, ranging from 1.5 to over 20 mgC $l^{-1}$, and much of this material is of allochthonous origin (Meili 1992). If phytoplankton is considered as the sole food source for the plankton community, the dissolved organic matter derived from higher plants is ignored and the energetic base of the pelagic community is underestimated. Since the heterotrophic detritivores and grazers are aggregated in the plankton, DOC should also be considered as a component of the community food base.

The amount of DOC that is "labile" or readily available to the biota ranges from less than 5 to over 40% of the total DOC pool (Laird and Scavia 1990; Tranvik 1992; Jones 1992). In the 18 Québec lakes we sampled, DOC concentrations ranged from 2.5 to 7.5 mgC $l^{-1}$ (table 2). The total potential food base (F) for consumers in these lakes can be estimated as the sum of phytoplankton standing stock and the labile DOC. Algal biomass varies sixteen-fold in the Québec lakes, whereas the concentration of dissolved organic carbon varies less than three-fold and is relatively high even in the most oligotrophic lakes (table 2). Thus, the addition of even a small labile fraction of DOC tends to dominate the estimated food base, particularly in oligotrophic lakes where algal biomass is very low. If we assume that 5% of the DOC is biologically labile, the estimated food base would vary only five-fold among lakes. Heterotrophic biomass increases with F with a slope not significantly different from unity (fig. 6), and the H/F ratio remains constant along a gradient of increasing plant carbon. The constancy of the ratio of heterotrophic biomass to food base suggests that heterotrophic biomass follows a resource gradient composed of both phytoplankton biomass and dissolved organic carbon. This pattern remains unchanged if the labile DOC is assumed to be greater than 5%.

This result is particularly interesting, because it suggests that the low slopes and high intercepts characteristic of empirical models that relate heterotrophic to autotrophic biomasses (tables 3 and 4) may result from an incomplete description of the resource base, rather than from trophic interactions within planktonic food webs. When both DOC and phytoplankton biomass are considered, planktonic consumers show an almost perfect ratio-dependency, suggesting that planktonic communities are primarily bottom-up controlled, and also supporting the notion that external carbon inputs are a key aspect of plankton community function in lakes (Jones 1992). Likewise, the log-log slopes of regressions between chlorophyll and phosphorus concentrations, which are characteristically above 1 (table 4), become indistinguishable from unity once the effect of lake mean depth has been removed (Smith 1990), so both autotrophic and heterotrophic biomass would seem to follow almost perfect ratio-dependency with their respective resources. The high intercepts of heterotrophic vs autotrophic relationships probably reflect a greater influence of carbon subsidies in oligotrophic lakes. Because DOC concentrations are relatively high and homogeneous among lakes, compared to the variation in chlorophyll and primary production, this organic carbon may become the major source of energy for the pelagic community where phytoplankton biomass is low. As phytoplankton carbon increasingly dominates the system along gradients of enrichment, the contribution of DOC to overall plankton metabolism probably declines. These high intercepts would tend to lower the slopes of the relationships between autotrophic and heterotrophic biomass in lakes, even if the carbon transfer efficiency from phytoplankton to heterotrophs, remained constant across gradients of enrichment.

There is increasing evidence that the carbon requirements of the planktonic heterotrophs in oligotrophic lakes exceed the production capacity of the phytoplankton (Hessen et al. 1990; Ahrens and Peters 1991; Baines and Pace 1991; del Giorgio and

Peters 1993; del Giorgio and Peters, in press). This imbalance is less apparent in more productive lakes, again suggesting that oligotrophic plankton communities depend more on external sources of carbon, and that the observed biomass structure reflects these energetic subsidies. Food subsidies are not restricted to lakes, however, and are likely to be important in any habitat with a high edge to area ratio (Power 1992). Many riverine, estuarine and coastal marine communities, for example, have been shown to be strongly dependent on external organic carbon inputs (Findlay et al. 1986; Hopkinson et al. 1989). In such cases, as in lakes, it is necessary to assess the entire resource base before any analysis of trophic interactions can effectively be made. The difficulty in determining resource subsidies in aquatic ecosystems is somewhat analogous to the problem of the spatial circumscription of communities in terrestrial systems. Consumer mobility beyond the spatial boundaries arbitrarily set for any given community may also be considered as a variant of energetic subsidies to the system, and could result in a distortion in the local patterns between autotrophic and heterotrophic biomass.

**COMPARISON WITH OTHER SYSTEMS:** To compare freshwater plankton with other systems, we used data on total auto- and heterotrophic biomass for marine and terrestrial systems (Whittaker and Likens 1973), forests (Reichle et al. 1973), and marine plankton (Holligan et al. 1984). Since biomass estimates for these terrestrial and aquatic systems are in gC $m^{-2}$, we converted the volumetric biomass estimates for the Québec lakes into areal units by integrating over the depth of the epilimnion. This comparison also included those lake literature data that were originally presented in areal units.

**Marine plankton:** Marine plankton followed the same pattern of declining H/A ratios with increasing phytoplankton biomass described for freshwater pelagic communities

Figure 7. The ratio of heterotrophic to autotrophic biomass (H/A Ratio) as a function of plant biomass for a wide range of systems: Freshwater plankton data from this study: Q=Québec lakes, L=literature data; o=oceanic plankton data extracted from Holligan et al. (1984); data extracted from Whittaker and Likens (1973) and Reichle et al. (1973): F=forests, G=grasslands, D=desert, T=tundra, C=cultivated land, E=estuaries, S=swamp, R=reef, O=marine plankton, H=hypertrophic lake.

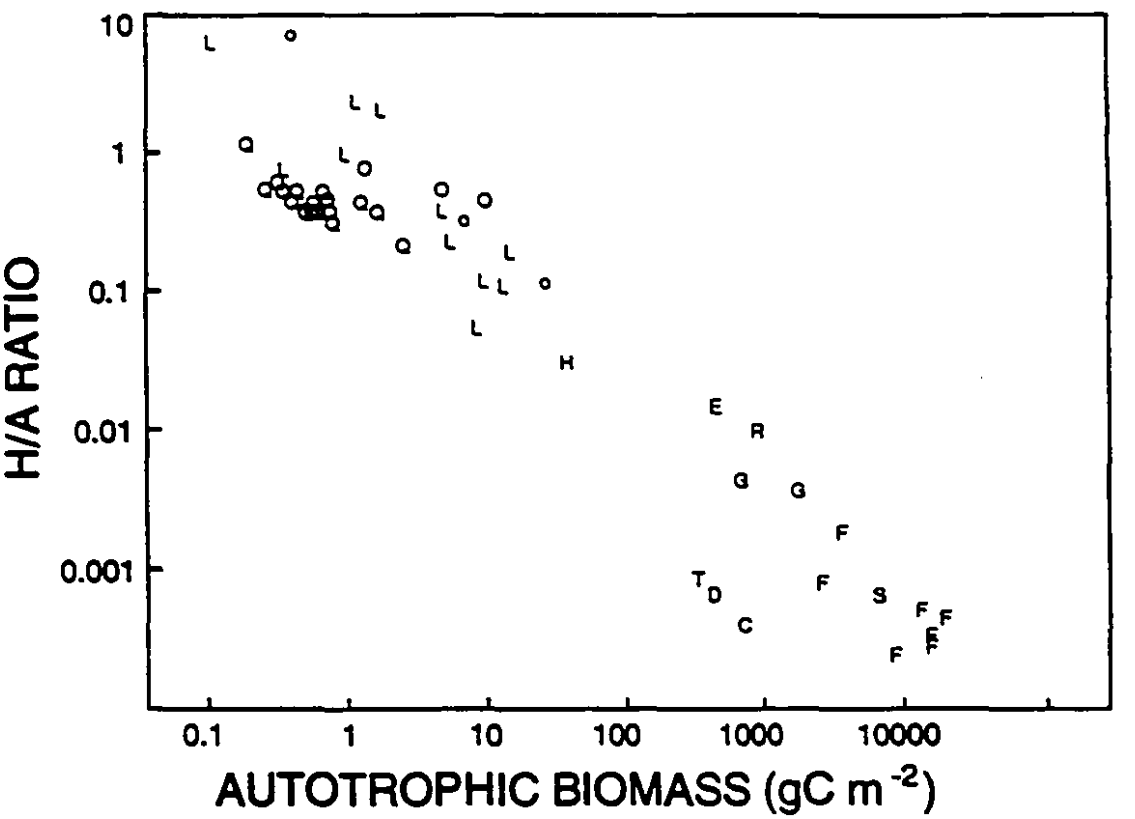

10
1
0.1
0.01
0.001
H/A RATIO
0.1
1
10
100
1000
10000
AUTOTROPHIC BIOMASS (gC m -2)

Figure 8. Bacterial biomass (filled circles) and zooplankton biomass (open circles) as functions of phytoplankton biomass based on literature data for lakes. Data in volumetric units (fig. 8A) and in areal units (fig. 8B). The parameters of the linear regressions are summarized in table 3.

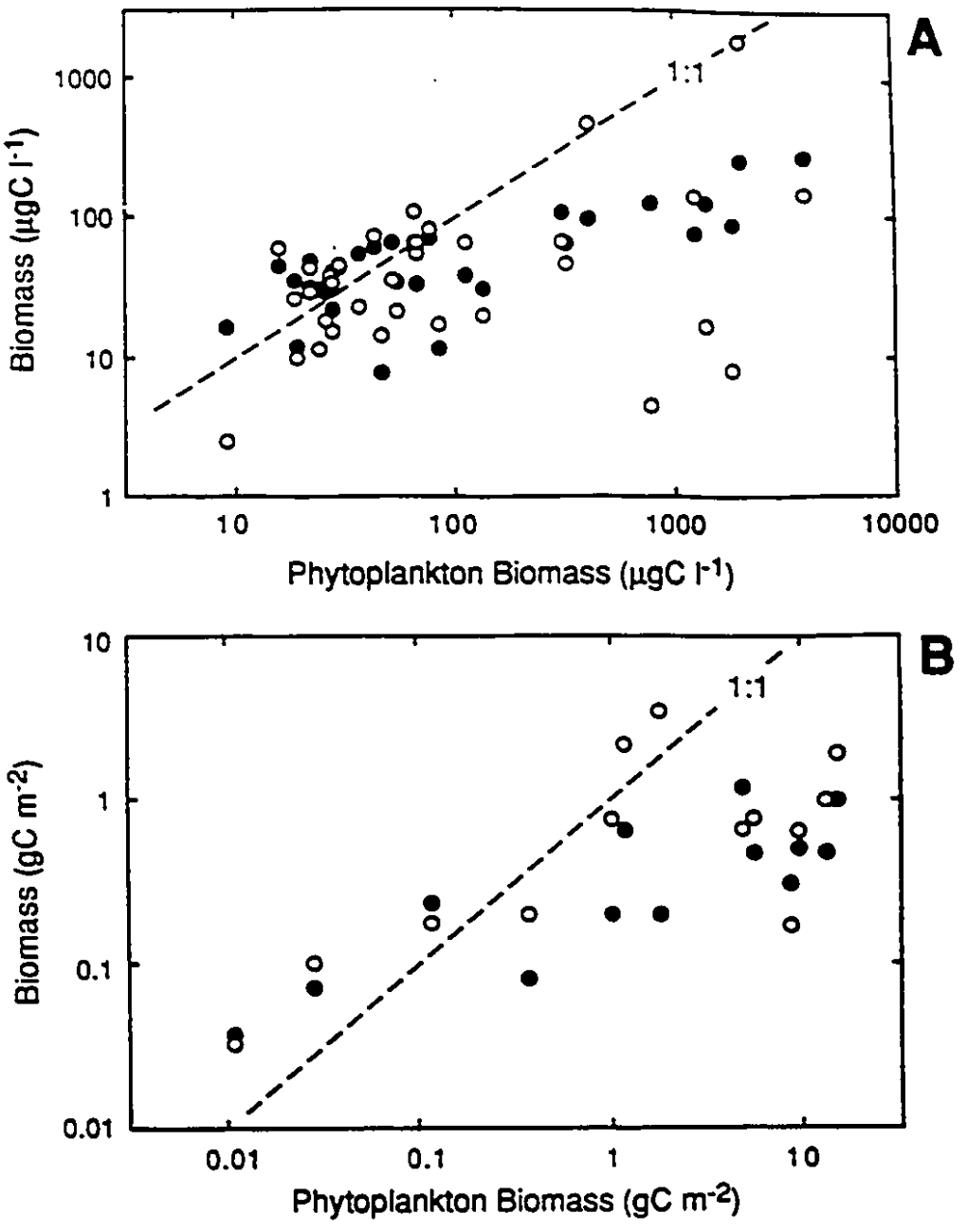
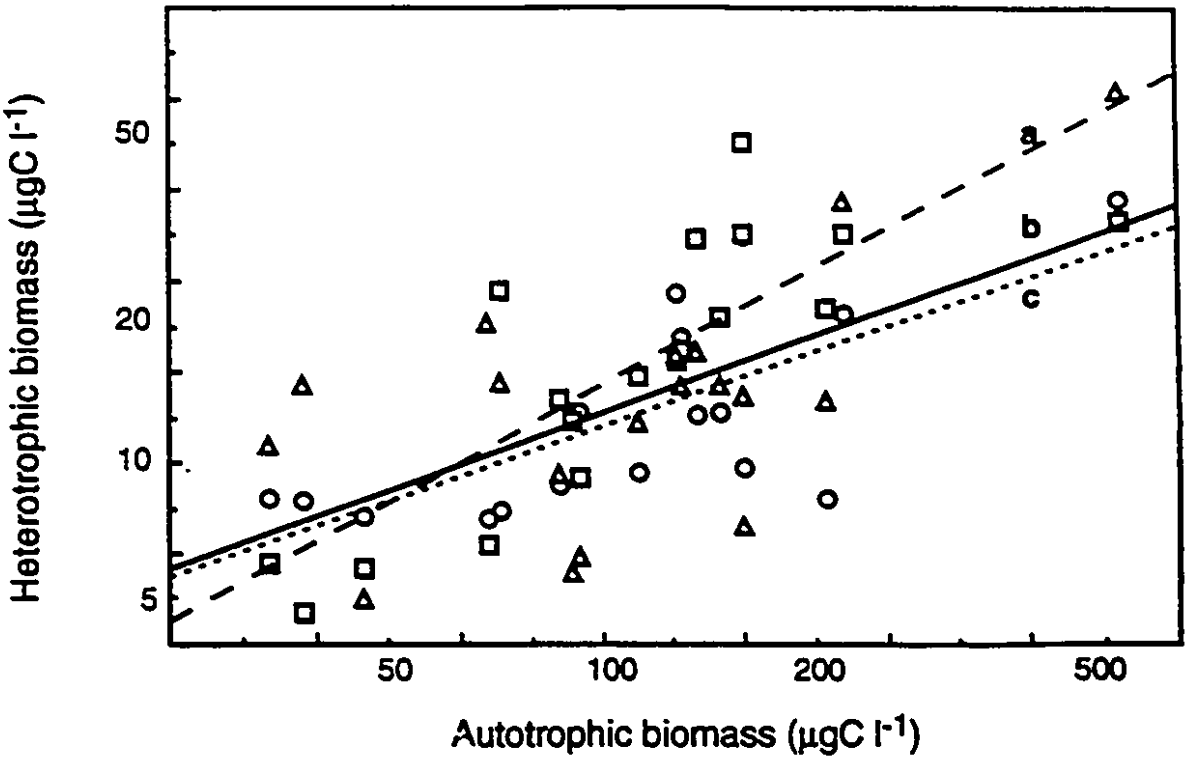

A
1:1
1000
100
10
1
Biomass (µgC l-1)
10
100
1000
10000
Phytoplankton Biomass (µgC l-1)
B
1:1
10
1
0.1
0.01
Biomass (gC m-2)
0.01
0.1
1
10
Phytoplankton Biomass (gC m-2)

Figure 9. Relationship between summer mean (geometric) autotrophic biomass and microzooplankton biomass (squares, line a), bacterial biomass (circles, line b), and macrozooplankton biomass (triangles, line c), for the 18 lakes sampled in southern Québec (data in table 2). The parameters of the linear regressions are summarized in table 3.


Heterotrophic biomass (µgC l-1)
50
20
10
5
50
100
200
500
Autotrophic biomass (µgC l-1)
a
b
c

(fig. 7). H/A ratios for marine communities usually fell within the same order of magnitude as their freshwater counterparts, whereas ratios for estuaries were lower and closer to estimates for terrestrial systems. Several authors have noted inverted biomass pyramids in oligotrophic areas of the oceans (Campbell et al. 1979; Fuhrman et al. 1989; Cho and Azam 1990) and that heterotrophic biomass increases relative to autotrophic biomass towards more oligotrophic marine areas (Dortch and Packard 1989).

Although the overall pattern of decreasing H/A ratios with trophy seems a feature shared by marine and freshwater plankton communities, the underlying processes may not be the same. The relatively high heterotrophic biomass in oligotrophic oceans has been explained by high turnover rates of the phytoplankton that dominate these areas (Holligan et al. 1984), but as we suggested earlier, this pattern may not apply to lakes. Moreover, there is some evidence that the distribution of biomass among individual heterotrophic components may differ between lakes and oceans. In oligotrophic areas of the oceans, bacteria seem to dominate living particulate carbon (Cho and Azam 1990), so the high H/A ratios there could be almost exclusively due to bacteria. In the 39 literature lakes we surveyed, bacterial and zooplankton biomasses increased similarly across the entire trophic span, so total heterotrophic biomass was distributed roughly equally between the two components, both for volumetric (fig. 8A) and areal estimates (fig. 8B, table 3). The 18 lakes sampled in Québec showed a similar pattern (fig. 9, table 3). There is no indication that marine systems support substantially less total heterotrophic biomass than do freshwater planktonic communities (fig. 7), at comparable levels of autotrophic biomass. This observation does not agree with other empirical evidence that lakes support substantially more bacterial biomass than do marine systems with similar

chlorophyll concentrations (Simon et al. 1992), but the small number of marine data points in our study limits the generality of this comparison.

**Terrestrial ecosystems:** There is a strong pattern of declining H/A ratios with increasing plant biomass across systems, from ultraoligotrophic lakes and oceans (autotrophic biomass < 0.1 gC $m^{-2}$), to tropical rain forests (plant biomass > 20 kgC $m^{-2}$) (fig. 7). H/A ratios decrease from >1 in extremely unproductive lakes and seas, to less than $4.5x10^{-4}$ in tropical forests. Overall, H/A ratios decline as $A^{-0.7}$. Heterotroph biomass, however, varies only 1.5 orders of magnitude across this range of systems, and the declining H/A ratios are the result of low slope that characterizes the H vs A relationship. The overall trend is consistent with the hypothesis that the heterotrophic standing crop per unit of autotrophic standing crop should be highest where plant biomass turns over most rapidly (O'Neill and DeAngelis 1981). The data on terrestrial autotrophic biomass, however, includes both living and dead tissue, and in the case of forests, this results in a high overall biomass with an extremely low turnover rate. If only living tissue were considered, the H/A ratios of terrestrial systems, particularly of forests, would be higher and probably somewhat closer to those measured in aquatic systems.

Another major difference between planktonic and terrestrial systems is the composition of the heterotrophic component of the community. As described above, the detrital subsystem contributes heavily to the total heterotrophic biomass in planktonic systems. In contrast, terrestrial heterotrophs generally represent herbivorous invertebrates and vertebrates that directly consume the plant biomass. In terrestrial systems, decomposition operates mainly in the soil, and so it is spatially segregated from the above-ground carbon pathways. The terrestrial detrital food web plays a fundamental role in the remineralization of nutrients and organic matter, but its

role in transferring carbon to higher trophic levels above ground is not well understood (Swift et al. 1979). Plankton communities still exhibit H/F ratios that are one to two orders of magnitude higher than the H/A ratios of terrestrial systems, suggesting that even with the inclusion of DOC, the base for the plankton must still turn over rapidly to support the observed biomass. In many terrestrial systems, however, decomposers are a major component of the total heterotrophic biomass (Heal and McLean 1975). The inclusion of this component would not alter the overall pattern, but could certainly narrow the distance between H/A ratios of aquatic and terrestrial communities. At present, the paucity of data on total decomposer biomass in terrestrial systems hampers this comparison.

## SUMMARY

Our results indicate that the ratio of total heterotrophic to autotrophic biomass (H/A ratio) in freshwater plankton communities declines systematically along gradients of increasing phytoplankton biomass. Marine plankton exhibit the same trend, and in the past, this trend has been attributed to high turnover of oligotrophic phytoplankton. However, the pattern in freshwater H/A ratios may not be linked to declining turnover rates of the autotrophic biomass along gradients of enrichment, but rather to energetic subsidies. Our results suggest that total heterotrophic biomass follows a gradient of food resources, composed of algal biomass and detrital carbon as dissolved organic carbon (DOC). Because DOC concentrations are relatively high and homogeneous among lakes, this organic carbon may become the major source of energy for the pelagic community where phytoplankton biomass is low. Since the dependency of phytoplankton biomass on nutrient availability in lakes is well established, the biomasses of both autotrophs and heterotrophs seem to be primarily resource controlled in freshwater plankton communities. Top-down regulation may still occur, and is not incompatible with broad trends in bottom-up control of planktonic

components (McCauley et al. 1988; Arditi et al. 1988, Hunter and Price 1992). A portion of the relatively large scatter that characterizes the regressions between autotrophic and heterotrophic biomass may be eventually explained by food web interactions.

Quantification of patterns in biomass allocation over a broader scale is limited by the lack of comparable data for terrestrial ecosystems. Our analysis, based on a rather small data set, indicates a systematic decline in the relative contribution of heterotrophic biomass as plant biomass increases from pelagic to forest ecosystems. More data on total auto- and heterotrophic biomass for terrestrial and marine systems are needed to further these comparisons. In terrestrial systems, plant biomass and primary production may be appropriate indicators of the community food base. In most lakes, however, scaling plankton processes to autotrophic production or biomass is inappropriate, because it ignores much of the energetic base of the community. Such incomplete scaling may result in patterns that could be misinterpreted as top-down control within planktonic communities. This warning, however, extends to food web studies in general, because the risk of underestimating the resource base is not restricted to freshwater plankton communities.

## ACKNOWLEDGEMENTS

We thank R. H. Peters and H. Cyr, D. Tilman and several anonymous referees for their valuable comments on the manuscript, and A. Simons, S. Clinton and M. Schallenberg for their assistance in the field. This research was supported by National Science and Engineering Research Commission and FCAR grants, a Spanish Government postdoctoral fellowship to J. M. Gasol., and a Vineberg Fellowship to P. A. del Giorgio.

## REFERENCES

Ahrens, M., and R. H. Peters. 1991. Plankton community respiration: relationships with size distribution and lake trophy. Hydrobiologia 224: 77-87.

Aizaki, M. 1985. Total number of bacteria as a trophic state index. Verhandlungen der Internationale Vereinigung Limnologie 22: 2732-2738.

Arditi, R., L. R. Ginzburg, and H. R. Akçakaya. 1991. Variation in plankton densities among lakes: a case for ratio-dependent predation models. American Naturalist 138: 1287-1296.

Baines, S. B., and M. L. Pace. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnology and Oceanography 36: 1078-1090.

Bannister, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnology and Oceanography 19: 1-12.

Banse, K. 1977. Determining the carbon-to-chlorophyll ratio of natural phytoplankton. Marine Biology 41: 199-212.

Beaver, J. R., and T. L. Crisman. 1989. Analysis of the community structure of planktonic ciliated protozoa relative to trophic state in Florida lakes. Hydrobiologia 174: 177-184.

----., and ----. 1991. Importance of latitude and organic color on phytoplankton primary productivity in Florida lakes. Canadian Journal of Fisheries and Aquatic Sciences 48: 1145-1150.

Bergmann, M., and R. H. Peters. 1980. A simple reflectance method for the measurement of particulate pigments in lake water and its application to phosphorus-chlorophyll-seston relationships. Can. J. Fish. Aquat. Sci. 37: 111-114.

Berryman, A. A. 1992. The origins and evolution of predator-prey theory. Ecology 73:

1530-1535.

Bird, D., and J. Kalff. 1984. The empirical relationships between bacterial abundance and chlorophyll concentrations in aquatic systems. Canadian Journal of Fisheries and Aquatic Sciences 41: 1015-1023.

Bjørnsen, P. K. 1986. Automatic determination of bacterioplankton biomass by image analysis. Applied and Environmental Microbiology 51: 1199-1204.

Blackburn, M. 1991. Low latitude gyral regions. Pages 3-29 in A. R. Longhurst, ed. Analysis of marine ecosystems. Academic Press, New York.

Børsheim, K. Y., and G. Bratbak. 1987. Cell volume to cell carbon conversion factors for a bacterivorous Monas sp. enriched from seawater. Marine Ecology Progress Series 36: 171-175.

Brock, T. D. 1985. A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, NY.

Campbell, W. B., T. R. Jacobsen, and L. R. Pomeroy. 1979. Heterotrophic-autotrophic index: a qualitative parameter of microbial interactions applied to a Gulf Stream intrusion. Marine Science Communications 5: 383-398.

Canfield, D. E., and L. M. Hodgson. 1983. Prediction of Secchi disc depths in Florida lakes: impact of algal biomass and organic color. Hydrobiologia 99: 51-60.

Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. BioScience 38: 764-769.

Cho, B. C., and F. Azam. 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Marine Ecology Progress Series 63: 253-259.

Christoffersen, K., B. Riemann, L. R. Hansen, A. Klysner, and H. B. Sørensen. 1990. Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. Microbial Ecology 20: 253-272.

Cole, J. J., S. Findlay, and M. L. Pace. 1988. Bacterial production in freshwater and saltwater ecosystems: a cross-system overview. Marine Ecology Progress

Series 43: 1-10.

Coveney, M. J., G. Cronberg, M. Enell, K. Larsson,, and L. Olofsson. 1977. Phytoplankton, zooplankton and bacteria-standing crop and production relationships in an eutrophic lake. Oikos 29: 5-21.

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

Cuthbert, I. D., and P. A. del Giorgio. 1992. Toward a standard method of measuring color in freshwater. Limnol. Oceanogr. 37: 1319-1326.

Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361: 148-150.

del Giorgio, P. A., and R. H. Peters. 1993. The balance between phytoplankton production and plankton respiration in lakes. Canadian Journal of Fisheries and Aquatic Sciences 50: 282-289.

del Giorgio, P. A., and R. H. Peters. In press. Patterns in planktonic P/R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnology and Oceanography.

Dillon, P. J., and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnology and Oceanography 19: 767-773.

Dortch, Q., and T. Packard. 1989. Differences in biomass structure between oligotrophic and eutrophic marine ecosystems. Deep-Sea Research 36: 223-240.

Elton, C. 1927. Animal ecology. MacMillan, New York.

Fee, E. J., R. E. Hecky, and H. A. Welch. 1987. Phytoplankton photosynthesis parameters in central Canadian lakes. Journal of Plankton Research 9: 305-316.

Findlay, S., L. Carlough, M. T. Crocker, H. K. Gill, J. L. Meyer, and P. J. Phillip. 1986.

Bacterial growth on macrophyte leachate and the fate of bacterial production. Limnology and Oceanography 31: 1335-1341.

Flynn, K. J. 1988. The concept of "primary production" in aquatic ecology. Limnology and Oceanography 33: 1215-1216.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos 50: 291-301.

Fuhrman, J. A., T. D. Sleeter, C. A. Carlson, and L. M. Proctor. 1989. Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. Marine Ecology Progress Series 57: 207-217.

Gasol, J. M., F. Peters, R. Guerrero, and C. Pedrós-Alió. 1992. Community structure in lake Cisó: biomass allocation to trophic groups and differing patterns of seasonal succession in the meta- and epilimnion. Archiv für Hydrobiologia 123: 275-303.

Gates, M. A., A. Rogerson, and J. Berger. 1982. Dry to wet biomass conversion constant for Tetrahymena elliotti (Ciliophora, Protozoa). Oecologia 55: 145-148.

Geller, W., R. Berberovic, U. Gaedke, H. Müller, H-R. Pauli, M. M. Tilzer, and T. Weisse. 1991. Relations among the components of autotrophic and heterotrophic plankton during the seasonal cycle 1987 in Lake Constance. Verhandlungen der Internationale Vereinigung Limnologie 24: 831-836.

Ginzburg, L. R., and H. R. Akcakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. Ecology 73: 1536-1543.

Griesbach, S. J., and R. H. Peters. 1991. The effects of analytical variations on estimates of phosphorus concentration in surface waters. Lake Res. Manag. 7: 97-106.

Hanson, J. M., and W. C. Leggett. 1984. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39: 257-263.

----., and R. H. Peters. 1984. Empirical prediction of zooplankton biomass in lakes.

Canadian Journal of Fisheries and Aquatic Sciences 41: 439-445.

Hargrave, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. Journal of the Fisheries Research Board of Canada 30: 1317-1326.

Harris, G. P. 1984. Phytoplankton productivity and growth measurements: past, present and future. Journal of Plankton Research 6: 219-237.

Heal, O. W., and S. F. McLean. 1975. Comparative productivity in ecosystems - secondary productivity, Pages 69-108 in W. H. van Dobben and R. H. Lowe-McConnell, eds. Unifying concepts in ecology. Junk, The Hague.

Hessen, D. O., T. Andersen, and A. Lyche. 1990. Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. Limnology and Oceanography 35: 84-99.

Hillbricht-Ilkowska, A. 1977. Trophic relations and energy flow in pelagic plankton. Polish Ecological Studies 3: 3-98.

Hobbie, J. E. 1984. Polar limnology. Pages 63-105 in F.B.Taub, ed. Lakes and reservoirs. Ecosystems of the World #23. Elsevier, Amsterdam.

Holligan, P. M., and others. 1984. Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. Marine Ecology Progress Series 14: 111-127.

Hopkinson, C. S., B. Sherr, and W. J. Wiebe. 1989. Size fractioned metabolism of coastal microbial plankton. Marine Ecology Progress Series 51: 155-166.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Jones, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73-91.

Laird, G. A., and D. Scavia. 1990. Distribution of labile dissolved organic carbon in

lake Michigan. Limnology and Oceanography 35: 443-447.

Lean, D. R. S., H-J. Fricker, M. N. Charlton, R. L. Cuhel, F. R. Pick. 1987. The lake Ontario life support system. Canadian Journal of Fisheries and Aquatic Sciences 44: 2230-2240.

Likens, G. E. (ed.) 1985. An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer-Verlag, New York.

Malthus, T. J., and S. F. Mitchell. 1990. On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. Freshwater Biology 22: 383-394.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton samples. Pages 228-265 in J. A. Downing and F. Rigler, eds. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook 17. Blackwell, Oxford.

----, and J. Kalff. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Canadian Journal of Fisheries and Aquatic Sciences 38: 458-463.

----., W. W. Murdoch, and S. Watson. 1988. Simple models and variation in plankton densities among lakes. American Naturalist 132: 383-403.

McNaughton, S.J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341: 142-144.

Meili, M. 1992. Sources, concentrations and characteristics of organic matter in softwater lakes and streams of the Swedish forest region. Hydrobiologia 229: 23-41.

Mittelbach, G. G., C. W. Osenberg, and M. A. Leibold. 1988. Trophic relations and ontogenic niche shifts in aquatic ecosystems. Pages 219-235 in B. Ebenman and L. Persson, eds. Size-structured populations. Springer-Verlag, Berlin.

Mori, S., Y. Saijo, and T. Mizuno. 1984. Japanese lakes and ponds. Pages 303-329 in F. B. Taub, ed. Lakes and reservoirs. Ecosystems of the world #23. Elsevier, Amsterdam.

Odum, E. P. 1971. Fundamentals of ecology. Saunders Co, New York.

OECD. 1980. OECD eutrophication programme, alpine lakes. Swiss Federal Institute for Water Resources and Water Pollution Control, Dübendorf.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240-261.

O'Neill, R. V. 1976. Ecosystem persistence and heterotrophic regulation. Ecology 57: 1244-1253.

----., and D. L. DeAngelis. 1981. Comparative productivity and biomass relations of forest ecosystems. Pages 411-449 in D. E. Reichle, ed. Dynamic properties of forest ecosystems. Cambridge University Press.

Ostrofsky, M. L., and F. H. Rigler. 1987. Chlorophyll-phosphorus relationships for subarctic lakes in Western Canada. Canadian Journal of Fisheries and Aquatic Sciences 44: 775-781.

Pace, M. L. 1986. An empirical analysis of zooplankton community size-structure across lake trophic gradients. Limnology and Oceanography 31: 45-55.

Peters, R. H. 1977. The unpredictable problems of trophodynamics. Environmental Biology of Fishes 2: 97-101.

Porter, K. G., and others. 1988. Microbial interactions in lake food webs. Pages 209-227 in S. R. Carpenter, ed. Complex interactions in lake communities. Springer-Verlag, New York.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73: 733-746.

Prairie, Y. T., and D. F. Bird. 1989. Some misconceptions about the spurious correlation problem in the ecological literature. Oecologia 81: 285-288.

Quiros, R. 1990. Predictors of relative fish biomass in lakes and reservoirs of Argentina. Canadian Journal of Fisheries and Aquatic Sciences 47: 928-939.

----. 1991. Empirical relationships between nutrients, phyto-and zooplankton and relative fish biomass in lakes and reservoirs of Argentina. Verhandlungen der Internationale Vereinigung Limnologie 24: 1198-1206.

Reichle, D. E., and others. 1973. Carbon flow and storage in a forest ecosystem. Pages 345-365 in G. M. Woodwell and E. V. Pecan, eds. Carbon in the biosphere. AEC Symposium Series 30, United States Atomic Energy Commission.

Richman, S., and P. E. Sager. 1990. Patterns of phytoplankton-zooplankton interaction along a trophic gradient: II. Biomass and size distribution. Verhandlungen der Internationale Vereinigung Limnologie 24: 401-405.

Ricker, W. E. 1973. Linear regression in fishery research. Journal of the Fisheries Research Board of Canada 30: 409-434.

Riemann, B., M. Sondergaard, H. H. Schierup, S. Bosselmann, G. Christensen, J. Hansen, and B. Nielsen. 1982. Carbon metabolism during a spring diatom bloom in eutrophic Lake Mosso. Internationale Revue der gesamten Hydrobiologie 67: 145-185.

----., M. Sondergaard, L. Persson, and L. Johansson. 1986. Carbon metabolism and community regulation in eutrophic, temperate lakes. Pages 267-280 in B. Riemann and M. Sondergaard, eds. Carbon dynamics in eutrophic, temperate lakes. Elsevier, Amsterdam.

Rognerud, S., and G. Kjellberg. 1984. Relationships between phytoplankton and zooplankton biomass in large lakes. Verhandlungen der Internationale Vereinigung Limnologie 22: 666-671.

Seip, K. L., and H. Ibrekk. 1988. Regression equations for lake management-how far do we go? Verhandlungen der Internationale Vereinigung Limnologie 23: 778-

785.

Sheldon, R. W., P. Nival, and F. Rassoulzadegan. 1986. An experimental investigation of a flagellate-ciliate-copepod food chain with some observations relevant to the linear biomass hypothesis. Limnology and Oceanography 31: 184-188.

Sherr, E. B., and B. F. Sherr. 1988. Role of microbes in pelagic food webs: a revised concept. Limnology and Oceanography 33: 1225-1227.

Shortreed, K. S., and J. G. Stockner. 1986. Trophic status of 19 subarctic lakes in the Yukon territory. Canadian Journal of Fisheries and Aquatic Sciences 43: 797-805.

Simon, M., B. C. Cho, and F. Azam. 1992. Significance of bacterial biomass in lakes and the ocean: comparison of phytoplankton biomass and biogeochemical implications. Marine Ecology Progress Series 86: 103-110.

Smith, V. H. 1979. Nutrient dependence of primary productivity in lakes. Limnology and Oceanography 24: 1051-1064.

----. 1985. Predictive models for the biomass of blue green algae in lakes. Water Resources Research 21: 433-439.

----. 1990. Phytoplankton responses to eutrophication in inland waters. Pages 231-249 in I. Akatsuka, editor. Introduction to applied phycology. SPB Academic, The Hague.

----., and J. Shapiro. 1981. Chlorophyll-phosphorus relations in individual lakes. Their importance to lake restoration strategies. Environmental Science and Technology 15: 444-451.

Sprules, W. G., and R. Knoechel. 1984. Lake ecosystem dynamics based on functional representations of trophic components. Pages 383-403 in D. G. Meyers and J. R. Strickler, eds. Trophic interactions within aquatic ecosystems. AAAS Selected Symposium Series, Westview Press.

Stockner, J. G., and K. S. Shortreed. 1989. Algal picoplankton production and

contribution to food webs in oligotrophic British Columbia lakes. Hydrobiologia 173: 151-166.

Sundh. I., and R. T. Bell. 1992. Extracellular dissolved organic carbon released from phytoplankton as a source of carbon for heterotrophic bacteria in lakes of different humic content. Hydrobiologia 229: 93-106.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. Studies in terrestrial ecosystems 5. Blackwell Scientific Publications, Oxford.

Tolstoy, A. 1979. Chlorophyll a in relation to phytoplankton volume in some Swedish lakes. Archiv für Hydrobiologie 85: 133-151.

Tranvik, L. J. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

Vadstein, O., B. O. Harkjerr, A. Jensen, Y. Olsen, and H. Reinertsen. 1989. Cycling of organic carbon in the photic zone of a eutrophic lake with special reference to the heterotrophic bacteria. Limnology and Oceanography 34: 840-855.

Vörös, L., and J. Padisàk. 1991. Phytoplankton biomass and chlorophyll-a in some shallow lakes in central Europe. Hydrobiologia 215: 111-119.

Watson, S., and J. Kalff. 1981. Relationships between nanoplankton and lake trophic status. Canadian Journal of Fisheries and Aquatic Sciences 38: 960-967.

----., and E. McCauley. 1988. Contrasting patterns of net- and nanoplankton production and biomass among lakes. Canadian Journal of Fisheries and Aquatic Sciences 49: 915-920.

Welschmeyer, N. A., and C. J. Lorenzen. 1984. Carbon-14 labeling of phytoplankton carbon and chlorophyll a carbon: Determination of specific growth rates. Limnology and Oceanography 29: 135-145.

Westlake, D. F., and others. 1980. Primary production. Pages 141-246 in E. D. Le Cren

and R. H. Lowe-McConnell, eds. The functioning of freshwater ecosystems. IBP 22. Cambridge Press.

Wetzel, R. G. 1983. Limnology. Saunders.

----. 1992. Gradient-dominated ecosystems: sources and regulatory functions of organic matter in freshwater ecosystems. Hydrobiologia 229: 181-198.

Whittaker, R. H., and G. E. Likens. 1973. Carbon in the biota. Pages 281-300 in G. M. Woodwell, and E. Pecan, eds. Carbon in the biota. AEC Symposium Series 30. United States Atomic Energy Commission.

White, P. A., J. Kalff, J. B. Rasmussen, and J. M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbial Ecology 21: 99-118.

White, E., G. Payne, and S. Pickmere. 1988. A limitation to the usefulness of chlorophyll as a biomass indicator in eutrophication studies. Verhandlungen der Internationale Vereinigung Limnologie 23: 598-601.

Wilkinson, L. 1987. SYSTAT: The system for statistics. SYSTAT Inc., Evanston.

Willén, E. 1984. The large lakes of Sweden: Vävern, Vättern, Mälaren and Hjälmaren. Pages 107-134 in F. B. Taub, ed. Lakes and reservoirs. Ecosystems of the world #23. Elsevier, Amsterdam.

Winberg, G. G. 1972. Etudes sur le bilan biologique énergetique et la productivité des lacs en Union Soviétique. Verhandlungen der Internationale Vereinigung Limnologie 18: 39-64.

Yan, N. D. 1985. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian shield lakes. Canadian Journal of Fisheries and Aquatic Sciences 43: 788-796.

Chapter 3

# THE RELATIONSHIP BETWEEN ETS (ELECTRON TRANSPORT SYSTEM) ACTIVITY AND OXYGEN CONSUMPTION IN LAKE PLANKTON: A CROSS-SYSTEM CALIBRATION

## ABSTRACT

The ETS (Electron Transport System) assay to measure respiration of aquatic organisms has been widely applied in studies of marine metabolism, but its use in freshwaters has been much more limited. This method calculates oxygen consumption from the measured ETS activity using an empirical conversion factor. This factor has been calculated for various marine organisms, and for natural plankton communities, but calibrations for freshwater organisms are lacking. The aim of this paper was to determine the relationship between lake plankton respiration and ETS activity, based on measured epilimnetic plankton oxygen uptake and ETS activity in 20 southern Quebèc lakes. The relationship between plankton oxygen consumption and ETS varies significantly both within lakes over the growing season, and among lakes. The magnitude of the error associated with calculating respiration from ETS is, however, similar to the error in other standard limnological procedures used in plankton carbon flow studies. Oxygen consumption is not a linear function of ETS across the range of lakes, but is rather a power function. The respiration:ETS ratio for lake plankton is therefore not constant: it is high in oligotrophic and colored lakes, and declines with trophy. These results are consistent with the changes expected in the structure of the plankton along trophic gradients.

## INTRODUCTION

Although respiration is a key factor in organic carbon utilization and energy flow in plankton communities, progress in quantifying rates of respiration, especially in lakes, has been slow (King and Packard, 1975; Williams, 1984). This may be partly due to the difficulty of measuring *in situ* respiration of natural plankton communities, particularly in oligotrophic areas, where rates are often below the detection limits of conventional methods (Packard and Williams, 1981). Various attempts have been made to overcome the problems associated with the measurement of plankton respiration (reviewed by Williams, 1984). Among the more promising approaches is the method proposed by Packard (1971), which is based on the measurement of the activity of the electron transport system (ETS), and originally designed as an indirect measurement of marine phytoplankton respiration. The method is simple and extremely sensitive, and it may be performed on virtually any type of planktonic organism or community, since the basic ETS is ubiquitous (Kenner and Ahmed 1975a; Packard, 1985).

The ETS assay has been modified and improved by various authors (Owens and King, 1975; Kenner and Ahmed, 1975a; Christiansen and Packard, 1979; Span, 1986). Its use has been extended from specific components of marine plankton (King and Packard, 1975; Owens and King, 1975; Båmstedt, 1980; Christensen et al., 1980; Bidigare et al., 1982; Finlay et al., 1983; Packard et al., 1983; Brugeaille et al., 1987; Hernàndez-Leòn, 1988; Schalk, 1988), and freshwater plankton (Devol, 1979; James, 1987; Tòth and Drits, 1991), to plankton community respiration in oceans (Packard, 1979; Packard and Williams, 1981; Romano et al., 1987a; 1987b; Vosjan and Nieuwland, 1987; Mimura et al., 1988; Vosjan et al., 1990) and lakes (Devol and Packard, 1978; Jones and Simon, 1979; Span, 1984; Rai, 1986; 1988), benthic organisms and sediment respiration (Zimmermann, 1975; Andersen and Helder, 1987;

Ta and Ruger, 1989; Cammen et al., 1990) and even biofilms (Blenkinsopp and Lock, 1990).

In all these different applications of the ETS method, the conversion from activity measured by ETS to situ oxygen consumption by the organisms is a critical step and remains a problematic issue (Williams 1984, Packard 1985). The ETS method is designed to estimate the respiratory capacity of organisms (Packard 1985). The theoretical relationship between ETS activity and actual oxygen uptake, based in the kinetics of respiratory control, deviates from experimental results. Thus, it is still necessary to empirically determine the relation between this potential respiration and *in situ* oxygen consumption to interpret ETS data. Empirical conversion factors have been derived for bacteria, phyto- and zooplankton and protozoans (Table 1). Researchers using ETS to estimate plankton community respiration have either determined an empirical conversion factor themselves (Table 1), or have used one of several published R:ETS (respiration to ETS) ratios (Devol, 1979; Schalk, 1988; Vosjan, 1988). In some cases, it was assumed that most of the respiration was due to phytoplankton so that the conversion factor for algae could be applied (Devol and Packard, 1978; Packard, 1979). In most cases, however, a constant conversion factor has been used, regardless of the taxonomic composition of the community.

Empirical R:ETS ratios for bacteria, phyto- and zooplankton are very different (Table 1). The use of a constant R:ETS ratio for the plankton therefore assumes that the relative contribution of these different components to community respiration does not vary among sites. The few empirical calibrations of whole plankton communities show a wide range of R:ETS ratios, and large SD around each ratio (Table 1). This suggests that the relationship between ETS activity and respiration is not constant and may vary with the type of plankton community. Several authors have shown that the

Table 1. Published empirical respiration to ETS ratios (R:ETS) and standard deviations (SD) for various groups of marine organisms and for freshwater and marine plankton communities. 1) Packard (1985), 2) Vosjan & Nieuwland (1987) 3) Vosjan et al. (1990), 4) Jones & Simon (1979), 5) Span (1988), 6) Toth & Drit (1991). All R:ETS ratios have been standarized to the Christensen & Packard (1977) method, using the conversion factors in Christensen & Packard (1979).

| Type | R/ETS | SD | Comment | Ref |
|---|---|---|---|---|
| Bacteria | 0.75 | (0.16) | Marine/Freshwater | 1 |
| Diatoms | 0.12 | (0.05) | Marine | 1 |
| Green algae | 0.12 | (0.03) | Marine | 1 |
| Protozoa | 0.17 | (0.01) | Freshwater | 1 |
| Zooplankton | 0.34 | (0.01) | Marine | 1 |
| Plankton | 0.11 | - | Marine | 1 |
| Plankton | 0.23 | - | Marine | 1 |
| Plankton | 0.22 | (0.09) | Marine | 2 |
| Plankton | 0.16 | (0.05) | Marine | 3 |
| Plankton | 0.12 | - | Freshwater (eutrophic) | 4 |
| Plankton | 0.09 | - | Freshwater (eutrophic) | 5 |
| Plankton | 0.49 | (0.04) | Freshwater (oligotrophic) | 6 |
| Plankton | 0.22 | (0.11) | Freshwater (oligo- to eutrophic) | This study |

relative proportions of autotrophic and heterotrophic biomass vary systematically along trophic gradients in the oceans (Dortch and Packard, 1989; Fuhrman et al., 1989; Cho and Azam, 1990), and the R:ETS ratio should vary accordingly. Packard and Williams (1981) proposed an empirical function to account for some of this variability in ocean studies, because they showed that a constant conversion factor greatly increases the error of the method. One should also expect differences among lakes in the R:ETS ratios, but the scarcity of published empirical conversion factors for freshwaters does not allow an interlake comparison. The method has to be calibrated in a wider variety of systems before it becomes an effective tool in freshwater plankton metabolism studies.

The objectives of this paper are twofold: First, to provide an empirical relationship between ETS activity and respiration for freshwater plankton from lakes spanning a wide trophic range. Secondly, to analyze some of the factors that may affect the respiration:ETS relationship in lake plankton, such as chlorophyll, TP concentrations and water color. I hypothesized that the R:ETS ratio should not be constant among lakes, but should reflect the relative contributions of bacteria, zoo- and phytoplankton to community respiration. Thus, humic lakes were expected to have high R:ETS because the contribution of bacteria to total respiration should be high in these systems. Conversely, I expected to find ratios approaching those of algae in eutrophic lakes with phytoplankton blooms.

## MATERIALS AND METHODS

Integrated epilimnetic water samples were taken with a plastic tube from 20 southern Québec lakes in June, July and August 1991. Table 2 summarizes the range of limnological characteristics of the study lakes. Chlorophyll (CHA) concentrations

were measured spectrophotometrically in ethanol extracts following Bergmann and Peters (1980), and total phosphorus (TP) was measured using the ascorbic acid method following persulphate digestion (Griesbach and Peters, 1991). Color is reported as absorbance of the filtered lake water (0.45 µm membrane), read in a 10 cm cell at 440 nm.

**ETS analysis:** Analyses of enzyme activity followed Rai (1984), who adapted the methods of Owens and King (1975) and Kenner and Ahmed (1975a). Plankton samples were concentrated on Nuclepore 0.4 µm polycarbonate membrane filters (25 mm diam.) under very low vacuum. Other authors have used glass fibre GF/C or GF/F filters, but a considerable fraction of the free bacteria and picoplankton are not retained by these filters (Lignell, 1992). The homogenation buffer, termination solution, substrate buffer and INT (2-(4-iodophenyl)-3-(4-nitrophenyl)-5-phenyltetrazolium chloride) solution are exactly those used by Rai (1984); the latter two were prepared daily to avoid bacterial contamination. The volume of water filtered ranged from 100 to 500 ml, depending on the density of the plankton. Three separate filters were prepared for each sample of water. The filters were placed in a plastic tube with 2 ml of homogenation buffer, in the refrigerator at 4°C. Within no more than 60 min, the tubes were placed in an ice bath at <4 °C, and the samples were continuously sonicated for 3 min, using a Broun-Sonic 1510 model at 300 Watts. Routine checks showed that no additional ETS activity was obtained by increasing this sonication time. A 1 ml aliquot was taken from each cell homogenate and placed in a tube with 3 ml of substrate buffer and 1 ml of INT solution. The samples were then incubated for 10 minutes at the *in situ* temperature. Reaction was stopped by adding 1 ml of termination solution. The samples were then centrifuged for 10 minutes at 5000 rpm, and the absorbance of an aliquot was read in a spectrophotometer at 490 nm. Blanks for the absorbance readings were made by adding 1 ml of homogenation buffer to 3 ml of substrate buffer

and 1 ml of INT solution, incubating the mixture for 10 minutes and stopping the reaction with 1 ml termination solution. Readings for turbidity at 750 nm were always negligible. The absorbances of the samples were converted to rates of oxygen reduction using the equation given by Rai (1984).

Modification of different steps of the ETS assay yields different estimates of enzyme activity for the same samples. We have followed the procedure described by Rai (1984) except that we used sonication instead of mechanical grinding to break cellular membranes. In this regard, our procedure is roughly comparable to that employed by Christensen and Packard (1977). Christensen and Packard (1979) showed that sonication increases activity of the cell homogenates by an average of 1.46 times compared to mechanical grinding. This correction factor should therefore be used to compare our results with those based on grinding. The use of 0.4 μm membranes instead of glass fibre filters also may increase the measured activity, because fewer bacteria are lost, but data are needed to quantify this potential effect.

**Oxygen uptake:** Plankton respiration was measured as the decrease in oxygen concentration in bottles. For each water sample, eight 300-ml BOD bottles were filled using a siphon. Four were randomly chosen as controls and the remaining four were placed in an incubator at *in situ* temperature for approximately 24 hours. Dissolved oxygen concentrations were measured using the azide modification of the Winkler technique (Golterman, 1978). The volume of all the bottles was calculated to within 0.1% to correct for displacement of the sample by reagents.

**Data analysis:** The data were analyzed by ordinary least square regression using SYSTAT, after being log transformed to meet normality assumptions and to equalize variance. A correction factor for bias, necessary when back transforming data from log

transformed equations was calculated as follows: CF = antilog (1.1513 x RMS), where RMS is the residual mean square of the regression (Neyman and Scott, 1960).

## RESULTS AND DISCUSSION

**Precision of the methods:** The mean standard deviation (SD) for the three replicates of individual ETS analyses was 13.3%, with a range of 2.2-46%. These values are within the reported range for the method (Christensen and Packard, 1979; Span, 1986). The mean SD for the four replicate Winkler determinations of incubated samples was 12%, with a range of 2.6-36%. The smallest detectable change in dissolved oxygen concentration in the control bottles was 20 $\mu g\ l^{-1}$, which is in the lower limit reported for the conventional Winkler method. The mean SD for the individual R:ETS ratios is thus 18%, calculated by propagating the error of respiration and ETS measurements.

**The relationship between respiration and ETS:** The data on respiration and ETS for the three experiments carried out in the 20 lakes appear in Table 3. The relationship between the two variables is not linear, but rather respiration increases roughly with the square root of ETS (Fig. 1). The regression equation is:

$$\log \text{Respiration} = 0.96 + 0.48 \log \text{ETS} \quad \text{eq (1)}$$

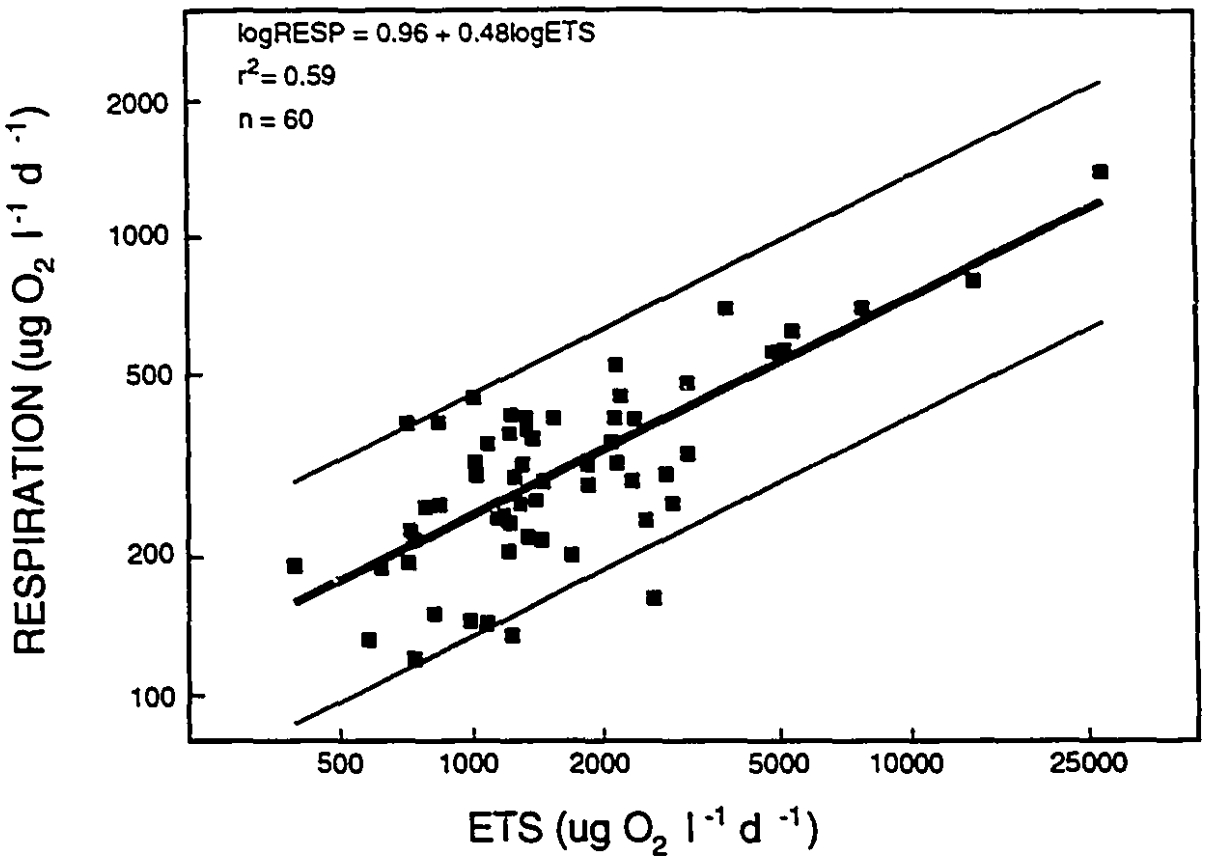
$$n = 60 \quad r^2 = 0.59 \quad S_{xy} = 0.13 \quad P < 0.0001 \quad CF = 1.05$$

There is considerable unexplained variance, particularly in the low range of ETS where many of the observations are clustered. Some of the observed scatter may be due to methodological problems. Whereas ETS is a measure of the respiratory potential of the community that reflects the immediate past prior to the sampling, the physiological measurement of respiration may also reflect changes in the community

Table 2. Range of limnological characteristics of the study lakes.

| Variable | Range |
|---|---|
| Latitude (degrees North) | 45 |
| Mean depth (m) | 3 - 42 |
| Area ($km^2$) | 0.3 - 47 |
| Mean summer chlorophyll ($\mu g\ l^{-1}$) | 0.7 - 37 |
| Mean summer TP ($\mu g\ l^{-1}$) | 5 - 50 |
| Color (absorbance at 440 nm, 10 cm cell) | 0.01 - 0.180 |

Figure 1. Plankton respiration as a function of ETS activity. Data are log-transformed, line of best fit and 95% confidence intervals shown.


logRESP = 0.96 + 0.48logETS
r2= 0.59
n = 60
RESPIRATION (ug O2 l-1 d -1)
2000
1000
500
200
100
500
1000
2000
5000
10000
25000
ETS (ug O2 l -1 d -1)

that occur during the incubation period. In most of our lakes, rather long incubation periods (20 to 24 h) were necessary to detect changes in the oxygen concentration. Short term oxygen uptake measurements would have been more appropriate, but were impractical in this study.

No significant relationship was found between the residuals and chlorophyll (CHA), TP or color. There was a significant negative correlation between temperature and the residuals of eq (1) (Fig. 2). Temperature was a significant variable ($p < 0.01$) in the following multivariate regression, which is a slight but significant improvement of eq (1):

$$\log \text{Respiration} = 1.33 + 0.55 \log \text{ETS} - 0.03 \text{ Temp} \qquad \text{eq (2)}$$
$$n = 60 \quad r^2 = 0.64 \quad S_{xy} = 0.12 \quad P < 0.0001 \quad CF = 1.04$$

The performance of equations 1 and 2 was compared with eight measurements which were not used in the original data analysis because their *in situ* temperature was well below the narrow temperature range of the original data (17-24°C). The mean error of the prediction using eq (1) was 18%, whereas the mean error using eq (2) was 45% (Table 4). Equation 2 grossly overestimates respiration at lower temperatures, suggesting that temperature is reflecting seasonality rather than a physiological effect. Equation 1 has thus a much wider range of application than equation 2, and should be more useful in calculating plankton respiration from ETS measurements.

The performance of equation 1 can also be assessed as a plot of predicted *vs* observed values (Fig. 3a). The slope of the regression equation is not significantly different from unity ($P < 0.001$) and 60% of the variance of the observed values is

Figure 2. Residuals of the respiration-ETS relationship as a function of water temperature.

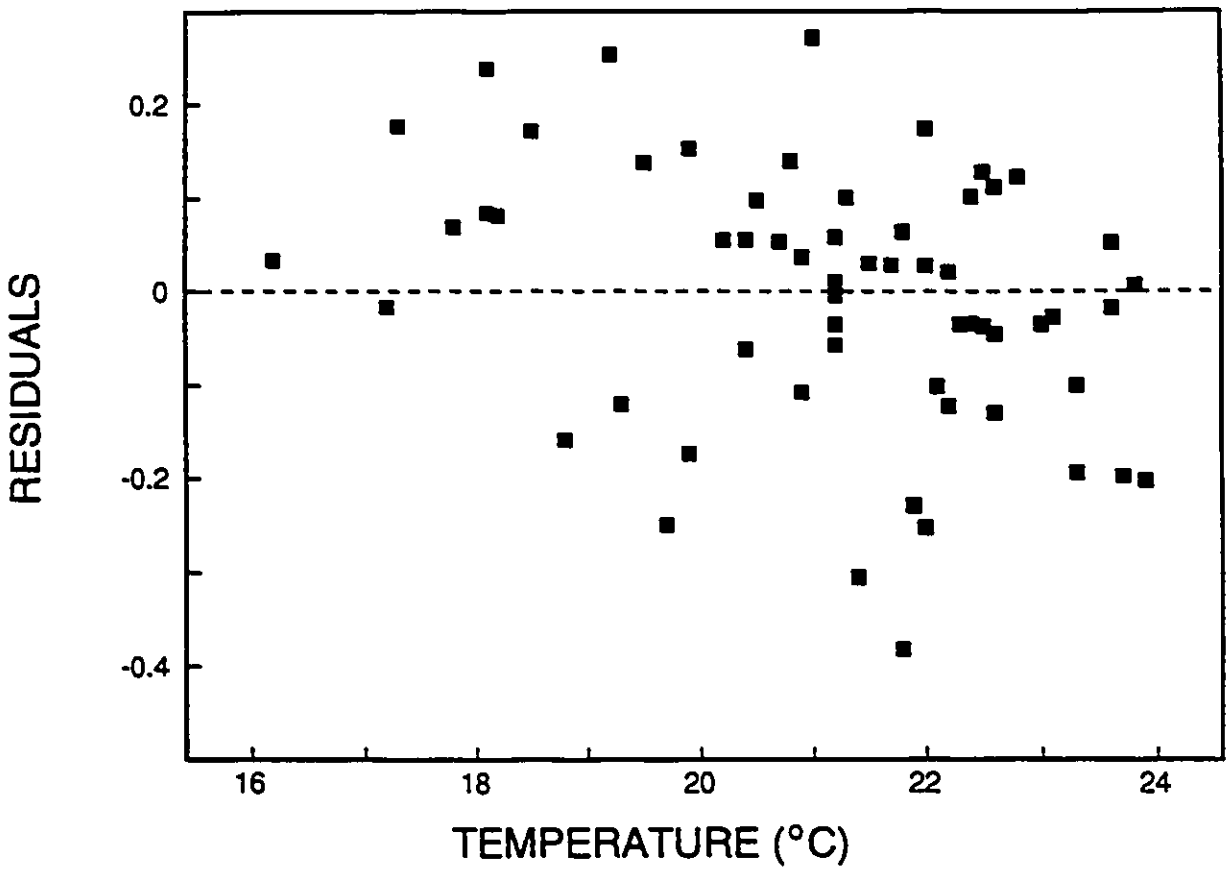
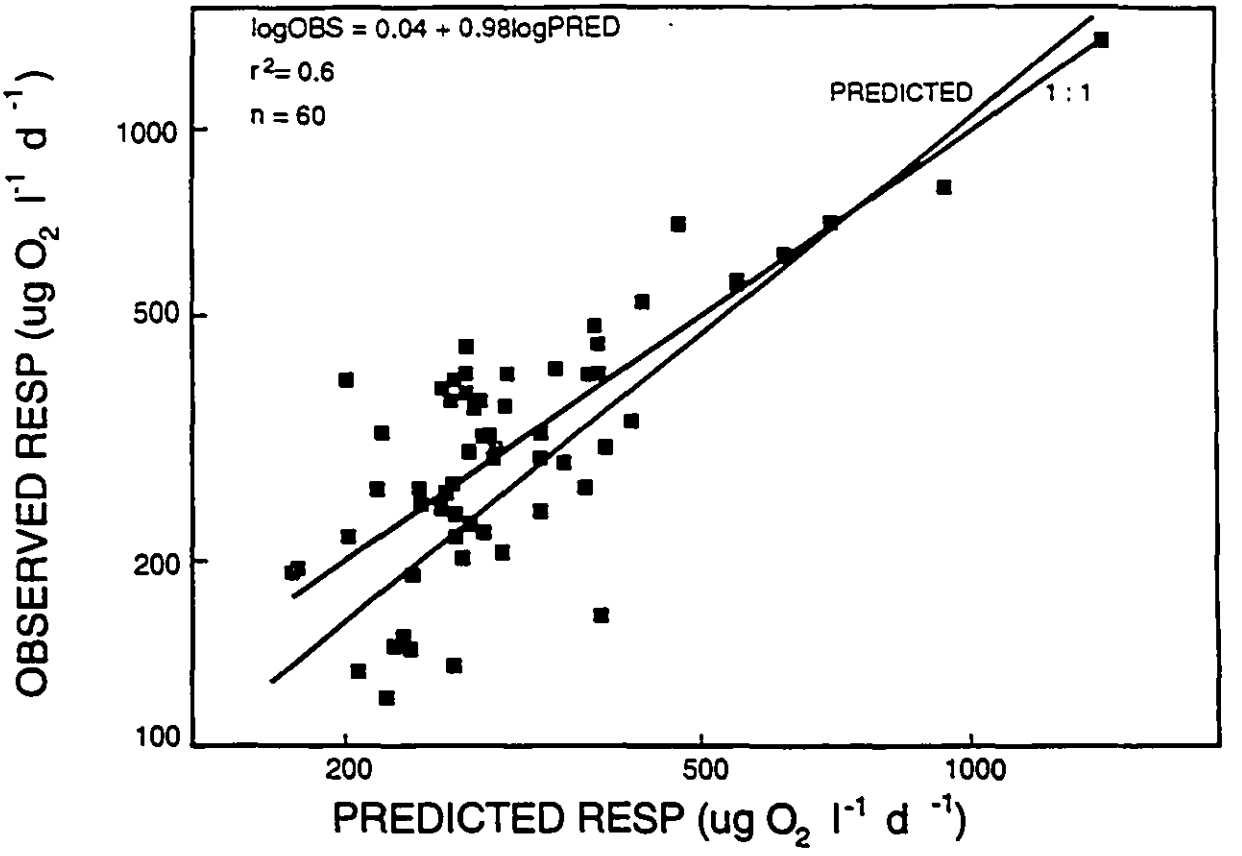
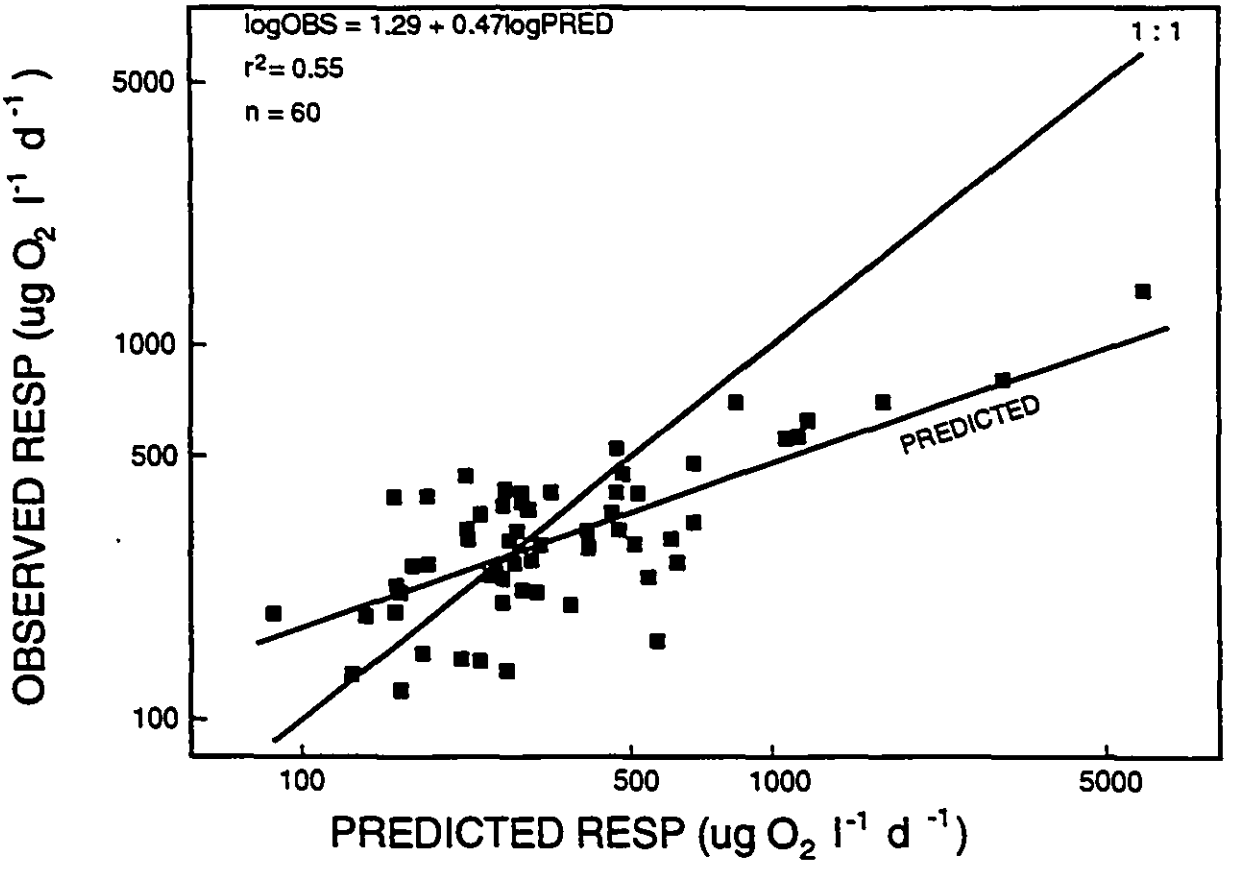

RESIDUALS
0.2
0
-0.2
-0.4
16
18
20
22
24
TEMPERATURE (°C)

Figure 3. Observed plankton respiration as a function of the predicted respiration calculated from equation 1 (3a). Data are log-transformed. Observed plankton respiration as a function of predicted respiration using the mean respiration to ETS ratio of all the experiments (3b) (R:ETS = 0.22, n = 60).


logOBS = 0.04 + 0.98logPRED
r2= 0.6
n = 60
PREDICTED
1 : 1
1000
500
200
100
200
500
1000
OBSERVED RESP (ug O2 l-1 d -1)
PREDICTED RESP (ug O2 l-1 d -1)


logOBS = 1.29 + 0.47logPRED
r2= 0.55
n = 60
1 : 1
PREDICTED
5000
1000
500
100
100
500
1000
5000
OBSERVED RESP (ug O2 l-1 d -1)
PREDICTED RESP (ug O2 l-1 d -1)

explained. Figure 3b shows a plot of predicted *vs* observed values using the mean R:ETS ratio of all the experiments (0.22). The use of a constant ratio more than doubles the error of the prediction, from a mean error of 24% for eq (1) to 54%, and the slope of the regression equation (0.4) is significantly different from 1 ($P < 0.001$).

There are limited published data with which to compare these results. Packard (1985) summarizes published empirical relationships for ETS and respiration, but all except one (Packard and Williams, 1981) are in units of oxygen consumption per unit biomass of different organisms, and can not be directly used. Packard and Williams (1981) and Mimura et al. (1988) provide two data sets on planktonic ETS and oxygen consumption for different oceanic sites, which are plotted in Figure 4. Equation 1 differs substantially from these two marine studies. The data in Mimura et al. (1988) yield the highest intercept, the data in Packard and Williams (1981) the lowest, and all three intercepts are significantly different ($P < 0.01$). The slope generated by the data in Packard and Williams is significantly greater than for the other two data sets ($P < 0.01$), whereas the slope of eq (1) is not significantly different from that generated by data in Mimura et al.

There is no clear explanation for the differences in the relationship between ETS and respiration within marine data, or between marine and freshwater data. This variability may be due to methodological differences in the three studies, although the data were standardized using the conversion factors in Christensen and Packard (1979). The two marine data sets have fewer points ($n < 14$), the range of plankton respiration is smaller, and include very low rates of respiration which we did not encounter in our lakes. It is conceivable that the freshwater relationship cannot be extrapolated to ultraoligotrophic areas. The communities sampled may not be comparable: this study represents integrated epilimnetic samples, Packard and

Williams (1981) provide estimates for different depths up to 30 m, and Mimura et al. (1988) sampled only the top 1 m, where microbial activity could potentially be higher. If this is the case, then the R:ETS ratio has to be regarded as very sensitive to changes in the composition of the plankton and highly site-specific, as Packard & Williams (1981) suggested.

**The R:ETS ratio:** The R:ETS ratios for the 20 lakes and the three sampling dates are listed in Table 3. The mean R:ETS ratio for all our experiments (n = 60) is 0.22 (SD = 0.11, range = 0.051-0.55). This value for the ratio is intermediate between the empirical conversion factors determined for algae and various heterotrophic components of the plankton (Table 1). Our mean R:ETS ratio also lies within the range of values reported for natural plankton communities (Table 1). It is higher than the values reported by James and Simon (1979) and Span (1988) for eutrophic freshwater sites, but lower than the ratio reported by Tòth and Drits (1991) for an oligotrophic lake. All the published R:ETS ratios have been standardized to the Christensen & Packard (1977) method using the conversion factors in Christensen & Packard (1979).

**The variation of the R:ETS ratio with trophy:** Over a trophic gradient of lakes, respiration increases less than ETS (Fig. 5). ETS and respiration are significantly correlated ($P < 0.0001$) with both CHA and TP. The slope of the ETS-CHA regression equation is significantly higher ($P < 0.001$) than the slope of the R-CHA relation (Fig. 5a); the same conclusion is drawn using TP instead of CHA (Fig. 5b). Thus the R:ETS ratio tends to decrease with increasing concentrations of chlorophyll and TP. For example, chlorophyll explains 30% of the variability in the ratio.

Table 3. Results of the experiments conducted in 20 southern Quebec lakes in June, July and August 1991. Temperature (Temp, °C), chlorophyll (CHA, µg $l^{-1}$), total phosphorus (TP, µg $l^{-1}$), water color (COLOR, absorbance at 440 nm, 10 cm cell), respiration (RESP, µg $O_2$ $l^{-1}$ $d^{-1}$), ETS activity (ETS, µg $O_2$ $l^{-1}$ $d^{-1}$), respiration to ETS ratio (R:ETS).

| Lake | Month | Temp | CHA | TP | Color | Resp | ETS | R:ETS |
|---|---|---|---|---|---|---|---|---|
| Massawippi | June | 17.3 | 5.6 | 11.2 | 0.042 | 409 | 1224 | 0.33 |
| | July | 20.9 | 2.5 | 11.7 | 0.028 | 299 | 1248 | 0.24 |
| | August | 22.5 | 2.8 | 7.4 | 0.027 | 266 | 1394 | 0.19 |
| Lovering | June | 18.1 | 5.2 | 13.5 | 0.095 | 393 | 835 | 0.47 |
| | July | 21.2 | 3.1 | 11.9 | 0.072 | 292 | 1450 | 0.20 |
| | August | 22.3 | 4.8 | 10.6 | 0.067 | 293 | 2316 | 0.13 |
| Baldwin | June | 18.1 | 3.1 | 8.2 | 0.031 | 302 | 1018 | 0.30 |
| | July | 20.4 | 1.6 | 11.1 | 0.019 | 287 | 1843 | 0.16 |
| | August | 20.9 | 1.5 | 6.5 | 0.019 | 221 | 1332 | 0.17 |
| Lyster | June | 17.2 | 0.7 | 5.3 | 0.026 | 189 | 619 | 0.30 |
| | July | 19.3 | 0.9 | 8.1 | 0.016 | 205 | 1209 | 0.17 |
| | August | 20.4 | 1.7 | 3.9 | 0.009 | 318 | 1296 | 0.24 |
| Aylmer | June | 17.8 | 1.1 | 11.9 | 0.198 | 257 | 778 | 0.33 |
| | July | 19.9 | 2.7 | 12.9 | 0.167 | 401 | 1325 | 0.30 |
| | August | 21.0 | 2.9 | 8.7 | 0.141 | 392 | 709 | 0.55 |
| St Francoise | June | 16.2 | 1.2 | 11.3 | 0.187 | 228 | 720 | 0.32 |
| | July | 19.5 | 2.0 | 11.2 | 0.161 | 352 | 1080 | 0.33 |
| | August | 21.2 | - | 7.6 | 0.147 | 260 | 840 | 0.31 |
| Waterloo | June | 20.7 | 6.7 | 39.5 | 0.069 | 627 | 5395 | 0.12 |
| | July | 22.4 | 27.1 | 41.2 | 0.053 | 807 | 13976 | 0.06 |
| | August | 21.8 | 106.5 | 68.6 | 0.079 | 1396 | 27256 | 0.05 |
| Yamaska | June | 20.5 | 8.3 | 22.1 | 0.068 | 450 | 2189 | 0.20 |
| | July | 22.2 | 6.5 | 26.6 | 0.050 | 570 | 5165 | 0.11 |
| | August | 22.0 | 15.3 | 34.2 | 0.047 | 705 | 7808 | 0.09 |
| Brome | June | 20.2 | 4.2 | 15.1 | 0.038 | 402 | 2120 | 0.19 |
| | July | 22.2 | 4.8 | 20.7 | 0.028 | 304 | 2776 | 0.11 |
| | August | 22.1 | 10.8 | 18.6 | 0.029 | 336 | 3096 | 0.11 |
| D'Argent | June | 20.8 | 2.4 | 12.5 | 0.101 | 373 | 1210 | 0.31 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | July | 23.8 | 3.3 | 13.5 | 0.066 | 356 | 2074 | 0.17 |
| | August | 23.1 | 2.9 | 11.9 | 0.064 | 261 | 1282 | 0.20 |
| Memphremagog | June | 18.5 | 3.5 | 19.1 | 0.048 | 526 | 2126 | 0.25 |
| | July | 22.4 | 1.4 | 12.7 | 0.022 | 362 | 1363 | 0.26 |
| | August | 22.5 | 3.5 | 13.1 | 0.026 | 380 | 1324 | 0.29 |
| Coulombe | June | 19.2 | 3.3 | 13.5 | 0.191 | 445 | 1006 | 0.44 |
| | July | 23.7 | 4.3 | 15.2 | 0.155 | 201 | 1686 | 0.12 |
| | August | 22.8 | 3.9 | 12.9 | 0.143 | 402 | 1533 | 0.26 |
| Nicolet | June | 18.2 | 0.6 | 3.9 | 0.026 | 191 | 395 | 0.48 |
| | July | 22.0 | 0.8 | 6.6 | 0.017 | 143 | 1075 | 0.13 |
| | August | 21.9 | 1.0 | 2.3 | 0.020 | 145 | 984 | 0.15 |
| Petite | June | 21.2 | 1.5 | 7.7 | 0.075 | 242 | 1133 | 0.21 |
| Brompton | July | 23.6 | 1.2 | 10.3 | 0.046 | 317 | 1832 | 0.17 |
| | August | 23.0 | 1.4 | 20.3 | 0.054 | 194 | 714 | 0.27 |
| Brompton | June | 21.2 | 2.3 | 7.5 | 0.101 | 237 | 1210 | 0.20 |
| | July | 23.3 | 3.2 | 11.9 | 0.077 | 261 | 2865 | 0.09 |
| | August | 22.3 | 2.6 | 14.7 | 0.078 | 246 | 1174 | 0.21 |
| Stukely | June | 19.9 | 1.6 | 5.1 | 0.046 | 150 | 813 | 0.18 |
| | July | 22.6 | 2.8 | 9.9 | 0.035 | 320 | 2143 | 0.15 |
| | August | 21.4 | 1.4 | 22.2 | 0.043 | 135 | 1229 | 0.11 |
| Bowker | June | 18.8 | 0.7 | 5.1 | 0.015 | 132 | 580 | 0.23 |
| | July | 21.3 | 0.9 | 7.5 | 0.009 | 362 | 1373 | 0.26 |
| | August | 21.2 | 1.1 | 4.9 | 0.013 | 218 | 732 | 0.30 |
| Magog | June | 22.0 | 4.1 | 20.8 | 0.039 | 701 | 3821 | 0.18 |
| | July | 23.6 | 2.1 | 18.1 | 0.027 | 480 | 3109 | 0.15 |
| | August | 21.7 | 13.7 | 48.1 | 0.030 | 563 | 4860 | 0.12 |
| Truite | June | 21.5 | 3.7 | 10.5 | 0.074 | 400 | 2354 | 0.17 |
| | July | 23.9 | 1.2 | 9.9 | 0.051 | 240 | 2486 | 0.10 |
| | August | 21.8 | 4.5 | 7.9 | 0.061 | 162 | 2592 | 0.06 |
| Orford | June | 19.7 | 0.5 | 5.1 | 0.019 | 120 | 735 | 0.16 |
| | July | 22.6 | 0.8 | 12.6 | 0.012 | 217 | 1429 | 0.15 |
| | August | 22.6 | 1.9 | 5.2 | 0.017 | 322 | 1015 | 0.32 |

Table 4. Independent data set and performance of equations 1 and 2 to calculate respiration from ETS measurements. Plankton respiration (RESP) and ETS (ug $O_2$ $l^{-1}$ $d^{-1}$) and temperature (T, °C) measured in 8 lakes, and respiration calculated from ETS using equation 1 (RESP1) and ETS and temperature using equation 2 (RESP2).

| Lake | T | Resp | ETS | Resp1 | %Error | Resp2 | %Error |
|---|---|---|---|---|---|---|---|
| Memphremagog | 8.6 | 476 | 2325 | 392 | 17.7 | 872 | 83.2 |
| Nicolet | 10.5 | 271 | 569 | 199 | 26.5 | 353 | 30.1 |
| Pet. Brompton | 14.9 | 231 | 1306 | 297 | 28.5 | 411 | 77.9 |
| Stukely | 13.5 | 265 | 1094 | 273 | 2.9 | 411 | 55.0 |
| Magog | 16.0 | 489 | 3144 | 453 | 7.4 | 617 | 26.3 |
| Truite | 17.9 | 217 | 1094 | 273 | 25.7 | 303 | 39.6 |
| Bowker | 11.0 | 301 | 636 | 210 | 30.1 | 362 | 20.3 |
| Orford | 15.8 | 275 | 1056 | 268 | 2.5 | 344 | 24.9 |
| | | | Mean | Error | 17.7 | | 44.7 |

Figure 4. Comparison of plankton respiration-ETS relationships for marine and freshwater data. Plankton respiration as a function of ETS activity for a) marine data extracted from Mimura et al. (1988). b) marine data extracted from Packard & Williams (1981). c) freshwater relationship using equation 1 (in text). Data are log-transformed. Both studies used variations of the Kenner and Ahmed (1975) method. For comparison with our freshwater data that utilized sonication instead of grinding, their data were standardized to the Christensen & Packard (1977) method using a conversion factors of 1.38 (Christensen & Packard, 1979).

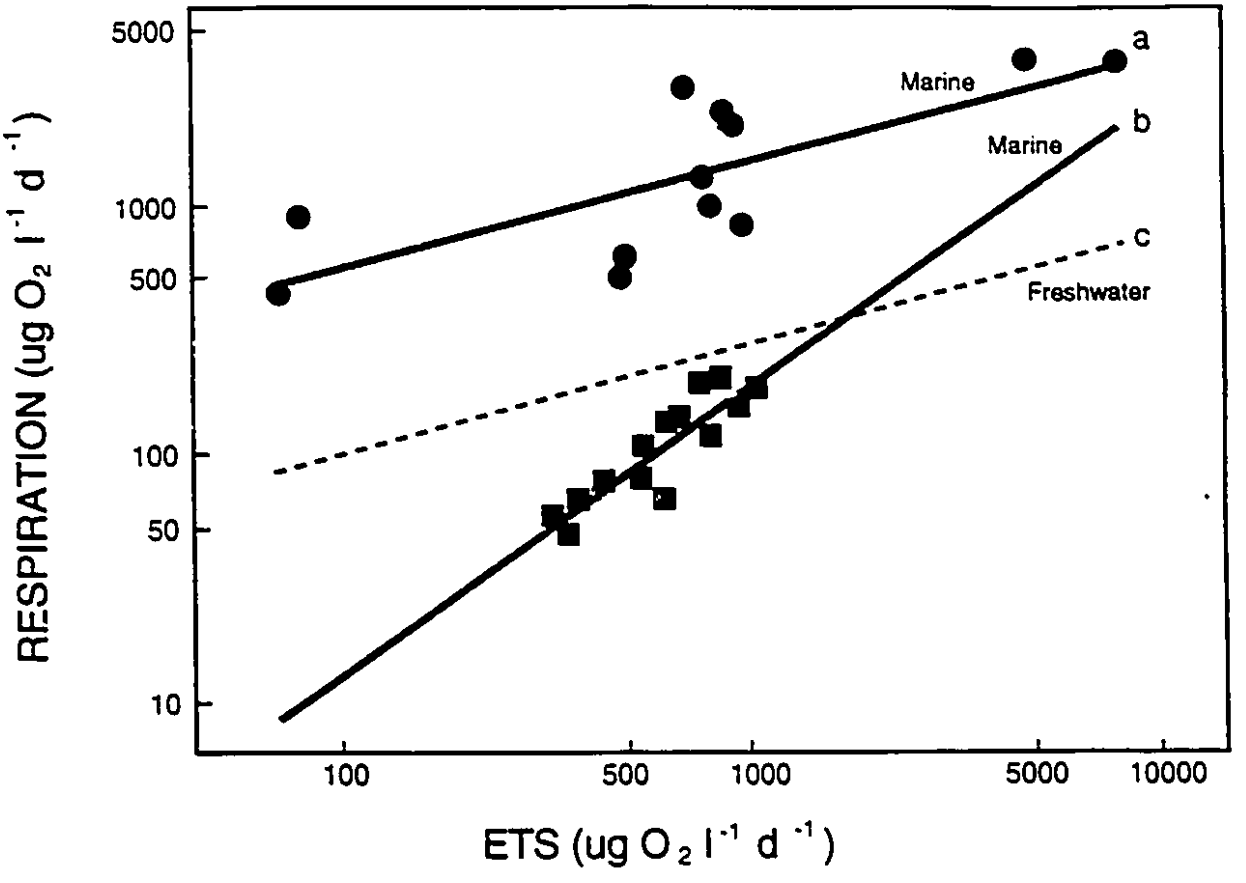

5000
1000
500
100
50
10
RESPIRATION (ug O2 l-1 d-1)
100
500
1000
5000
10000
ETS (ug O2 l-1 d-1)
a
Marine
b
Marine
c
Freshwater

Figure 5. Plankton respiration and ETS activity as functions of chlorophyll concentration (5a), and total phosphorus (TP) (5b). Data are log-transformed.

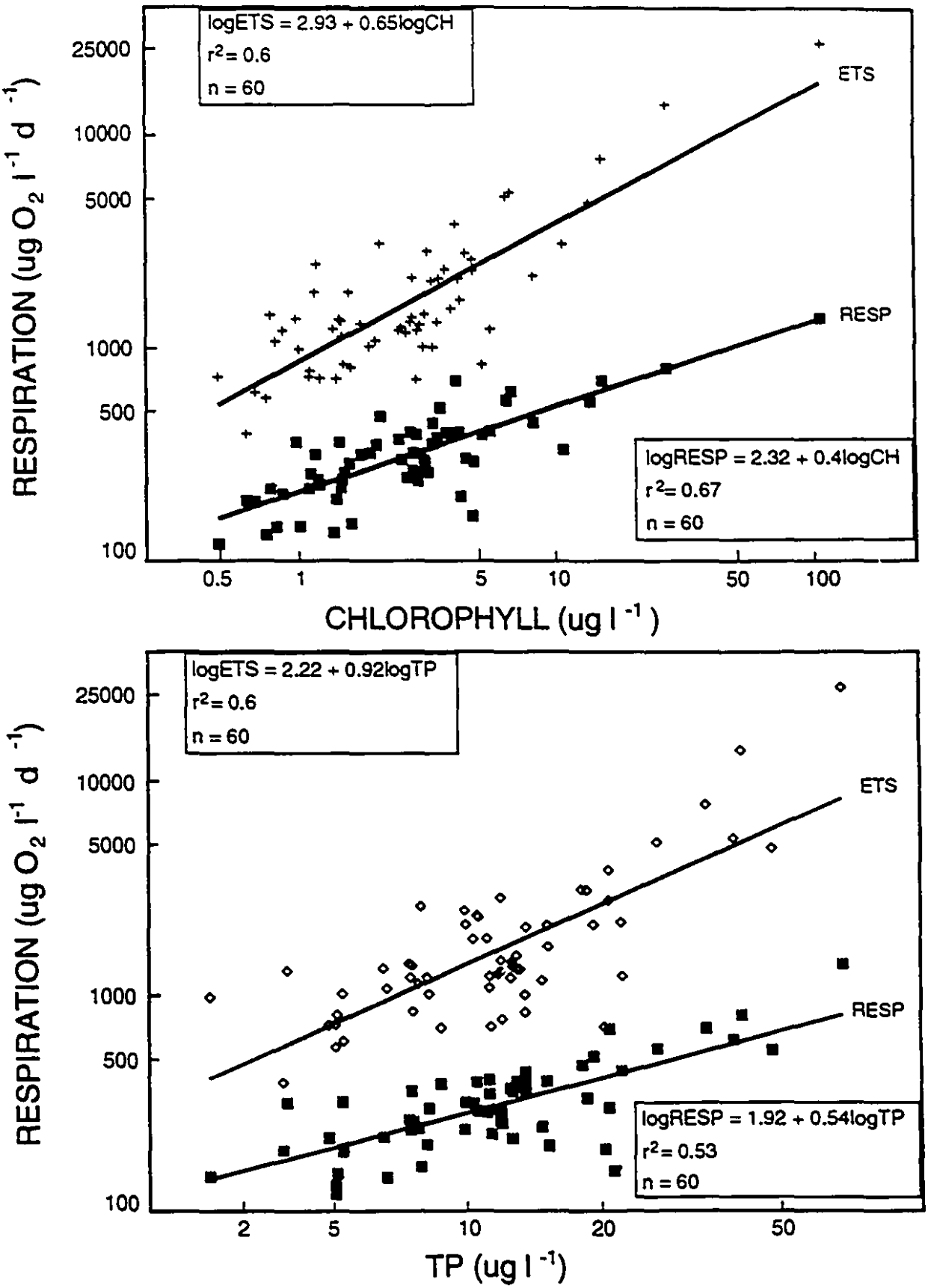
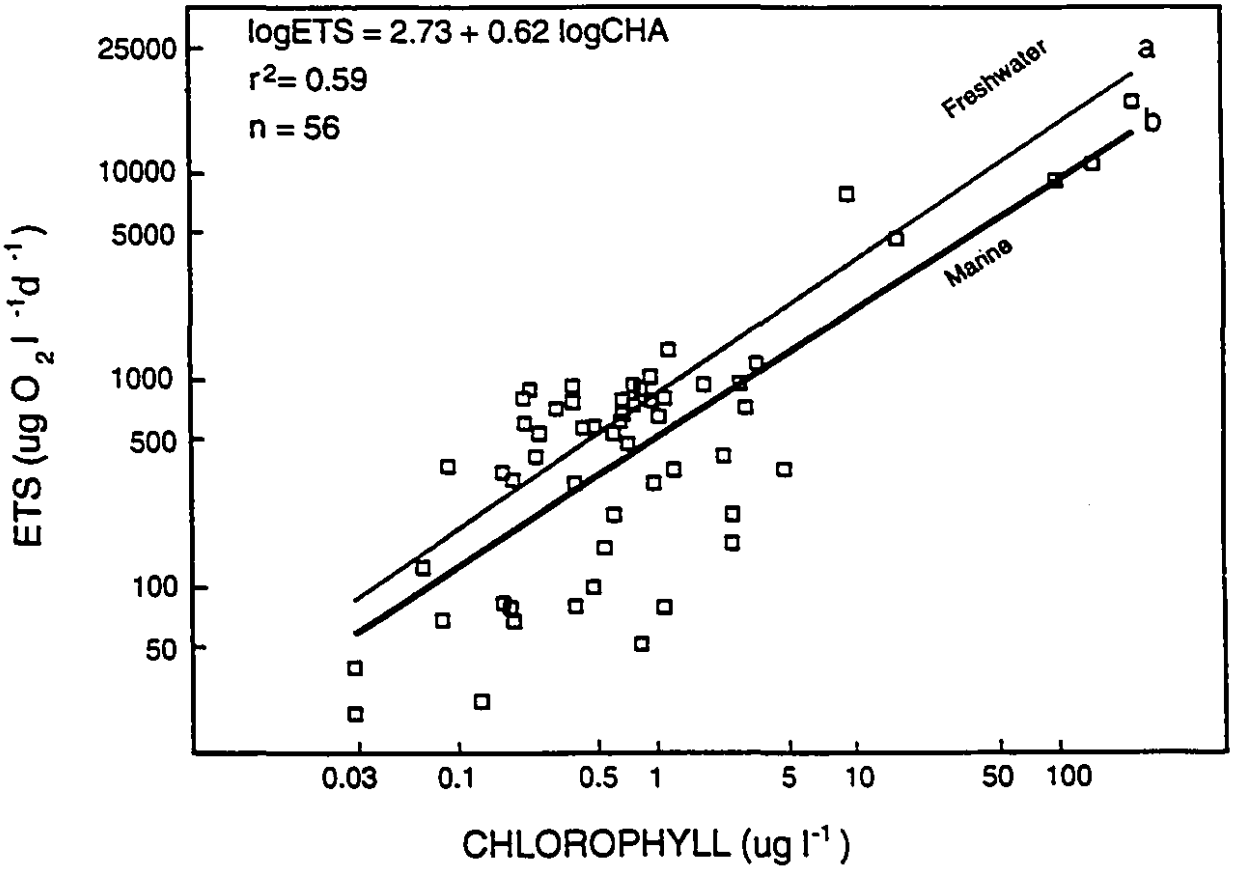

logETS = 2.93 + 0.65logCH
r2= 0.6
n = 60
ETS
RESP
logRESP = 2.32 + 0.4logCH
r2= 0.67
n = 60
RESPIRATION (ug O2 l-1 d -1)
25000
10000
5000
1000
500
100
0.5
1
5
10
50
100
CHLOROPHYLL (ug l -1 )
logETS = 2.22 + 0.92logTP
r2= 0.6
n = 60
ETS
RESP
logRESP = 1.92 + 0.54logTP
r2= 0.53
n = 60
RESPIRATION (ug O2 l-1 d -1)
25000
10000
5000
1000
500
100
2
5
10
20
50
TP (ug l -1)

Figure 6. Comparison of freshwater and marine ETS-chlorophyll relationships. a) Lake plankton ETS activity as a function of chlorophyll concentration from equation in Figure 5a. b) Marine plankton ETS activity as a function of chlorophyll. Data were extracted from Packard & Williams (1981), Mimura et al. (1990), Romano et al (1987a) and Christensen & Packard (1979). All marine ETS values have been converted to the Christensen & Packard (1977) method. Data are log-transformed.


logETS = 2.73 + 0.62 logCHA
r2= 0.59
n = 56
Freshwater
a
b
Marine
25000
10000
5000
1000
500
100
50
0.03
0.1
0.5
1
5
10
50
100
ETS (ug O2 l-1d-1)
CHLOROPHYLL (ug l-1)

The R:ETS ratio approaches the empirical conversion factor determined for algae (Table 1) in the most eutrophic lakes, suggesting that algal contribution to community respiration increases in more productive systems. The two most eutrophic lakes sampled, Yamaska and Waterloo, had ratios as low as 0.05 during phytoplankton blooms. Kenner and Ahmed (1975b) found similarly low ratios in algal cultures in late log phase, and suggested that respiration tended to decline in these populations, whereas ETS remained essentially unchanged. It is reasonable to expect a similar pattern during massive algal developments in lakes.

The low R:ETS ratio found in eutrophic lakes can also be interpreted as an increase in overall photosynthetic capacity relative to the respiratory potential of the plankton. The ETS assay is performed on homogenates of whole plankton samples, which include algal chloroplasts. Photosynthesis, like respiration, involves an electron transport system, and the ETS assay will measure the activity of both systems (Packard 1985). Thus, for algae, ETS compounds the respiratory and the photosynthetic electron transport activity, resulting in R:ETS ratios that are lower than for all the other heterotrophic components of the plankton. Likewise, at a community level, a decrease in R:ETS ratios with trophy can be interpreted as an increase in photosynthetic capacity relative to respiratory potential of the plankton, or a shift from predominantly heterotrophic communities in oligotrophy to predominantly autotrophic communities in eutrophy.

ETS has been correlated to chlorophyll concentrations in previous studies of marine plankton (Packard et al., 1974; Setchell and Packard, 1979; Packard and Williams, 1981; Packard, 1985). Data extracted from four published marine studies (Fig. 6) show good agreement between the marine and freshwater ETS-CHA data, and the parameters of the two regression equations are not significantly different ($P <$

0.01), although the marine data include much lower chlorophyll concentrations than those encountered in our freshwater study. Our slightly higher intercept may be the result of using a 0.4 um membrane instead of glass fibre filters to concentrate the plankton samples. This result is in marked contrast with the striking differences discussed above in the respiration-ETS relationships between marine and freshwater systems.

Packard and Williams (1981) and Packard (1985) suggested that a close correlation between ETS and chlorophyll would only be expected in areas where activity was dominated by phytoplankton. There is evidence, however, that plankton biomass in oligo- to ultraoligotrophic areas of the oceans is dominated by heterotrophs, particularly bacteria ( Dortch and Packard, 1989; Cho and Azam, 1990), but the ETS-CHA relationship from Figure 6 still applies to these areas. Likewise, in the present study, the ETS-CHA covers a wide range of lakes, from oligotrophic systems where the larger fraction of the plankton biomass is in the form of heterotrophs, to eutrophic lakes where algae overwhelmingly dominate planktonic biomass and activity (del Giorgio and Peters, 1993). The ETS-CHA relationship, both for marine and for freshwater plankton, does not seem merely to indicate algal dominance over community metabolism. Rather, the structure of the plankton communities varies along a gradient of chlorophyll concentrations, and also of TP in lakes, and the ETS seems to vary concomitantly.

**The variation of the R:ETS ratio with temperature:** The R:ETS ratio declines with increasing temperature (Fig. 7). This pattern explains a substantial portion of the variability within lakes along the summer. Although King and Packard (1975) found that temperature had a negligible effect on marine zooplankton R:ETS ratios, Båmstedt (1980) showed a strong temperature-dependence of the R:ETS ratio

Figure 7. The lake plankton R:ETS ratio as a function of mean summer lake temperature. Ratios are log-transformed.

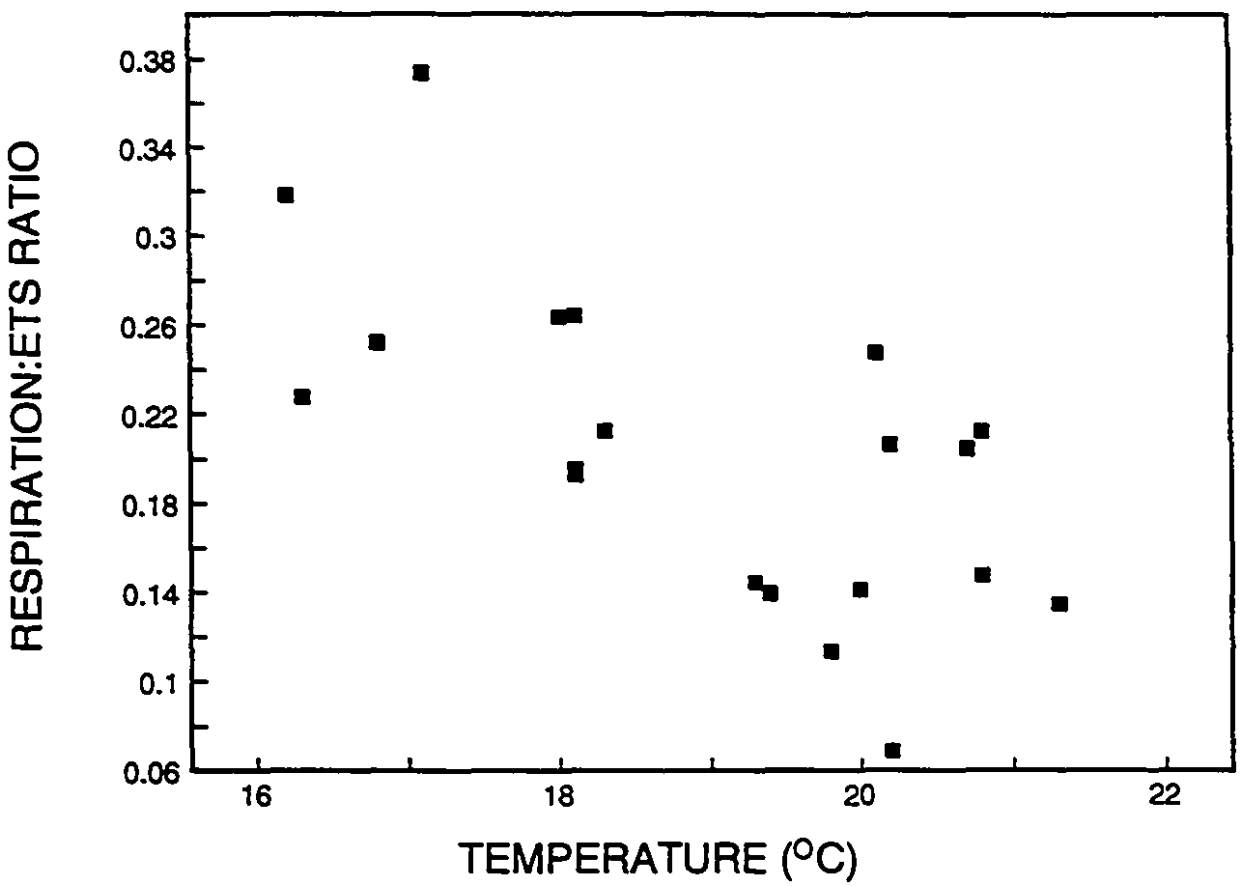
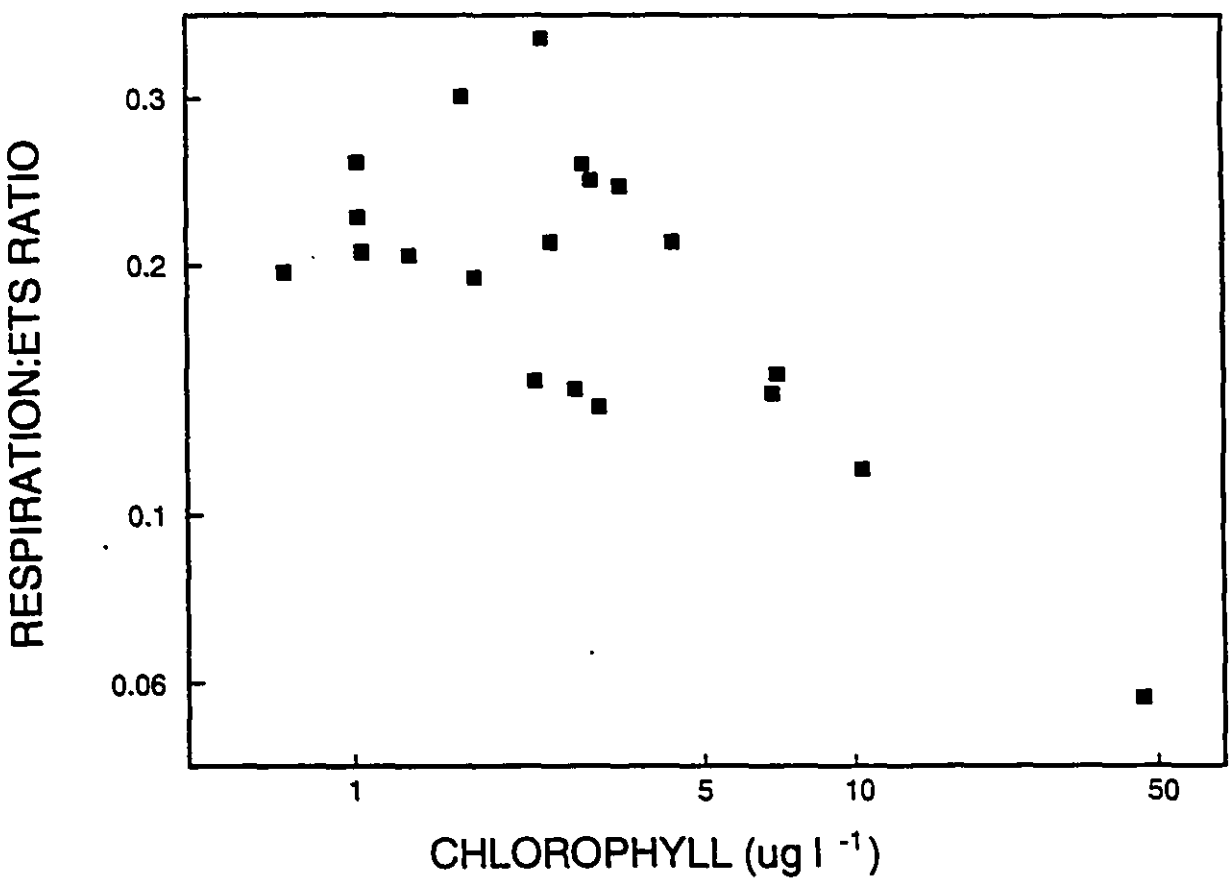

RESPIRATION:ETS RATIO
0.38
0.34
0.3
0.26
0.22
0.18
0.14
0.1
0.06
16
18
20
22
TEMPERATURE (°C)

Figure 8. The lake plankton R:ETS ratio as a function of mean summer chlorophyll concentration, log-log plot.


RESPIRATION:ETS RATIO
0.3
0.2
0.1
0.06
1
5
10
50
CHLOROPHYLL (ug l -1)

in zooplankton samples. The dependency of the ratio on temperature implies that the response of ETS is greater than the response of respiration, and that the $Q_{10}$ of the two processes is different. The temperature-dependence of ETS has been well documented and is described by an Arrhenius equation (Ahmed and Kenner 1977), which has been used to convert ETS measurements to *in situ* temperatures in several studies (Båmstedt 1980, James 1987). The temperature-dependence of lake plankton respiration is less well established, however, and a wide range of $Q_{10}$ values for natural communities have been reported (Ganf 1974). It is conceivable that temperature is reflecting the seasonality of factors that affect the R:ETS ratios, and that temperature itself does not play such an important role.

**Overall patterns in R:ETS ratios across lakes:** Previous sections have noted that the R:ETS ratio is negatively correlated to both chlorophyll concentrations and temperature. In addition, the ratio tends to be high in lakes with high humic content, as indicated by the color of the water. All three variables were selected by a stepwise multiple regression procedure ($P < 0.01$), to yield the following model:

$$\log (R:ETS) = 0.66 - 0.05\ TEMP + 0.18 \log COLOR - 0.24 \log CHA$$
$$n = 60 \quad r^2 = 0.51 \quad S_{xy} = 0.16 \quad P < 0.0001 \quad CF = 1.07 \qquad \text{eq (3)}$$

This model explains 50% of the variation in the ratio, and indicates some of the major trends to be expected in the relationship between respiration and ETS. Thus the R:ETS ratio tends to decline along the summer within lakes as the temperature of the water increases. Lakes with the highest chlorophyll concentrations tend to have the lowest ratios, and within oligotrophic lakes, colored lakes have the highest ratios observed. The dependency of the R:ETS ratio on lake trophy and humic content is statistically stronger if the data for the three experiments carried out in each lake

during the summer are averaged. A stepwise multiple regression on the lake means yields the equation:

$$\log (R:ETS) = -0.33 - 0.36 \log CHA + 0.17 \log COLOR \qquad eq\ (4)$$
$$n = 20 \quad r^2 = 0.61 \quad S_{xy} = 0.12 \quad P < 0.0001 \quad CF = 1.04$$

Temperature is not significant in this model, but chlorophyll and color explain 61% of the variation in the ratio across lakes. Thus it would seem that the pattern in R:ETS ratios reflects major changes in plankton community structure. The high ratios, approaching the empirical factors for heterotrophs, found in colored lakes are consistent with elevated heterotrophic activity known to occur in these systems, fueled by allochthonous organic inputs (Salonen and Hammar, 1986; Hessen et al., 1990). Clear oligotrophic lakes, however, also show high ratios relative to more eutrophic systems (Fig. 8), suggesting that along a trophic gradient of lakes, the contribution of heterotrophs to plankton community metabolism decreases as algal productivity increases. These results are consistent with the growing evidence, both for marine and freshwater systems, that there is a progressive shift from plankton communities dominated by heterotrophs in oligotrophy, to communities dominated by autotrophs in nutrient-rich waters (Dortch and Packard, 1989; Cho and Azam, 1990; Currie, 1991; del Giorgio and Peters, 1993).

## CONCLUSIONS

Lake plankton respiration may be calculated from ETS measurements to within a mean error of 25%, using equation 1. This equation should be applied with caution in lakes outside the range covered in this study (Table 2). Our empirical equation may be applied to ETS measurements performed with another variant of the method, if the data are transformed using one of the published inter-method conversions, but this step will most likely increase the error around the predicted respiration. There is considerable scatter around the R *vs* ETS regression line, with 95% confidence limits around individual predictions amounting to around ± 60%. Nevertheless, the magnitude of the error associated with calculating respiration from ETS measurements in lake plankton is similar to the error in other standard limnological procedures used in plankton carbon flow studies, such as the $^{14}C$ technique to measure rates of primary production, or the thymidine uptake procedure to measure bacterial production. Since ETS is very sensitive at low metabolic rates, and easily and rapidly performed, its use in plankton metabolism studies is encouraged, particularly for extensive comparative research on plankton respiration in lakes.

Respiration is not a linear function of ETS but rather increases roughly as the square root of ETS, and thus the R:ETS ratio does not remain constant. The R:ETS ratio varies significantly both within and among lakes. The ratio declines with temperature (in the 16-24 °C range), and this trend explains a considerable portion of the within-lake variability of the ratio along the summer. Many factors covary with temperature in lakes, however, so that temperature may integrate various effects on the R:ETS ratio.

Around 61% of the variability of the mean R:ETS ratios is explained by the average chlorophyll concentrations and water color. The variation in the R:ETS ratio

thus seems to indicate changes in the relative contribution of the different components of the plankton to community respiration, over a trophic gradient of lakes. Lakes with high heterotrophic activity, such as humic lakes, tend to have high ratios, whereas eutrophic systems show lower R:ETS ratios. The overall pattern in the R:ETS ratios suggests a declining contribution of heterotrophs to community respiration with increasing algal productivity.

## ACKNOWLEDGEMENTS

I wish to thank W. Everett for his valuable assistance in the field, and R.H. Peters and two anonymous reviewers for their critical comments on the manuscript. This research has been supported by grants from FCAR and NSERC, and is a contribution of the McGill Limnology Research Center.

## REFERENCES

Andersen,F.O. and Helder,W. (1987) Comparison of oxygen microgradients, oxygen flux rates and electron transport system activity in coastal marine sediments. Mar. Ecol. Prog. Ser., 37, 259-264.

Båmstedt,U. (1980) ETS activity as an estimator of respiratory rate of zooplankton populations. The significance of variations in environmental factors. J. exp. mar. Biol. Ecol., 42, 267-283.

Bergmann,M. and Peters,R.H. (1980) A simple reflectance method for the measurement of particulate pigments in lake water and its application to phosphorus-chlorophyll-seston relationships. Can. J. Fish. Aquat. Sci., 37, 111-114.

Bidigare,R.R., King,F.D. and Biggs,D.C. (1982) Glutamate dehydrogenase (GDH) and respiratory electron-transport-system (ETS) activities in Gulf of New Mexico zooplankton. J. Plankton Res., 4, 895-911.

Blenkinsopp,S.A. and Lock,M.A. (1990) The measurement of electron transport system activity in river biofilms. Wat. Res., 24, 441-445.

Brugeaille,M., Relexans,J.C., His,E. and Lin,R.G. (1987) ETS activities and biomasses of ten marine phytoplankters cultured *in vitro*. C.R. Acad. Sc. Paris, Ser. III, 13, 351-354.

Cammen,L.M., Corwin,S. and Christensen,J.P. (1990) Electron transport system (ETS) activity as a measure of benthic macrofaunal metabolism. Mar. Ecol. Prog. Ser., 65, 171-182.

Christensen,J.P., Owens,T.G., Devol,A.H. and Packard,T.T. (1980) Respiration and physiological state in marine bacteria. Mar. Biol., 55, 267-276.

Christensen,J.P. and Packard,T.T. (1977) Sediment metabolism from the northwest African upwelling system. Deep-Sea Res., 24, 339-347.

Christensen,J.P. and Packard,T.T. (1979) Respiratory electron transport activities in phytoplankton and bacteria: Comparison of methods. Limnol. Oceanogr., 24, 576-583.

Cho,B.C. and Azam,F. (1990) Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Mar. Ecol. Prog. Ser. 63, 253-259.

Currie,D.J. (1991) Large-scale variability and interactions among phytoplankton, bacterioplankton, and phosphorus. Limnol. Oceanogr., 35, 1437-1455.

del Giorgio, P.A. and Peters, R.H. (1993). The balance between phytoplankton production and plankton respiration in lakes. Can. J. Fish. Aquat. Sci. 50: 282-289.

Devol,A.H. (1979) Zooplankton respiration and its relation to plankton dynamics in two lakes of contrasting trophic state. Limnol. Oceanogr., 24, 893-905.

Devol,A.H. and Packard,T.T. (1978) Productivity, chlorophyll, and respiration in Lake Washington. Limnol. Oceanogr. 23, 104-111.

Dortch,Q. and Packard,T.T. (1989) Differences in biomass structure between oligotrophic and eutrophic marine ecosystems. Deep-Sea Res., 36, 223-240.

Finlay,B.J., Span,A. and Ochsenbein-Gattlen,C. (1983) Influence of physiological state on indices of respiration rate in protozoa. Comp. Biochem. Physiol., 74A, 211-219.

Fuhrman,J.A., Sleeter,T.D., Carlson,C.A. and Proctor,L.M. (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. Mar. Ecol. Prog. Ser., 57, 207-217.

Ganf,G.G. (1974) Rates of oxygen uptake by the plankton community of a shallow equatorial lake (Lake George, Uganda). Oecologia, 15, 17-32.

Golterman,H.L., Clymo,R.S. and Ohnstad,M.A.M. (1978) Methods for physical and chemical analysis of freshwaters. IBP 8, Blackwell, London.

Hernàndez-Leòn,S. (1988) Gradients of mesozooplankton biomass and ETS activity in the wind-shear area as evidence of an island mass affect in the Canary Island waters. J. Plankton Res., 10, 1141-1154.

Hessen,D.O., Andersen,T. and Lyche,A. (1990) Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. Limnol. Oceanogr., 35, 84-99.

James,M.R. (1987) Respiratory rates in the cladoceran *Ceriodaphnia dubia* in Lake Rotongaio, a monomictic lake. J. Plankton Res., 9, 573-578.

Jones,J.G. and Simon,B.M. (1979) The measurement of electron transport system activity in freshwater benthic and planktonic samples. J. Appl. Bacter., 46, 305-315.

Kenner,R.A. and Ahmed,S.I. (1975a) Measurements of electron transport activities in marine phytoplankton. Mar. Biol., 33, 119-127.

Kenner,R.A. and Ahmed,S.I. (1975b) Correlation between oxygen utilization and electron transport activity in marine phytoplankton. Mar. Biol., 33, 129-133.

King,F.D. and Packard,T.T. (1975) Respiration and respiratory electron transport system in marine zooplankton. Limnol. Oceanogr., 20, 849-854.

Lignell, R. (1992) Problems in filtration fractionation of $^{14}C$ primary productivity studies. Limnol. Oceanogr., 37, 172-178.

Mimura,T., Romano,J.C. and de Souza-Lima,Y. (1988) Microbiomass structure and respiratory activity of microneuston and microplankton in the northwestern Mediterranean Sea influenced by the Rhone river water. Mar. Ecol. Prog. Ser., 49, 151-162.

Neyman,J. and Scott,E.L. (1960) Correction of bias introduced by a transformation of variables. Ann. Math. Stat., 31, 643-661.

Owens,T.G. and King,F.D. (1975) The measurement of respiratory electron-transport-system activity in marine zooplankton. Mar. Biol., 30, 27-36.

Packard,T.T. (1971) The measurement of respiratory electron transport activity in marine phytoplankton. J. Mar. Res., 29, 235-244.

Packard,T.T. (1979) Respiration and respiratory electron transport activities in plankton from the N. W. African upwelling area. J. Mar. Res., 37, 711-742.

Packard,T.T. (1985) Measurement of electron transport activity of microplankton. Adv. Aquat. Microbiol., 3, 207-261.

Packard,T.T. and Williams,P.J.leB. (1981) Rates of respiratory oxygen consumption and electron transport in surface seawater from the northwest Atlantic Ocean. Oceanol. Acta, 4, 351-358.

Packard,T.T., Garfield,P.C. and Martinez,R. (1983) Respiration and respiratory enzyme activity in aerobic and anaerobic cultures of the marine denitrifying bacterium, *Pseudomonas perfectomarinus*. Deep-Sea Res., 30, 227-243.

Packard,T.T., Harmon,D. and Boucher,J. (1974) Respiratory electron transport activity in plankton from upwelled waters. Tethys, 6, 213-222.

Rai,H. (1984) Size-dependent respiratory-enzyme activity and primary production of microplankton in Schohsee (a North German Baltic lake). Arch. Hydrobiol., 102, 137-153.

Rai,H. (1988) Activity of respiratory electron transport system (ETS) in different size particles as a measure of carbon losses from primary producers. Verh. Internat. Verein. Limnol., 23, 503-504.

Romano,J.C., Mimura,T. and de Souza-Lima,Y. (1987a) Discriminating approach of various microplanktonic-stage contributions to whole ETS measurements in sea-water samples. a. Phytoplankton. Int. Revue ges. Hydrobiol., 72, 457-472.

Romano,J.C., Laborde,P., Mimura,T. and de Souza-Lima,Y. (1987b) Discriminating approach of various microplanktonic-stage contributions to whole electron transport system (ETS) measurements in sea-water samples. b. Bacteria. Int. Revue ges. Hydrobiol., 72, 607-630.

Salonen,K. and Hammar,T. (1986) On the importance of dissolved organic matter in the nutrition of zooplankton in some lake waters. Oecologia, 68, 246-253.

Schalk,P.H. (1988) Respiratory electron transport system (ETS) activities in zooplankton and micronekton of the Indo-Pacific region. Mar. Ecol. Prog. Ser., 44, 25-35.

Setchell,F.W. and Packard,T.T. (1979) Phytoplankton respiration in the Peru upwelling. J. Plankton Res., 1, 343-354.

Span,A.S.W. (1986) Optimization of the electron transport system (ETS) method for natural phytoplankton assemblages tested with some species of freshwater phytoplankton. Wat. Res., 20, 1497-1503.

Span,A.S.W. (1988) Metabolic activity as reflected by ETS and BOD in a shallow eutrophic lake. Arch. Hydrobiol., 31, 141-147.

Tan,T.L. and Ruger,H.J. (1989) Benthic studies of the Northwest African upwelling region: bacteria standing stock and ETS-activity, ATP-biomass and Adenylate Energy Charge. Mar. Ecol. Prog. Ser., 51, 167-176.

Tòth,L.G. and Drits,A.V. (1991) Respiratory energy loss of zooplankton in Lake Balaton (Hungary) estimated by ETS-activity measurements. Verh. Internat. Verein. Limnol., 24, 993-996.

Vosjan,J.H. (1988) The ATP and ETS method in the study of surface layers and deep-sea basins of East Indonesian waters. Arch. Hydrobiol., 31, 221-228.

Vosjan,J.H. and Nieuwland,G. (1987) Microbial biomass and respiratory activity in surface waters of the East Banda Sea and North West Arafura Sea (Indonesia) at the time of the South East Monsoon. Limnol. Oceanogr., 32, 767-775.

Vosjan,J.H., Tijssen,S.B., Nieuwland,G. and Wetsteyn,F.J. (1990) Oxygen regime, respiratory activity and biomass of microorganisms, and the carbon budget in the Fladen Ground area (Northern North Sea) during spring. Neth. J. Sea. Res., 25, 89-99.

Williams,P.J.leB. (1984) A review of measurements of respiration of marine plankton populations. In Hobbie,J.A. and Williams,P.J.leB. (eds), Heterotrophic Activity in the Sea. Plenum Press, New York, pp. 357-389.

Zimmerman,A.P. (1975) Electron transport analysis as an indicator of biological oxidations in freshwater sediments. Verh. Internat. Verein. Limnol., 19, 1518-1523.

Chapter 4

# PATTERNS IN PLANKTONIC P/R RATIOS IN LAKES: INFLUENCE OF LAKE TROPHY AND DISSOLVED ORGANIC CARBON .

## ABSTRACT

A comparative analysis of planktonic metabolism in 20 southern Quebec lakes was carried out to test the hypothesis that planktonic P/R ratios reflect gradients of both nutrient enrichment and dissolved organic carbon. Mean epilimnetic phytoplankton photosynthesis ranged from 8 to 377 mg C $m^{-3}$ $d^{-1}$, and the amount of carbon respired by the plankton in excess of phytopiankton photosynthesis ranged from 30 to 86 mg C $m^{-3}$ $d^{-1}$. Plankton community respiration was 2 to 10 times greater than phytoplankton photosynthesis in all oligotrophic and mesotrophic lakes during the growing season, and this imbalance narrowed towards the more productive lakes. P/R ratios were positively related to chlorophyll and TP concentration, and inversely related to water color and dissolved organic carbon (DOC) concentration. The strong influence of DOC on planktonic P/R ratios was almost exclusively due to its depressing effect on phytoplankton photosynthesis; DOC had no statistical effect on respiration. The calculated DOC loading for these lakes suggests that organic carbon loss through epilimnetic respiration in excess of phytoplankton photosynthesis is comparable to the estimated DOC loss within the lakes, and that summer plankton metabolism could be supported by external DOC inputs in most lakes. The highly significant intercept of the respiration to production relationship, 27 mg C $m^{-3}$ $d^{-1}$, may indicate the baseline metabolism supported by external sources of carbon that occurs in these temperate lakes. Estimates of respiratory $CO_2$ production from the pelagial of southern Quebec lakes range from 11 to 60 mmol $CO_2$ $m^{-2}$ $d^{-1}$, depending on lake trophy and DOC concentration. These estimates suggest that planktonic metabolism of allochthonous DOC probably constitutes a major source of $CO_2$ in lakes.

## INTRODUCTION

The potential of external carbon inputs to influence lake metabolism and plankton community function has long been recognized in limnology. Birge and Juday (1927) distinguished between autotrophic lakes, which derive their organic matter from internal sources, and allotrophic lakes, which derive a large portion of the organic matter from the drainage basin. Subsequently, several authors have shown that both dissolved and particulate detrital organic carbon comprise a large reservoir of energy that stabilizes aquatic ecosystems (Wetzel 1992), and fuels lake metabolic processes (Wetzel and Richey 1978, Odum and Prentki 1978, Likens and Bormann 1979). Some aspects of this paradigm, however, have seldom been quantified. For example, limnologists recognize that plankton community respiration may exceed phytoplankton photosynthesis in lakes, but the magnitude and frequency of this discrepancy remains largely unknown. Far from being a closed issue, the influence of dissolved organic carbon on freshwater planktonic food webs has received renewed attention in recent years (Jones 1992, Salonen et al. 1992).

Dissolved organic carbon (DOC) influences lake plankton metabolism through physical, chemical and biological processes: humic DOC affects the underwater light climate by reducing the depth of the trophogenic layer, and competes with phytoplankton for light. DOC has also been shown to scavenge limiting nutrients, including iron and other micronutrients, from the water. These physical and chemical processes may depress primary production (Jackson and Hecky 1980). At the same time, DOC can also serve as a carbon source for bacteria (Tranvik 1992), and indirectly, for other heterotrophic components of the plankton, so DOC should contribute to plankton community respiration (Hessen 1992). Jones (1992) reviewed these processes, and hypothesized that planktonic P/R ratios should generally increase with trophy in lakes, and that at comparable nutrient or chlorophyll

concentrations, colored lakes should have lower P/R ratios than clear-water lakes. A review of the literature on plankton primary production and respiration (del Giorgio and Peters 1993) supports the first part of this hypothesis: planktonic P/R ratios are generally below unity in oligotrophic and mesotrophic lakes, and are greater than one in eutrophic lakes. The impact of allochthonous carbon on lacustrine planktonic metabolism is greater in colored lakes (Sarvala et al. 1981, Salonen et al. 1983, Rask et al. 1986), but the distinction between clear-water and brown-water lakes is arbitrary, because DOC is found in all water bodies. Most lakes lie somewhere between the brown polyhumic boreal lakes and the ultra-clear oligotrophic alpine lakes, so it is uncertain where they fall in Jones' (1992) scheme.

Overall, the evidence suggests that planktonic P/R ratios reflect two distinct resource gradients: the first is a nutrient gradient, which relates to phytoplankton biomass and production, and the second is a gradient of dissolved organic carbon concentration and/or water color, related mainly to lake morphometry and characteristics of the drainage basin. These two gradients are not necessarily coherent: high DOC concentration may occur at high or low TP concentration, and vice versa (Meili 1992, De Haan 1992).

In this paper we tested the hypothesis that planktonic P/R ratios are directly related to total phosphorus and chlorophyll a concentrations, and inversely related to water color or DOC concentrations. This hypothesis is a quantitative test of the conceptual model proposed by Jones (1992) for patterns in freshwater planktonic P/R ratios. To test the hypothesis, we have measured phytoplankton photosynthesis and plankton community respiration along the growing season in southern Quebec lakes. These lakes span a wide trophic range, and also a wide range in water color and dissolved organic carbon concentrations.

## MATERIALS AND METHODS

**Study sites:** Twenty lakes in southern Quebec, Canada, were sampled for this study. These lakes lie approximately 45° latitude North and 72° West; most stratify during the summer (except shallow lakes like Waterloo, Baldwin and Brome), and are covered with ice from mid-December to mid-April. Mean depth ranged from 2.9 to 48 m, and lake area from 0.3 to 47.1 $km^2$ . Their watersheds are dominated by rolling hills in the Appalachian region, with mixed farmland and woodland. A few, such as lakes Waterloo, Magog and Brome, receive large anthropogenic nutrient inputs. Lake Memphremagog is divided into three distinct basins, and only the Central basin was sampled; the morphometric data therefore corresponds only to this basin and not to the entire lake.

**Sampling and chemical analyses:** All the lakes were sampled monthly from May 10 to August 30, 1991, and four of the lakes were sampled until mid-October; the depth of the thermocline was determined from the thermal and oxygen profiles taken with a Orion 840 combined meter, and integrated 40 l samples of epilimnetic water were collected with a plastic tube from the deepest point of each lake. In shallow lakes that did not stratify the entire water column was sampled. The underwater PAR intensity was determined with a LiCor quantum meter equipped with an Li-192S underwater photocell ($2\pi$ collector). In the laboratory, chlorophyll (CHL) concentration was measured spectrophotometrically in ethanol extracts following Bergmann and Peters (1980), and total phosphorus (TP) was measured using the ascorbic acid method following persulphate digestion (Griesbach and Peters 1991); dissolved organic carbon (DOC) was measured from filtered (0.45 µm membrane) and acidified water samples using a Dorhman Carbon Analyzer; color (COL) is reported as absorbance of the filtered lake water (0.45 µm membrane), read in a 10 cm cell at a wavelength of 440 nm (Cuthbert and del Giorgio 1992); the concentration of total

inorganic carbon (TIC) was determined from total alkalinity, pH and temperature (Wetzel and Likens 1991).

**Phytoplankton photosynthesis**: Rates of phytoplankton photosynthesis were measured following Fee (1990). In the laboratory, and no more than 2 h after collection, lake water was siphoned into 10 60-ml quartz bottles, and 0.5 ml of $NaH^{14}CO_3$ containing approximately 2.8 µCi were injected into each bottle. The bottles were placed in a chamber having four different PAR levels (ranging from 10 to 982 µEin $m^{-2}$ $sec^{-1}$), and incubated for 3 h at *in situ* lake temperature; two of the bottles were completely darkened with masking tape. At the end of the incubation period, a 10-ml aliquot from each bottle was acidified with HCl (to pH < 2) and bubbled with air for 2 h, to eliminate inorganic $^{14}C$. A 1-ml aliquot of the bubbled sample was then mixed with 10 ml of scintillation cocktail (Beckman, Ready Safe) and counted in a Model 1215 RackBeta II Liquid Scintillation Counter, with external channel correction. Rates of C uptake were determined using the equation:

$$\text{Photosynthesis } (\mu g\ C\ l^{-1}\ h^{-1}) = (^{14}C\ assim/^{14}C\ avail) \times 1.06 \times TIC \times 1/T$$

where $^{14}C$ assim = DPMs in the bubbled samples; $^{14}C$ avail = total DPMs added; 1.06 = fractionation factor for $^{14}C$; TIC = total inorganic carbon (µg $l^{-1}$); T = incubation time (hours). Computer programs developed by Fee (1990) were used to analyze the laboratory and field data: the initial slope of the photosynthesis *vs* light curve, normalized to biomass ($\alpha^B$, in mg C mg $CHL^{-1}$ $Ein^{-1}$ $m^{-2}$), and the biomass-specific maximum rate of photosynthesis ($P^B_m$, in mg C mg $CHL^{-1}$ $h^{-1}$) were estimated from chlorophyll and incubator data; *in situ* rates of photosynthesis were calculated from solar PAR, PAR extinction in the lake, chlorophyll and the above photosynthetic parameters. The program calculates solar PAR for each location and date, assuming

70% cloudless days during the summer (Energy, Mines and Resources Canada 1974). The program finally integrates photosynthetic rates over the mixed layer, in mg C $m^{-2}$ $d^{-1}$, and calculates the mean volumetric rates for this layer, in mg C $m^{-3}$ $d^{-1}$.

**Plankton respiration:** Plankton respiration was measured as the decrease in oxygen concentration in bottles. For each integrated epilimnetic water sample, eight 300-ml BOD bottles were filled using a siphon. Four were randomly chosen as controls and the remaining four were placed in an incubator at *in situ* temperature for approximately 24 h. Dissolved oxygen concentrations were measured using the azide modification of the Winkler technique (Golterman et al. 1978). The volume of all the bottles was calculated to within 0.1% to correct for displacement of the sample by reagents. The minimum change in oxygen concentration that could be detected using this technique was 18 µg $O_2$ $l^{-1}$. Rates of oxygen uptake were converted to rates of C production (mg C $m^{-3}$ $d^{-1}$) assuming RQ = 0.8 (Schwaerter et al. 1988).

**Carbon loading model:** The annual dissolved organic carbon loading from the drainage basin was calculated for each lake, using the approach developed by Engstrom 1986. The change in the lake dissolved organic carbon concentration [DOC] (gC $m^{-3}$) can be stated as the sum of gains and losses through inflow, outflow and sedimentation or degradation:

$$d[DOC] / dt = J - Q \,.\, [DOC] - S$$

where J is the rate of dissolved organic input from the drainage basin (gC $y^{-1}$), S is the rate of internal DOC loss through sedimentation or mineralization (gC $y^{-1}$), and Q is the water outflow rate ($m^{-3}$ $y^{-1}$). J is defined as:

$$J \ (gC\ y^{-1}) = DOC_{exp}\ (gC\ m^{-2}\ y^{-1}).\ A_d\ (m^2)$$

DOC export from watersheds in this area of southern Quebec varies between 6 and 18 gC $m^{-2}$ $y^{-1}$ (Eckhardt and Moore 1990); we use the midpoint of these values

(12 gC $m^{-2}$ $y^{-1}$) in these calculations. Q is the water inflow and outflow rate ($m^{-3}$ $y^{-1}$), and is defined as:

$$Q = R \cdot A_d + (p - e) \cdot A_l$$

where R is the annual water runoff ($m^{-3}$ $m^{-2}$), $A_d$ is the area of the drainage basin ($m^2$), p is precipitation and e is evaporation, both in mm $y^{-1}$, and $A_l$ is the lake area ($m^2$); runoff in southern Quebec averages 500 mm, and the net input of rain to the lake (p - e) is 400 mm (Energy, Mines and Resources Canada 1974).

Under steady state conditions, d[DOC] / dt = 0; and the internal loss rate through sedimentation and degradation (S, in gC $y^{-1}$) can be calculated as:

$$S = J - (Q \cdot [DOC])$$

The resulting rates of input (J) and internal loss of allochthonous organic carbon (S), normalized to lake area (gC $m^{-2}$ $y^{-1}$), were then compared to the measured rates of plankton respiration in excess of phytoplankton photosynthesis during the summer. Excess plankton respiration (E, in gC $m^{-2}$ $summer^{-1}$) is defined as:

$$E = [R\ (mgC\ m^{-3}\ d^{-1}) - P\ (mgC\ m^{-3}\ d^{-1})] \cdot Z_{int}\ (m) \cdot 150\ (days)$$

where R and P are the mean summer epilimnetic plankton respiration and phytoplankton photosynthesis, respectively, $Z_{int}$ is the depth of the epilimnion or the sampling depth, and 150 days integrate the summer period, from May to September. S and E were compared to determine if excess organic carbon respired by the plankton in the epilimnion of lakes could originate from the allochthonous DOC pool. If S exceeds E, then DOC input is sufficient, but if E exceeds S, then some other source, or an artifact, should be considered.

**Statistical analyses:** All the data shown are arithmetic means of four to seven samples taken during the study. The data were log-transformed to meet normality assumptions and to equalize variance, and analyzed by ordinary least squares using

SYSTAT. The conclusions of our analyses are drawn from the parameters of the ordinary least square regressions because we are mainly interested in the predictive nature of these relationships. However there is error in both our independent and dependent variables, so we also provide the parameters of the functional regressions (Model II) and their confidence limits for our univariate equations, calculated following McArdle (1988) and Ricker (1975). These regressions are only referred to if they suggest a qualitatively different result than that indicated by the least square regressions. Unless otherwise stated, the significance level for all hypothesis tests was $p < 0.05$. The full data set used in this analysis appears in Appendix 3 of this thesis.

## RESULTS

The lakes sampled were diverse in terms of trophic status. Mean summer TP concentration ranged in these lakes from 4.9 to 45.7 μg $l^{-1}$, chlorophyll ranged from 0.7 to 37.2 μg $l^{-1}$, and DOC from 2.7 to 7.5 mg C $l^{-1}$ (Table 1). All volumetric data are means integrated over the sampling depth ($Z_{int}$, Table 1), which corresponds either to the mixing depth or approximately to mean depth in the case of very shallow lakes.

**Phytoplankton photosynthesis and plankton respiration**: Mean summer epilimnetic plankton respiration rates ranged from 56 to 280 mg C $m^{-3}$ $d^{-1}$, whereas mean summer epilimnetic phytoplankton photosynthetic rates ranged from 8 to 377 mg C $m^{-3}$ $d^{-1}$ (Table 1). Plankton respiration increased much more slowly than photosynthesis in this set of 20 lakes (Fig. 1). The slope of the relationship between photosynthesis and respiration was significantly lower than 1 (Table 2), and its intercept (27.1 mg C $m^{-3}$ $d^{-1}$) was substantially above 0, suggesting that in the absence of phytoplankton production, there would still be measurable rates of plankton respiration in lakes.

Table 1. Mean summer physico-chemical and biological data for the mixed layer of 20 southern Quebec lakes: TP (total phosphorus, $\mu g\ l^{-1}$), CHL (chlorophyll, $\mu g\ l^{-1}$), DOC (dissolved organic carbon, $mg\ l^{-1}$), COL (water color, measured as absorbance at 440 nm in a 10 cm cell), Temp (water temperature, °C), RESP (plankton community respiration, $mgC\ m^{-3}\ d^{-1}$), PHOT (phytoplankton photosynthesis, $mgC\ m^{-3}\ d^{-1}$), and $Z_{int}$ (depth of the thermocline, and of sampling integration). Central is the central basin of lake Memphremagog.

| Lake | TP | CHL | DOC | COL | Temp | RESP | PHOT | $Z_{int}$ |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 4.9 | 0.7 | 3.3 | 0.022 | 18.1 | 56.2 | 12.5 | 7.5 |
| Bowker | 5.4 | 1.0 | 2.7 | 0.014 | 18.1 | 76.1 | 14.8 | 7.0 |
| Lyster | 5.7 | 1.1 | 3.6 | 0.018 | 16.3 | 58.7 | 20.7 | 7.5 |
| Orford | 7.0 | 1.1 | 3.3 | 0.015 | 20.2 | 70.1 | 24.1 | 6.2 |
| Baldwin | 8.4 | 1.7 | 3.8 | 0.025 | 18.1 | 66.8 | 32.2 | 4.0 |
| Truite | 8.6 | 3.1 | 5.1 | 0.068 | 21.2 | 76.4 | 45.8 | 4.5 |
| Brompton | 10.3 | 2.3 | 5.5 | 0.092 | 20.1 | 68.7 | 19.5 | 7.3 |
| Massawippi | 10.9 | 3.1 | 4.2 | 0.033 | 16.8 | 108.1 | 44.1 | 7.2 |
| Stukely | 11.2 | 2.3 | 4.5 | 0.042 | 19.3 | 65.3 | 22.2 | 6.7 |
| Petite Brompton | 12.1 | 1.3 | 5.1 | 0.065 | 20.7 | 73.9 | 19.6 | 5.2 |
| D'Argent | 12.3 | 2.5 | 5.3 | 0.079 | 20.8 | 86.3 | 30.2 | 4.2 |
| St. Francoise | 12.8 | 1.86 | 7.2 | 0.168 | 16.2 | 82.6 | 8.4 | 8.0 |
| Aylmer | 12.9 | 2.4 | 7.3 | 0.179 | 17.1 | 94.9 | 8.5 | 8.0 |
| Coulombe | 13.9 | 3.4 | 7.5 | 0.164 | 20.1 | 112.1 | 28.6 | 4.0 |
| Lovering | 14.2 | 4.4 | 5.9 | 0.083 | 18.3 | 86.1 | 32.5 | 6.5 |
| Central | 16.2 | 3.4 | 4.3 | 0.033 | 18.0 | 125.4 | 41.1 | 8.5 |
| Brome | 19.1 | 6.9 | 4.1 | 0.031 | 19.9 | 101.2 | 109.6 | 5.0 |
| Magog | 26.4 | 6.9 | 4.5 | 0.034 | 20.8 | 167.5 | 80.4 | 7.0 |
| Yamaska | 28.9 | 10.4 | 5.2 | 0.058 | 19.8 | 202.1 | 127.2 | 5.0 |
| Waterloo | 45.7 | 37.2 | 5.4 | 0.065 | 20.2 | 279.6 | 377.3 | 4.0 |

Table 2. Parameters of regression equations for the model log (y) = b log (x) + c, where y = Dependent variable (Dep var), x = independent variable (Indep var), b = slope, and c = intercept. All variables are log-transformed. The proportion of variance explained ($r^2$) and the standard error of the estimate ($S_{xy}$) for each equation are given, together with b and c ± 95% confidence intervals for the parameter estimates. For univariate regressions, the parameters for both model I (I) and model II (II) are provided. The variables are total phosphorus (TP, µg $l^{-1}$), chlorophyll (CHL, µg $l^{-1}$), plankton respiration (RESP, mgC $m^{-3}$ $d^{-1}$), phytoplankton photosynthesis (PHOT, mgC $m^{-3}$ $d^{-1}$), P/R ratio (P/R), water color (COL, absorbance 440 nm, 10 cm cell), dissolved organic carbon (DOC, mg $l^{-1}$).

| Indep var | Dep var | $r^2$ | $S_{xy}$ | Slope | Intercept |
|---|---|---|---|---|---|
| TP | RESP | 0.823 | 0.079 | 0.673 ± 0.153 (I) | 1.240 ± 0.172 |
| | | | | 0.742 ± 0.155 (II) | 1.164 ± 0.172 |
| TP | PHOT | 0.565 | 0.275 | 1.242 ± 0.540 (I) | 0.165 ± 0.599 |
| | | | | 1.652 ± 0.536 (II) | -0.281 ± 0.599 |
| CHL | RESP | 0.824 | 0.078 | 0.411 ± 0.095 (I) | 1.787 ± 0.057 |
| | | | | 0.453 ± .94 (II) | 1.768 ± 0.057 |
| CHL | PHOT | 0.762 | 0.203 | 0.879 ± 0.244 (I) | 1.121 ± 0.145 |
| | | | | 1.007 ± 0.243 (II) | 1.065 ± 0.145 |
| TP | P/R | 0.242 | 0.254 | 0.569 ± 0.497 (I) | -1.075 ± 0.555 |
| | | | | 1.157 ± 0.499 (II) | -1.714 ± 0.555 |
| CHL | P/R | 0.442 | 0.218 | 0.469 ± 0.260 (I) | -0.666 ± 0.155 |
| | | | | 0.705 ± 0.261 (II) | -0.772 ± 0.155 |

Table 2 (continuation)

| | | | | | |
|---|---|---|---|---|---|
| PHOT | RESP | 0.628 | 0.114 | 0.356 ± 0.137 (I) | 1.432 ± 0.212 |
| | | | | 0.449 ± 0.136 (II) | 1.291 ± 0.212 |
| CHL, | P/R | 0.732 | 0.155 | 0.594 ± 0.195 (CHL) | -1.346 ± 0.351 |
| COL | | | | -0.475 ± 0.233 (COL) | |
| CHL, | P/R | 0.713 | 0.161 | 0.620 ± 0.208 (CHL) | 0.164 ± 0.449 |
| DOC | | | | -1.328 ± 0.695 (DOC) | |
| TP, COL | P/R | 0.560 | 0.199 | 0.872 ± 0.431 (TP) | -2.089 ± 0.746 |
| | | | | -0.521 ± 0.311 (COL) | |
| TP, DOC | P/R | 0.550 | 0.201 | 0.946 ± 0.458 (TP) | -0.460 ± 0.579 |
| | | | | -1.517 ± 0.935 (DOC) | |
| TP, COL | PHOT | 0.785 | 0.199 | 1.601 ± 0.431 (TP) | -1.039 ± 0.746 |
| | | | | -0.618 ± 0.311 (COL) | |
| CHL, | PHOT | 0.923 | 0.119 | 1.012 ± 0.149 (CHL) | 0.398 ± 0.269 |
| COL | | | | -0.505 ± 0.178 (COL) | |

**Plankton respiration and trophy**: Mean summer epilimnetic rates of plankton respiration were positively related to both TP and chlorophyll concentrations (Fig. 2a-b). Plankton respiration rates did not increase proportionally with either TP or CHL. In both cases, the slopes of the regression equations (Table 2) were significantly lower than 1. Rates of respiration increased more slowly with chlorophyll than with TP, and the slopes of the two relationships differed significantly (Table 2). The regression equations of respiration as a function of TP or CHL were also characterized by high intercepts (17.4 mg C $m^{-3}$ $d^{-1}$ for TP, and 61.2 mg C $m^{-3}$ $d^{-1}$ for CHL) that differed significantly from 0 (Table 2). The functional relationships between plankton respiration rates and TP and CHL showed essentially the same trends, although only the slope for CHL was significantly lower than 1 (Table 2).

**Phytoplankton photosynthesis with trophy**: Mean summer epilimnetic rates of phytoplankton photosynthesis were positively correlated with both TP and chlorophyll concentrations (Fig. 2a-b). The slopes for both TP and CHL were not significantly different from 1, and the ordinary least square slopes were not significantly different from each other (Table 2). The functional slope of the production-TP relationship was significantly greater than 1 (Table 2).

**Planktonic P/R ratios with trophy**: Along a gradient of increasing chlorophyll concentrations, phytoplankton photosynthesis increased more rapidly than plankton respiration (Fig. 2a). The two slopes differed significantly (Table 2), and the intercept of the respiration-CHL relationship was significantly higher than that of the photosynthesis-CHL relationship (Table 2). As a result, the P/R ratio (ratio of

Figure 1. Mean summer epilimnetic plankton community respiration as a function of phytoplankton photosynthesis for the epilimnion of 20 southern Québec lakes. Data are log-transformed and the line of best fit is plotted. The parameters of the regression equation appear in Table 2.

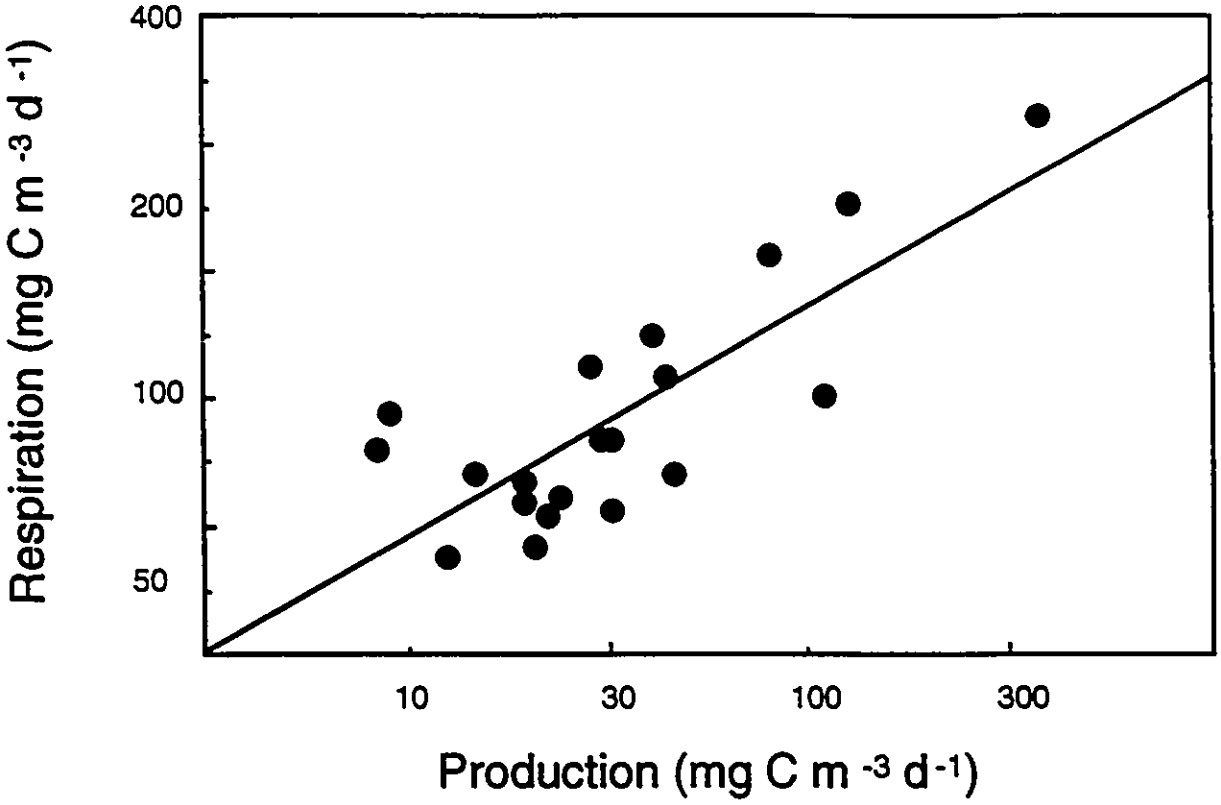
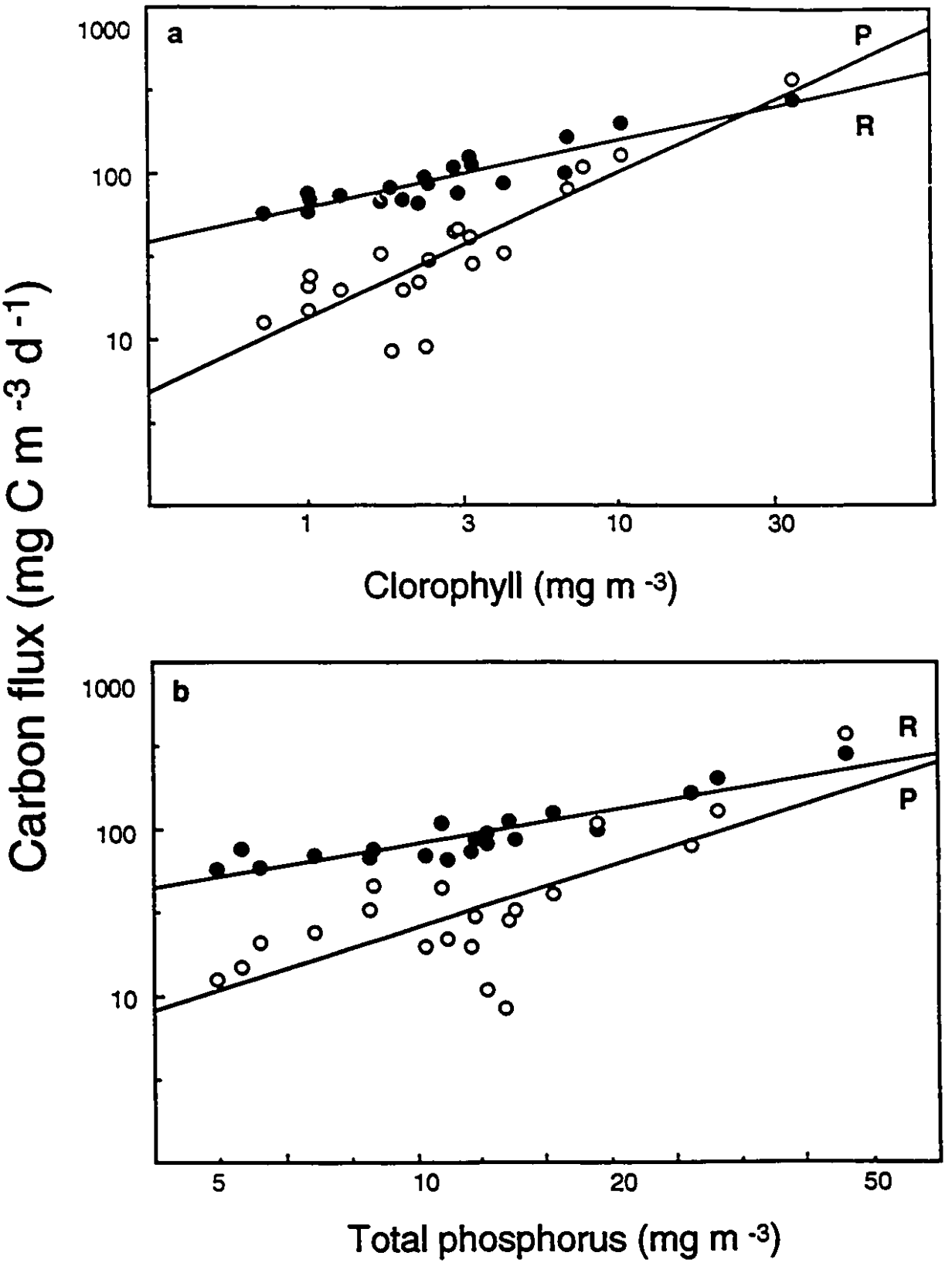

400
200
100
50
Respiration (mg C m -3 d -1)
10
30
100
300
Production (mg C m -3 d -1)

Figure 2. Mean summer epilimnetic plankton respiration (R) and phytoplankton photosynthesis (P) as functions of epilimnetic chlorophyll concentration (fig. 2a) and total phosphorus (TP) concentration (fig. 2b). Data are log-transformed and lines of best fit are plotted. The parameters of the regression equations appear in Table 2.


a
P
R
1000
100
10
1
3
10
30
Clorophyll (mg m -3)
Carbon flux (mg C m -3 d -1)
b
R
P
1000
100
10
5
10
20
50
Total phosphorus (mg m -3)

phytoplankton photosynthesis to plankton respiration) was significantly and positively correlated to CHL (Fig. 3a, Table 2). The same trend in respiration and photosynthesis occurred along the gradient of TP (Fig. 2b), so the P/R ratios tended to increase with TP concentration (Fig. 3b), although the slope of this relationship was only marginally significantly greater than 0 (Table 2).

**Effect of DOC and color on the P/R ratio:** The best multivariate predictive model for freshwater planktonic P/R ratios had CHL and COL as independent variables, and explained 73% of the variation in the ratio across lakes (Table 2). The regression coefficient for CHL in this model was positive, whereas the coefficient for COL was negative; both were significantly different from 0 (Table 2). DOC performs almost as well as COL (Table 2); this is not surprising, given the tight correlation that exists between COL and DOC in these lakes (Cuthbert and del Giorgio 1992). COL or DOC also considerably improved the relationship between the P/R ratio and TP, but overall, the multivariate regressions involving TP did not perform as well as those that included CHL (Table 2).

The strong influence of color on the P/R ratios across lakes was almost exclusively due to its effect on the rates of phytoplankton photosynthesis. Water color did not seem to influence plankton respiration in this set of lakes: rates of respiration were not significantly correlated to color, and the residuals of the respiration-CHL relationship did not show any pattern with COL (Fig. 4a). Thus, for any given level of chlorophyll there was no indication that rates of plankton respiration were elevated in the more colored lakes. Color did have a strong effect on epilimnetic rates of phytoplankton production: although photosynthesis and COL were not significantly correlated, the residuals of the photosynthesis-CHL relationship (Table 2) showed a strong negative trend with color (Fig. 4b). COL thus considerably improved the

Figure 3. The ratio of mean summer epilimnetic plankton respiration to phytoplankton photosynthesis as functions of (fig. 3a) epilimnetic chlorophyll concentration, and of (fig. 3b) total phosphorus (TP) concentration. Data are log-transformed, and the parameters of the regression equations appear in Table 2.

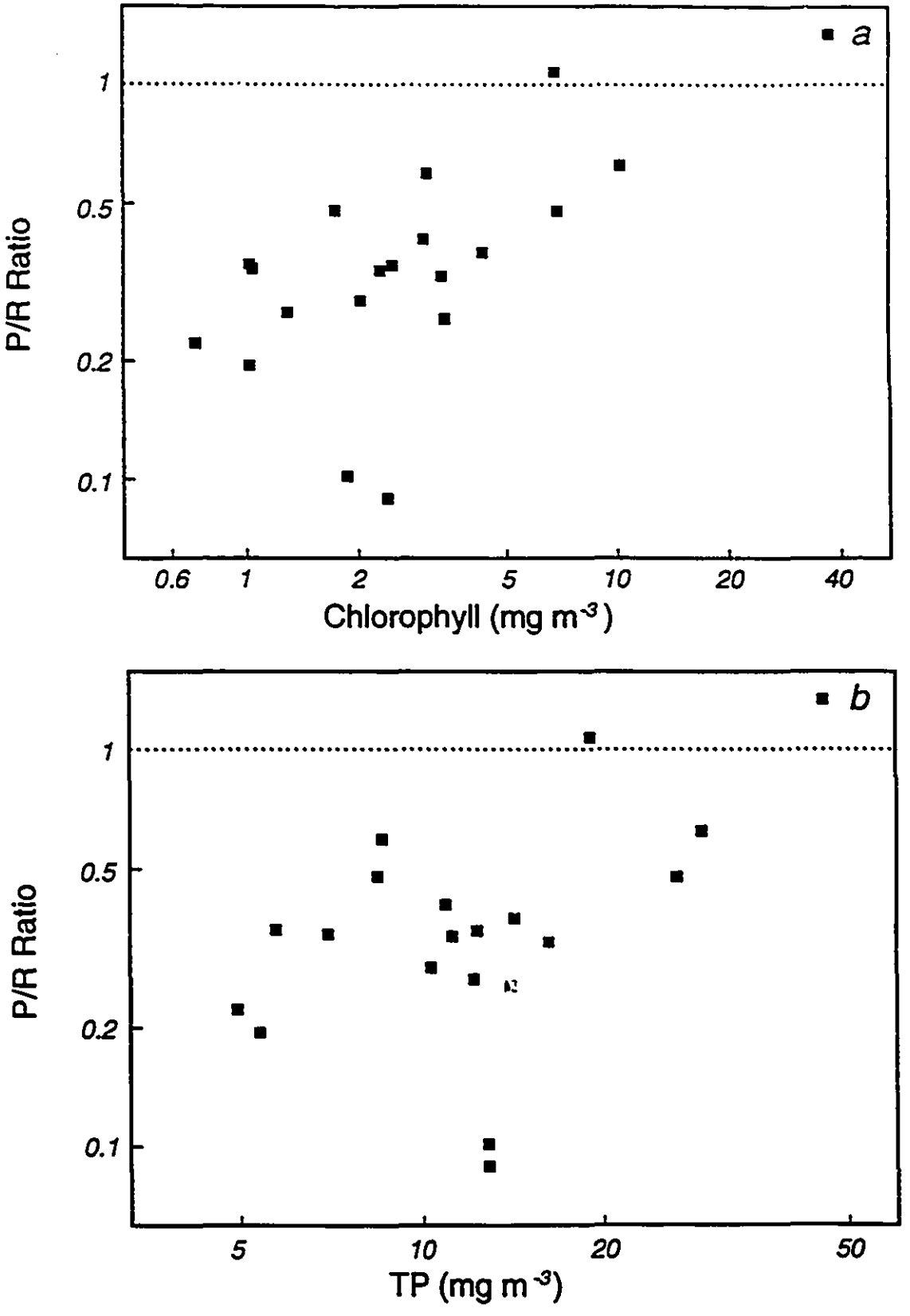
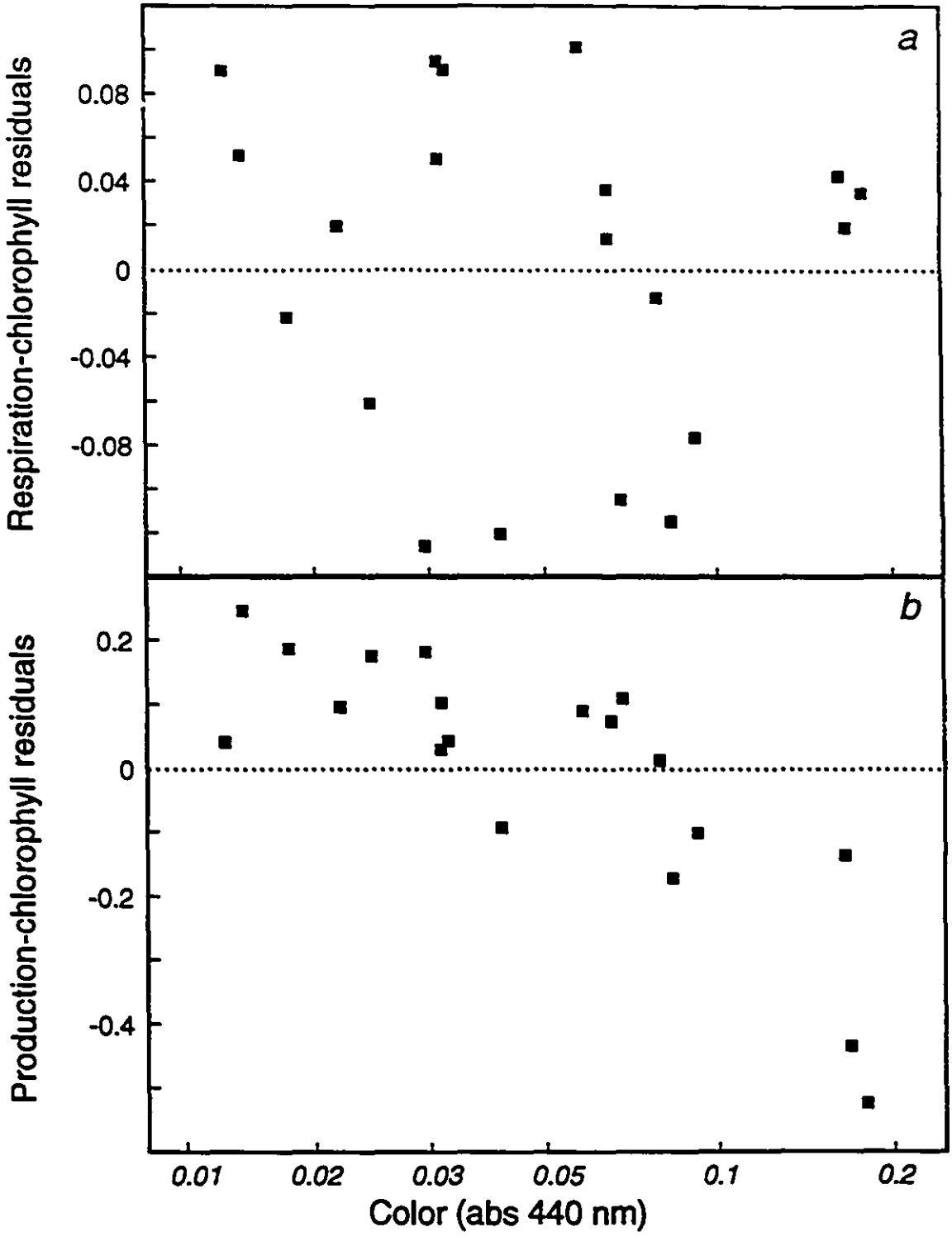

a
1
0.5
0.2
0.1
P/R Ratio
0.6
1
2
5
10
20
40
Chlorophyll (mg m-3)
b
1
0.5
0.2
0.1
P/R Ratio
5
10
20
50
TP (mg m-3)

Figure 4. The residuals of the relationship between (fig. 4a) plankton respiration and chlorophyll and (fig. 4b) phytoplankton photosynthesis and chlorophyll, as functions of log-color, measured as absorbance at 440nm in a 10 cm cell.

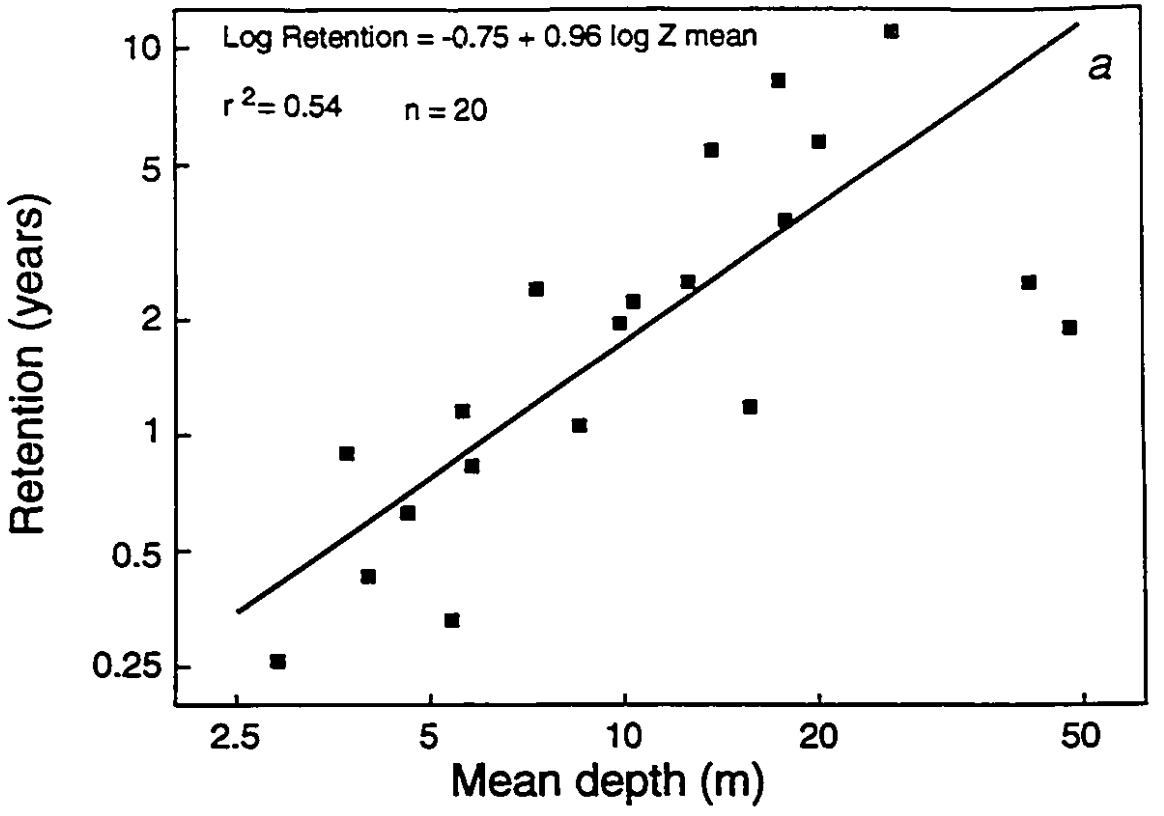

a
b
Respiration-chlorophyll residuals
Production-chlorophyll residuals
0.08
0.04
0
-0.04
-0.08
0.2
0
-0.2
-0.4
0.01
0.02
0.03
0.05
0.1
0.2
Color (abs 440 nm)

photosynthesis-CHL relationship, and in conjunction with CHL, accounted for 93% of the variation of phytoplankton photosynthesis across lakes (Table 2).

**Influence of lake morphometry on the P/R ratios**: The patterns in P/R ratios described above may ultimately be linked to morphometric characteristics of the lakes and their drainage basins. In this set of lakes, water retention time integrated the effects of several morphometric variables (Table 3): after logarithmic transformation it was directly related to the logarithm of mean depth (Fig. 5a), and inversely related to the logarithm of $A_d/A_l$ (the ratio of drainage area to lake area, Fig. 5b). It was also inversely related to the percent littoral area of the lake and to the ratio of lake area to lake volume, so water retention is a convenient variable to summarize the influence of morphometry on planktonic P/R ratios.

Significant negative relationships were found between water retention time and both chlorophyll and water color (Figs. 6a-b). Not surprisingly, photosynthesis and plankton respiration rates were also negatively related to retention time (Figs. 6c-d). Shallow lakes, which had short retention times and high $A_d/A_l$ ratios, tended to have higher concentrations of chlorophyll and DOC, and higher rates of both photosynthesis and respiration, in contrast with lakes with longer water residence times, which were typically deeper, and had lower $A_d/A_l$ ratios and percent littoral area. It is not clear from these relationships, however, whether lake morphometry influenced CHL, COL, PHOT and RESP in the same way. The four slopes were negative, but they were not significantly different from each other. The influence of lake morphometry on planktonic P/R ratios may have been direct, on photosynthesis and respiration, or indirect, through its effect on chlorophyll and color.

Figure 5. Water retention time as a function of mean depth (fig. 5a), and the ratio of drainage basin area:lake area (fig. 5b). Data are log-transformed and lines of best fit are plotted.


Log Retention = -0.75 + 0.96 log Z mean
r 2= 0.54
n = 20
a
Retention (years)
10
5
2
1
0.5
0.25
2.5
5
10
20
50
Mean depth (m)

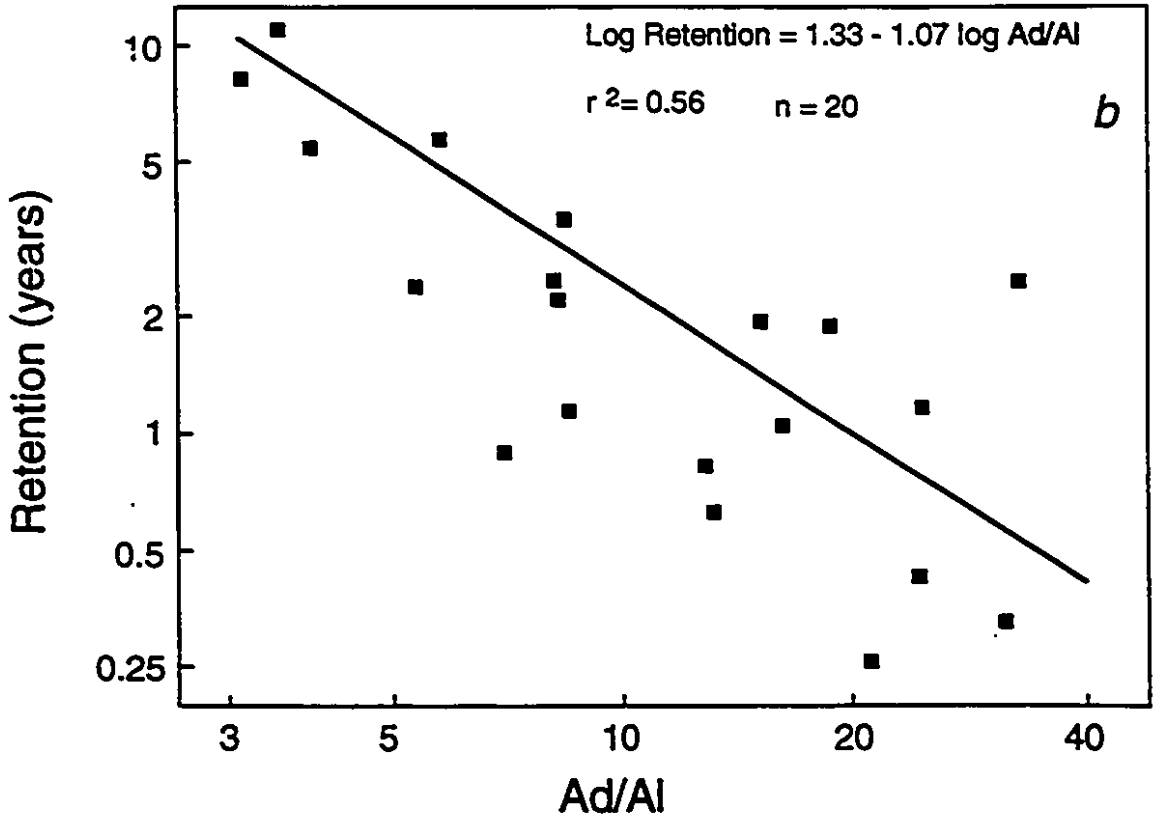

Log Retention = 1.33 - 1.07 log Ad/Al
r 2= 0.56
n = 20
b
Retention (years)
10
5
2
1
0.5
0.25
3
5
10
20
40
Ad/Al

Figure 6. The relationship between water retention time and epilimnetic chlorophyll concentration (fig. 6a), water color (fig. 6b), mean summer epilimnetic plankton respiration (fig. 6c), and mean summer epilimnetic phytoplankton photosynthesis (fig. 6d). Data are log-transformed.

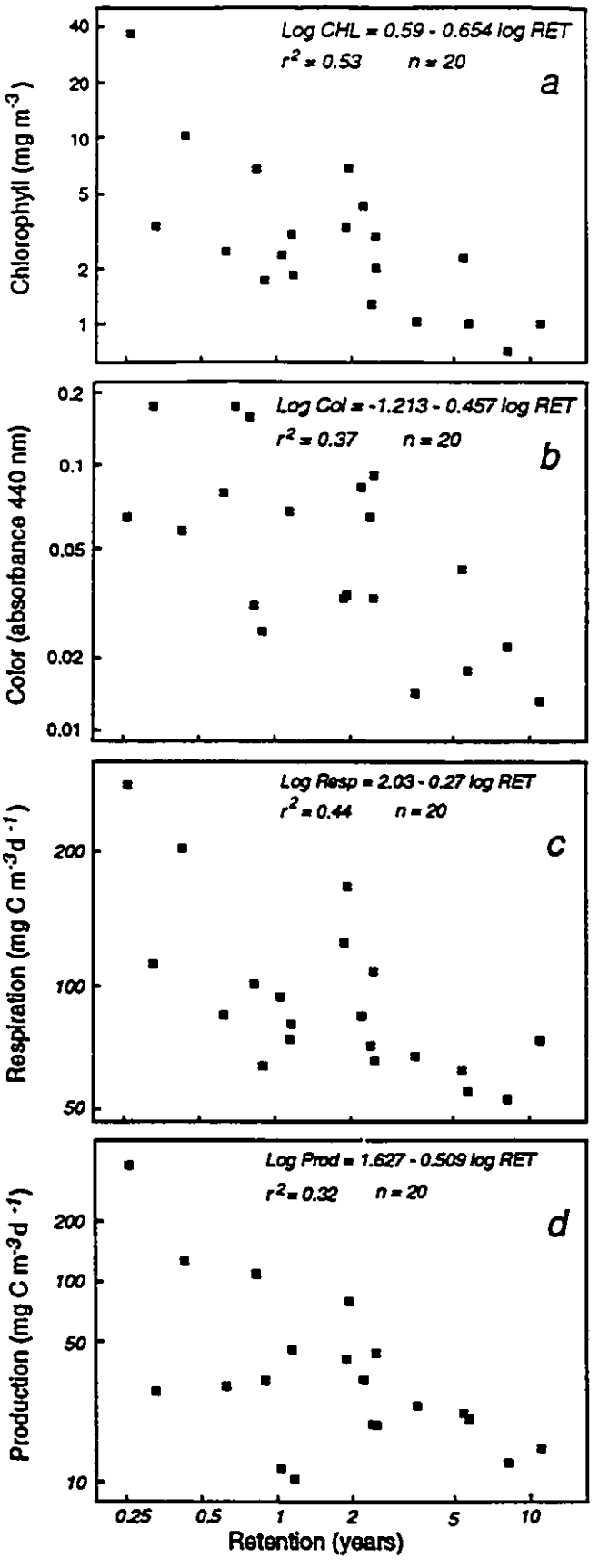
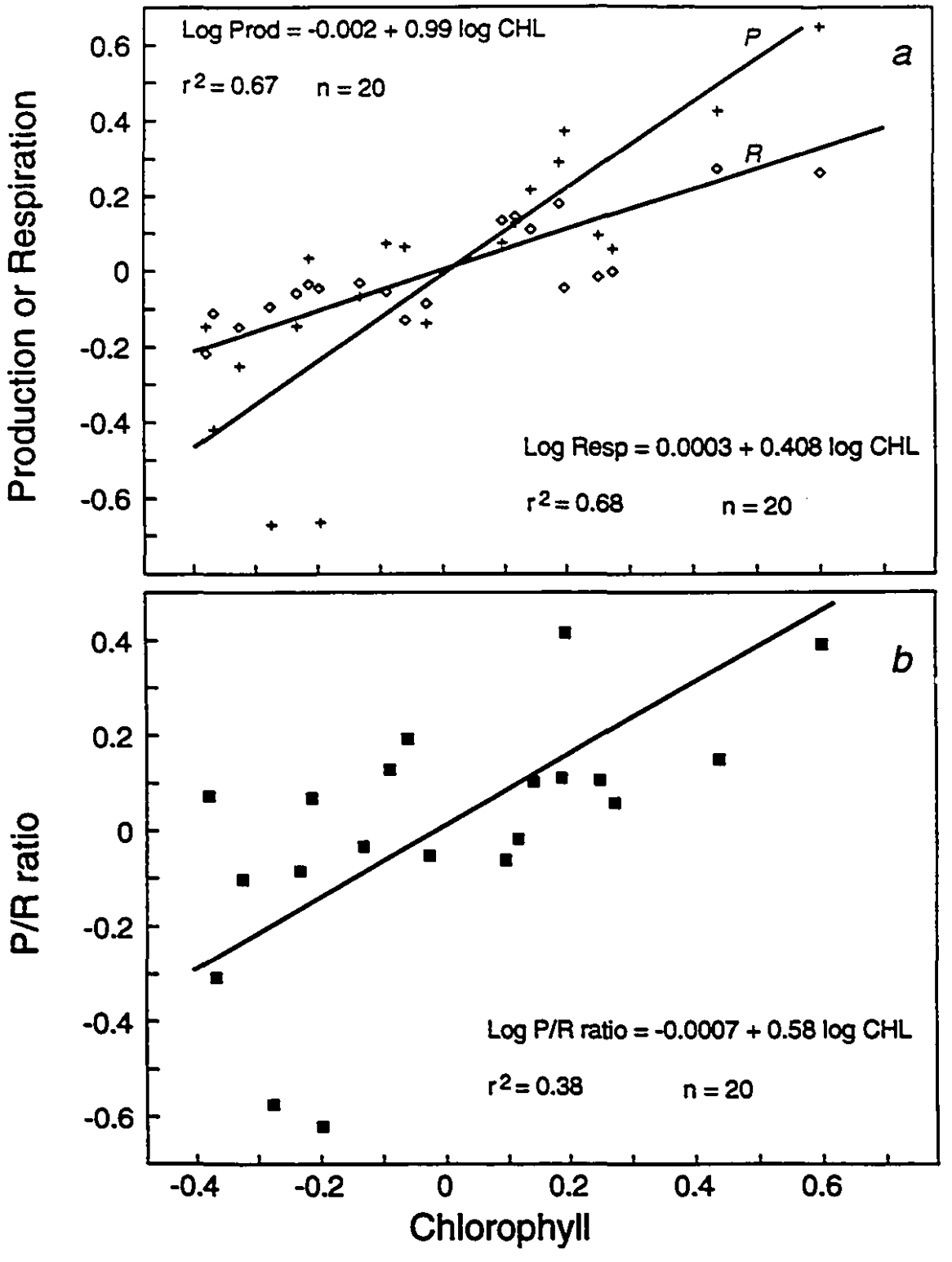

Log CHL = 0.59 - 0.654 log RET
r² = 0.53 n = 20
a
Chlorophyll (mg m⁻³)
40
20
10
5
2
1
Log Col = -1.213 - 0.457 log RET
r² = 0.37 n = 20
b
Color (absorbance 440 nm)
0.2
0.1
0.05
0.02
0.01
Log Resp = 2.03 - 0.27 log RET
r² = 0.44 n = 20
c
Respiration (mg C m⁻³d⁻¹)
200
100
50
Log Prod = 1.627 - 0.509 log RET
r² = 0.32 n = 20
d
Production (mg C m⁻³d⁻¹)
200
100
50
10
0.25
0.5
1
2
5
10
Retention (years)

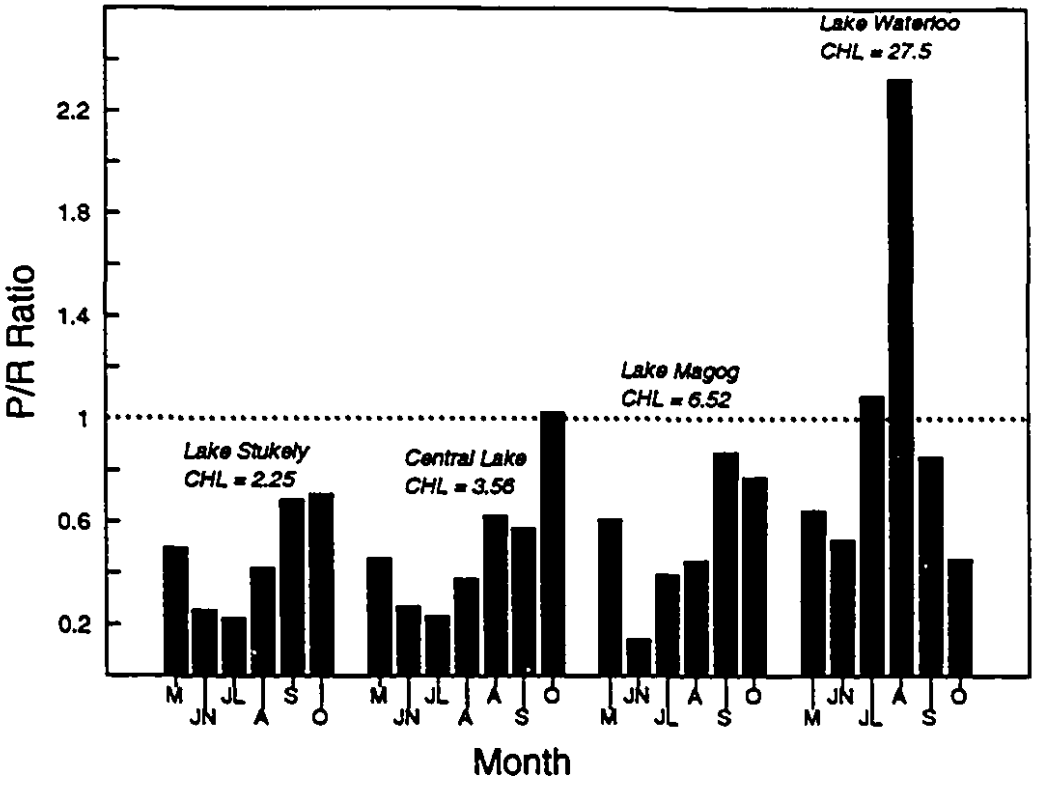
Figure 7. The relationship between the residuals of the chlorophyll-retention regression and the residuals of the respiration-retention (R) and photosynthesis-retention (P) regressions (fig. 7a), and the residuals of the P/R ratio-retention regression (fig. 7b).


Log Prod = -0.002 + 0.99 log CHL
r2 = 0.67 n = 20
P
R
a
Log Resp = 0.0003 + 0.408 log CHL
r2 = 0.68 n = 20
Production or Respiration
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
b
Log P/R ratio = -0.0007 + 0.58 log CHL
r2 = 0.38 n = 20
P/R ratio
0.4
0.2
0
-0.2
-0.4
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
Chlorophyll

The influence of morphometry on planktonic P/R ratios was explored by correcting for water retention time (RET) all four variables mentioned above, and reanalysing the patterns in P/R ratios with trophy and DOC. To do this, we calculated the residuals of the regressions between water retention time and CHL, COL, PHOT, and RESP; by allowing for RET, any relationship between these four variables and mean depth, $A_d/A_l$ ratio, percent littoral, and the lake area/lake volume ratio was effectively removed. These residual rates of phytoplankton photosynthesis and plankton respiration were significantly correlated with the residual chlorophyll concentrations (Fig. 7a), and the patterns were essentially the same as for the uncorrected variables: photosynthesis increased faster with chlorophyll concentration than respiration. The two slopes (0.99 and 0.41, for production and respiration, respectively) were significantly different from each other, and very similar to those found for the uncorrected data (0.88 and 0.41, for photosynthesis and respiration, respectively). As a result, after removing the effect of water retention time, planktonic P/R ratios still increased with chlorophyll concentrations (Fig. 7b), so patterns in P/R ratios cannot be explained solely by differences in lake and drainage basin morphometry.

**Seasonal variation of P/R ratios:** The variation of P/R ratios from early May to late October is shown in Figure 8, for the 4 lakes that were sampled from May to October. P/R ratios were relatively high in May, after the spring chlorophyll peak, lowest during June and July, as the lakes warmed, and gradually increased again toward the fall, when temperature declined and a second chlorophyll peak appeared, generally due to cyanobacteria. In oligotrophic lakes, however, P/R ratios were never above unity, whereas in the most eutrophic lake (Lake Waterloo), P/R ratios exceeded one, twice during phytoplankton blooms in July and August.

Figure 8. Seasonal variation of P/R ratios in four selected southern Quebec lakes, were measurements for May (M), June (JN), July (JL), August (A), September (S) and October (O) were carried out. The mean chlorophyll concentration (CHL) for the entire period is shown.


Lake Waterloo
CHL = 27.5
Lake Magog
CHL = 6.52
Lake Stukely
CHL = 2.25
Central Lake
CHL = 3.56
P/R Ratio
2.2
1.8
1.4
1
0.6
0.2
M
JN
JL
A
S
O
Month

## DISCUSSION

**Patterns in planktonic P/R ratios across lakes:** The hypothesis that planktonic P/R ratios are a function of both lake trophic status, and water color (or DOC) is fully supported by our results. P/R ratios increased with CHL and decreased with COL, but were always below unity in oligotrophic lakes, regardless of the DOC concentration or color of the water, and only exceeded one in the most eutrophic lakes that we studied. In lakes with summer chlorophyll concentrations below 6 mg $m^{-3}$, mean summer plankton respiration exceeded mean summer phytoplankton production by two- to tenfold, depending on the concentration of DOC in the water. Eutrophic lakes had P/R ratios that approached or exceeded unity, but if we assume sedimentation losses of 20 to 30% of the measured primary production (Baines and Pace in press), planktonic respiration would exceed the remaining phytoplankton production, even in the most eutrophic lakes. In any case, the plankton of eutrophic lakes does tend to approach autotrophy, as hypothesized by Jones (1992), whereas the plankton of clear-water oligotrophic lakes appears to be much more allotrophic than that author suggested.

There have been previous reports of high relative plankton respiration rates (Sarvala et al. 1981, Salonen et al. 1983, Rask et al. 1986, Ahrens and Peters 1991, Hessen 1992) and of low P/R ratios (Devol 1979, Bower and McCorkle 1980, del Giorgio and Peters 1993) in oligotrophic lakes, and reports of planktonic P/R ratios approaching or exceeding unity in eutrophic to hypertrophic systems (Gasith 1974, Radheyshyam and Naik 1992, del Giorgio and Peters 1993). Not all published reports support these findings: Cole et al. (1989), for example, found that inputs of organic carbon exceeded outputs, and that bacterial respiration was only a small fraction of phytoplankton production in the pelagial of oligotrophic clear-water Mirror Lake. Reports from other oligotrophic clear-water systems, however, indicate that bacterial

carbon demand often exceeds phytoplankton photosynthesis (Scavia and Laird 1989, Thomas et al. 1991).

Several methodological problems may influence the observed patterns in planktonic P/R ratios across lakes. Rates of phytoplankton photosynthesis were calculated for the epilimnion of lakes; in many of the lakes we sampled, including eutrophic and moderately to highly colored lakes, the euphotic zone was shallower than the epilimnion, so the production estimates for the two layers coincide. In several clear-water oligotrophic lakes, however, the euphotic zone extended beyond the epilimnion, and in these cases, total primary production was underestimated and mean volumetric rates for the entire mixed layer were then overestimated. Examples of such lakes are Bowker, Nicolet and Lyster. For these lakes, we recalculated production integrated over the entire euphotic depth, and found that it never exceeded our estimates for the mixed layer by over 10-15%, which is not enough to modify the patterns found.

The problem would be compounded, however, by the development of metalimnetic or hypolimnetic chlorophyll peaks. These clear-water, low-nutrient lakes could develop deep chlorophyll maxima (Pick et al. 1984, Gasol and Pedros-Alió 1991), that may equal or exceed the production in the overlying layers (Fee 1978). Occasional depth profiles of chlorophyll in these lakes never revealed such peaks, but their occurrence cannot be ruled out, and they could represent an important source of autochthonous organic carbon not included in our analysis. The patterns in P/R ratios remain unchanged, however, if we exclude from the analysis those lakes where deep chlorophyll peaks could potentially develop. Chemical oxygen demand could also potentially influence the respiration estimates, but tests using samples killed with 5%

formalin and incubated for over 20 h showed that chemical oxygen consumption was always negligible, never exceeding 4% of the oxygen consumed in the live samples.

The greatest methodological concern, however, may be the validity of the actual values of the P/R ratio. These ratios were constructed using data from short-term (3 h) $^{14}C$ incubations for photosynthesis, and long (> 20 h) incubations for oxygen uptake. It is still unclear whether short $^{14}C$ uptake experiments measure gross or net photosynthesis (Harris 1984), and long incubations for respiration may result in the underestimation of *in situ* rates of oxygen consumption by the plankton (Williams 1984). The use of a constant factor of 0.8 to convert oxygen to carbon units further complicates the problem, because the RQ has been shown to vary across natural communities (Rich 1984). In spite of these shortcomings, our field measurements are still in excellent agreement with other large-scale comparative analyses that have been published for both phytoplankton photosynthesis (Smith 1979, Beaver and Crisman 1991) and plankton respiration (del Giorgio and Peters 1993). These studies encompass a wide variety of lakes worldwide, and a variety of analytical and sampling techniques. The overall agreement among these empirical studies suggests that the measurements of photosynthesis and respiration are relatively robust, and so are the patterns in planktonic P/R ratios that are derived from these measurements. The absolute magnitude of the ratio should still be interpreted with caution, however, until these estimates can be independently corroborated, for example, by measurements of oxygen and $CO_2$ changes in the water column of lakes.

Organic color did not seem to influence rates of plankton respiration, but mean epilimnetic rates of phytoplankton photosynthesis were depressed in the more colored lakes, such as Coulombe, Aylmer and St. Francoise. The effect was twofold: the euphotic layer was extremely compressed in these lakes, and comprised only a

fraction of the mixing depth, so mean epilimnetic rates were consequently low. In addition, we found that in lakes with over 6 mg DOC $l^{-1}$, $P^B_m$ was low in relation to clear lakes with similar chlorophyll concentrations, and therefore photosynthetic rates integrated over the euphotic zone were also depressed. Both effects have been observed in colored lakes before (Jackson and Hecky 1980, Beaver and Crisman 1991). Overall, our estimates of phytoplankton photosynthesis are in good agreement with other reports on lakes of similar nutrient and chlorophyll concentrations. Published reports, however, indicate that volumetric rates of photosynthesis in lakes are generally related to chlorophyll concentrations with slopes significantly above one (Smith 1979, Beaver and Crisman 1991, del Giorgio and Peters 1993), whereas our slope of 0.88 (Table 2) is not significantly different from unity. This discrepancy probably reflects a difference in integration depth: previous studies have focused on the entire euphotic zone, whereas in the present study we have focused on the mixed layer. Because the euphotic zone becomes increasingly shallow in eutrophic lakes, rates integrated over the epilimnion tend to be much lower than those integrated over the euphotic zone in these lakes, and thus the slope of the relationship between volumetric rates and chlorophyll becomes less steep.

Rates of respiration and photosynthesis were inversely related to mean depth and water retention time (Fig. 6c-d), and positively related to the $A_D/A_l$ ratio. Morphometry has been previously shown to influence different aspects of lake metabolism: whole lake winter respiration rates are also inversely related to mean depth (Welch et al. 1976, Barica and Mathias 1979), and positively related to the ratio of sediment area:water volume (Mathias and Barica 1980, Welch and Bergmann 1985). Similarly, Fee (1979) reported a strong positive relationship between the sediment area:volume ratio and summer epilimnetic primary production. These inverse relationships between respiration or photosynthesis and mean depth reflect

the increased contribution in shallow lakes of highly productive zones, such as the sediment-water and littoral interfaces, with high rates of remineralization, nutrient resuspension and organic carbon supply (Mathias and Barica 1980). In the present data set, however, photosynthesis, respiration and planktonic P/R ratios were better predicted by chlorophyll, color, or both, than by any combination of morphometric variables, and the patterns of P/R ratios with chlorophyll and color remained after the effect of morphometry had been removed (Fig. 7a-b).

These results suggest that planktonic P/R ratios are primarily determined by factors that directly control phytoplankton production in lakes, such as nutrient concentrations and water color, which are in turn strongly influenced by lake morphometry and the characteristics of the drainage basin. Consequently, alterations in the characteristics of the drainage basin are likely to have a strong impact on plankton metabolism. For example, Rask et al. (1993) found that the plankton of an oligotrophic humic lake shifted from net heterotrophy (P/R ratios < 1) to net autotrophy (P/R ratios > 1) after clear-cutting in the drainage basin resulted in increased nutrient loads into the lake, with the consequent increase in phytoplankton photosynthesis. Overall, it is the potential for phytoplankton photosynthesis, rather than the inputs of external carbon, that determines the balance between autotrophy and heterotrophy in freshwater plankton. Exceptions may be found in the polyhumic lakes (DOC > 20-25 mgC $l^{-1}$), where the magnitude of allochthonous organic inputs may swamp autochthonous production (Odum and Prentki 1978).

**Sources of organic carbon:** In spite of the uncertainties in the measurements of photosynthesis and respiration which were discussed above, the calculated P/R ratios still provide a useful reference as to the magnitude of external organic carbon utilization by plankton communities across lakes. There are three likely sources of

organic carbon that may fuel the excess plankton respiration measured in most lakes during the summer: phytoplankton-derived carbon, fixed during early spring and not utilized until the summer; inputs of detrital carbon from the littoral of lakes, and inputs of organic carbon, mostly DOC, from the drainage basin. Work is under way to determine the relative importance of these three distinct carbon sources to the pelagial community in these lakes, using C and N stable isotopes. At present we can only comment on the contribution of phytoplankton and terrestrial vegetation to plankton community metabolism.

**Autochthonous sources: phytoplankton photosynthesis**: The seasonal pattern in P/R ratios (Fig. 8) suggests that the imbalance between phytoplankton photosynthesis and plankton respiration is greatest in mid-summer, and that the discrepancy is generally smaller during early spring and fall. Temperature is likely to play a major role in this seasonal pattern, because photosynthesis is less inhibited by low temperatures than respiration rates (Verduin 1956). There is considerable evidence to support this view. Whole lake winter respiration rates in Ontario lakes (Welch et al. 1976) were more than one order of magnitude lower than our summer epilimnetic rates, at comparable chlorophyll concentrations; likewise, rates of plankton respiration in late fall, winter, and early spring in Lake Wingra were only a fraction of the rates measured during the remainder of the growing season (Gasith 1974).

During early spring and late fall, however, temperate lakes typically have peaks of phytoplankton biomass and production (Reynolds 1984); many lakes also develop chlorophyll peaks under the ice (Welch 1974, Thomas et al. 1991). Several authors have reported lags between these peaks of phytoplankton production and increases in bacterial or zooplankton biomass and metabolism (Devol 1979, Scavia and Laird 1987); it is conceivable that at least a fraction of the summer excess respiration may be

Table 3. Lake and drainage basin morphometry, and components of the carbon loading model. Morphometric variables are $Z_m$ (mean depth, m), $A_d$ (area of the drainage basin, $km^2$), $A_l$ (lake area, $km^2$), Ret (water retention time in years); the terms of the DOC loading model (see materials and methods) are: E (excess plankton respiration per unit lake area, gC $m^{-2}$ $summer^{-1}$), Q (total annual input of water, x $10^9$ $m^3$), J (annual allochthonous DOC input per unit lake area, gC $m^{-2}$ $y^{-1}$), and S (annual internal loss of allochthonous DOC per unit lake area, gC $m^{-2}$ $y^{-1}$). Lakes Brome and Waterloo had mean P/R ratios > 1 and were excluded from the carbon loading calculations.

| Lake | $Z_m$ | $A_d$ | $A_l$ | Ret | E | Q | J | S |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 17.3 | 12.7 | 3.9 | 8.2 | 49.2 | 9 | 39.1 | 30.7 |
| Bowker | 25.9 | 8.1 | 2.3 | 11.1 | 64.4 | 5 | 42.3 | 36.1 |
| Lyster | 20.0 | 9.9 | 1.7 | 5.7 | 42.7 | 6 | 70.0 | 57.0 |
| Orford | 17.7 | 10.6 | 1.3 | 3.6 | 42.8 | 6 | 97.8 | 84.6 |
| Baldwin | 3.8 | 2.1 | 0.3 | 0.9 | 20.7 | 1 | 84.0 | 66.7 |
| Truite | 5.6 | 3.3 | 0.4 | 1.1 | 18.4 | 2 | 99.3 | 75.0 |
| Brompton | 12.5 | 97.1 | 11.9 | 2.5 | 53.8 | 56 | 98.4 | 72.3 |
| Massawippi | 41.6 | 584.2 | 17.9 | 2.5 | 69.1 | 300 | 391.2 | 318.4 |
| Stukely | 13.6 | 14.9 | 3.8 | 5.5 | 43.2 | 10 | 47.3 | 36.8 |
| Petite Brompton | 7.3 | 3.6 | 0.7 | 2.4 | 42.4 | 2 | 62.7 | 47.1 |
| D'Argent | 4.6 | 13.2 | 1.0 | 0.6 | 35.2 | 7 | 158.4 | 120.0 |
| St. Francoise | 15.6 | 1157 | 47.1 | 1.2 | 89.5 | 610 | 295.6 | 201.7 |
| Aylmer | 8.5 | 477.8 | 29.5 | 1.1 | 103.8 | 260 | 194.5 | 132.2 |
| Coulombe | 5.4 | 24.4 | 0.8 | 0.3 | 49.8 | 13 | 366.5 | 250.0 |
| Lovering | 9.7 | 38.1 | 4.6 | 2.2 | 52.6 | 22 | 99.7 | 71.7 |
| Central | 48.0 | 1607 | 21.6 | 1.3 | 107.1 | 810 | 893.9 | 740.7 |
| Brome | 5.8 | 185.7 | 14.5 | 0.8 | - | 1100 | 154.6 | 124.1 |
| Magog | 9.8 | 164.2 | 15.2 | 1.2 | 91.3 | 87 | 129.0 | 105.3 |
| Yamaska | 5.5 | 51.4 | 2.1 | 0.2 | 56.2 | 28 | 294.3 | 223.8 |
| Waterloo | 2.9 | 31.6 | 1.5 | 0.3 | - | 17 | 253.1 | 193.3 |

fueled by carbon fixed by phytoplankton early in the spring, when heterotrophic metabolism and biomass are still low. These early peaks in phytoplankton photosynthesis may have been missed in the present study and thus spring phytoplankton production may have been underestimated. Welch et al. (1976) used a similar argument to explain winter respiration under the ice in Ontario lakes, invoking storage of phytoplankton carbon fixed during the growing season. The lakes that we studied stratify around mid-May, so detrital phytoplankton carbon would have to persist for several months in the epilimnion in order to be utilized during mid-summer; the process that would allow such long-term storage remains unclear.

**Allochthonous sources: terrestrial vegetation:** Although the littoral contributes organic carbon to the pelagial of lakes, terrestrial inputs of organic carbon, mostly as DOC, dominate the detrital carbon pool in most lakes (Wetzel 1992). It is therefore important to determine whether the rates of carbon utilization and plankton metabolism, in excess of phytoplankton photosynthesis, are compatible with the rates of input and internal loss of terrestrial organic carbon. To do this comparison, the annual allochthonous organic carbon loading was calculated for each lake, using a mass-balance approach (Engstrom 1987), and the results are shown in Table 3. Annual areal DOC inputs (J, in gC $m^{-2}$ $y^{-1}$) and internal carbon loss (S, in gC $m^{-2}$ $y^{-1}$) were then compared with integrated summer (May to September) excess respiration (E, in gC $m^{-2}$ $summer^{-1}$). The two lakes (Waterloo and Brome) that had mean P/R ratios > 1 were excluded from this analysis since they had no imbalance . Details of calculations of J, S, and E, appear in the Materials and Methods section.

The fraction of the total annual allochthonous DOC input (J) that could potentially be respired during the summer in the epilimnion varies between 10% to slightly over 100%; it is negatively related to $A_d/A_l$ (the ratio of drainage basin

area:lake area, Fig. 9a), and positively related to water retention time (Fig. 9b). In lakes with high $A_d/A_l$ ratios and short water retention time, only a small fraction of the total allochthonous DOC inputs would tend to be respired by the epilimnetic plankton. Studies have shown that between 5 to 40 % of the total DOC pool is biologically labile and can be utilized by bacteria within days or weeks (Laird and Scavia 1990, Tranvik 1992). The bulk of the DOC is composed of more refractory compounds with much longer turnover times. Rasmussen et al. (1989) showed that lakes with water retention times greater than one year tend to be clear, whereas lakes with low water residence times usually have high water color, presumably because humic DOC flushes through the system without sedimenting or being broken down either chemically or biologically.

Consequently, the fraction of the total DOC inputs (J) that is lost internally through sedimentation or degradation (S, Table 3) tends to increase with water retention time (S ranges from 50% to over 80 % of J). Total summer excess respiration (E) tends to increase proportionally to this internal loss term (Fig. 10), and on average, E represents 54% (range = 15 to 140%) of the calculated internal loss of allochthonous DOC (S). These calculations suggest that organic carbon loss through epilimnetic respiration in excess of phytoplankton production is comparable to the estimated DOC loss within the lakes, and that summer plankton metabolism could be supported by external DOC inputs in most lakes, including lakes with relatively low water color and DOC concentrations. There are three lakes, however, in which excess plankton respiration appears to exceed the internal carbon loss (Lakes Bowker, Nicolet and Lyster). These lakes are deep and have steep slopes, and therefore do not have extensive macrophyte development, so inputs of carbon from the littoral are relatively small. The estimates of carbon loading and internal loss greatly depend on the choice of organic carbon export coefficients (see Materials and Methods section),

Figure 9. Summer excess respiration, E (gC $m^{-2}$ $summer^{-1}$), expressed as percent of the annual DOC input, J (gC $m^{-2}$ $y^{-1}$) as a function of the $A_d/A_l$ ratio (fig. 9a), and water retention time (fig. 9b). Data are log-transformed.

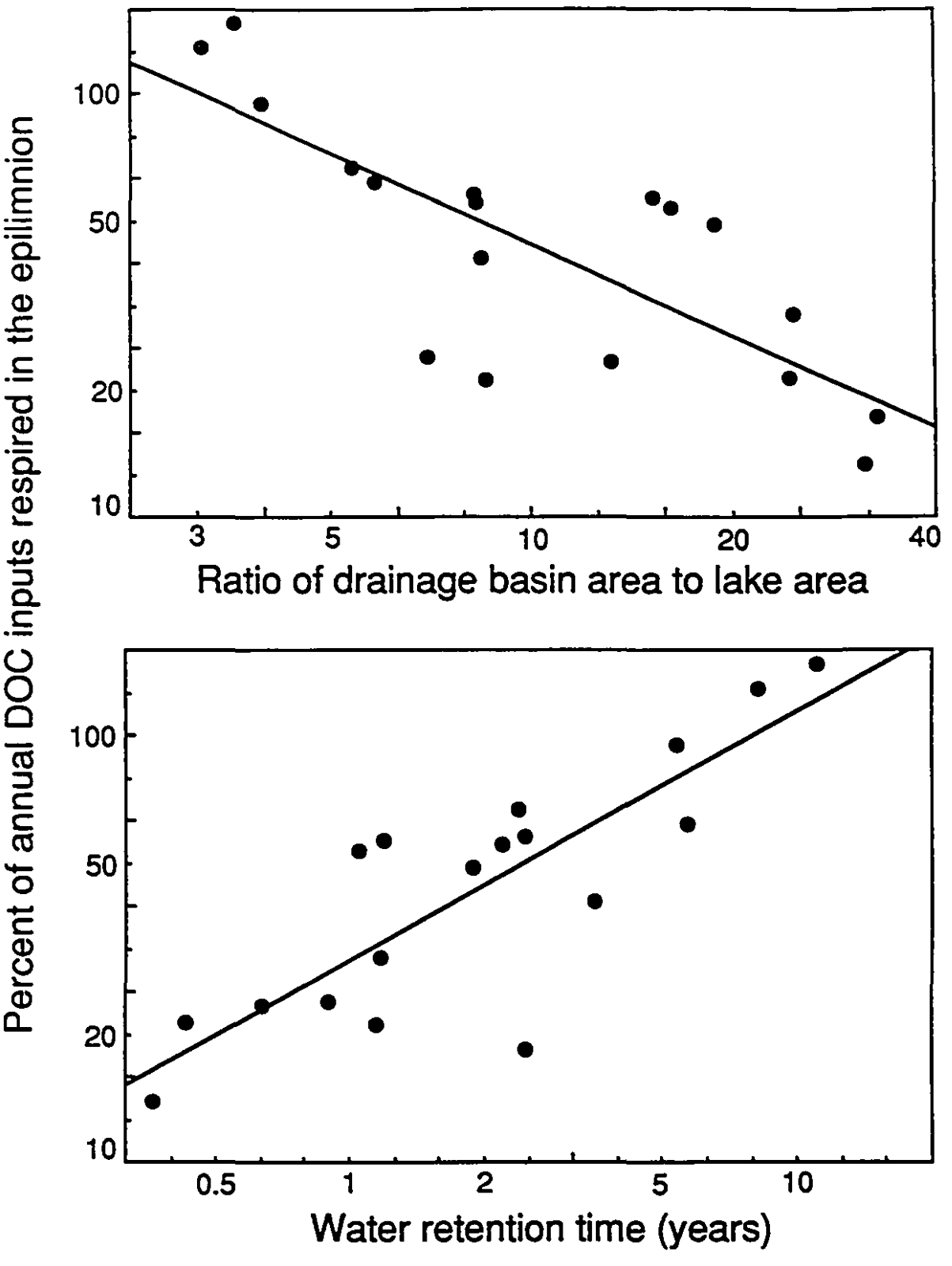
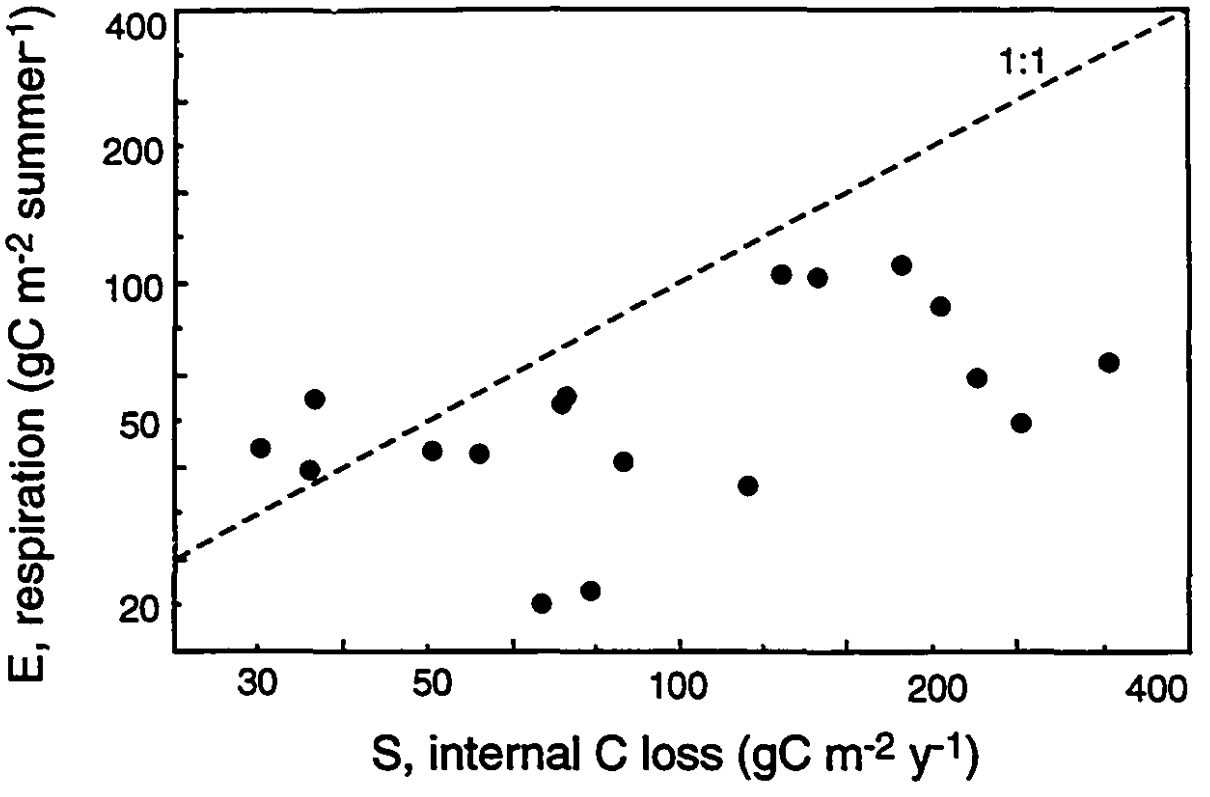

Percent of annual DOC inputs respired in the epilimnion
100
50
20
10
3
5
10
20
40
Ratio of drainage basin area to lake area
100
50
20
10
0.5
1
2
5
10
Water retention time (years)

Figure 10. Summer excess plankton respiration, E (gC $m^{-2}$ $summer^{-1}$), as a function of the annual internal loss of DOC, S (gC $m^{-2}$ $y^{-1}$), estimated from the DOC loading model (Table 3). The line of equal increase (1:1) is shown, and the data are log-transformed. E is the difference between plankton respiration and phytoplankton photosynthesis, integrated over the depth of the epilimnion and over the summer (from the beginning of May to the end of September, 150 days).


E, respiration (gC m-2 summer-1)
400
200
100
50
20
1:1
30
50
100
200
400
S, internal C loss (gC m-2 y-1)

which may vary considerably across drainage basins within the same region. It is possible that allochthonous carbon inputs were underestimated in some lakes, which, like Nicolet and Lyster, have a considerable portion of their drainage basins occupied by wetlands. Other sources of allochthonous DOC, such as rainfall and direct litterfall have not been considered in the carbon loading model, and this may result in an underestimation of 10 to 20% of the total organic carbon load (Likens and Bormann 1979).

Lakes with high $A_d/A_l$ ratios tend to have greater DOC inputs, but the residence time of this organic carbon in the lake is usually very low. Conversely, lakes with low $A_d/A_l$ ratios receive smaller inputs of DOC, but this carbon remains in the system longer, increasing the possibility of being degraded, chemically or biologically, within the water column. This pattern may explain the lack of statistical effect of DOC concentration on rates of plankton respiration. Within the range of DOC concentrations found in southern Quebec, clear water and colored lakes, which differ by threefold in their DOC concentrations, may not differ substantially in the amount of DOC that can be effectively utilized by the biota. The highly significant intercept of the respiration to production relationship (Fig. 1), of 27 mg C $m^{-3}$ $d^{-1}$, may indicate a baseline planktonic metabolism, independent of phytoplankton production, that we can expect to find in most lakes, supported by external inputs of carbon.

**Implications for $CO_2$ flux:** Net fluxes of $CO_2$ from lakes to the atmosphere have been reported for arctic and temperate lakes during the growing season (Coyne and Kelley 1974, Hesslein et al. 1980, Bower and McCorkle 1980, Kling et al. 1991, 1992), whereas net $CO_2$ invasion into lakes has only been documented for highly productive (Kling et al. 1992), or extremely soft-water lakes (Herczeg 1987). Overall, when $CO_2$ fluxes have been measured most oligotrophic and mesotrophic lakes appear to be

highly heterotrophic and evolve $CO_2$ during the ice-free period. This pattern in $CO_2$ fluxes in lakes agrees well with the trends in planktonic P/R ratios described in this paper, because the production of respiratory $CO_2$ exceeds the fixation of $CO_2$ through algal photosynthesis in the epilimnion of most lakes . Alternative explanations have been invoked, such as photochemical oxidations (Salonen and Tulonen 1990), and DIC inputs from groundwaters (Kling et al. 1992), but there is consensus that terrestrial DOC is likely to play a central role in patterns of $CO_2$ flux in lakes (Kling et al. 1991). The amount of $CO_2$ originating from plankton respiration in the southern Québec lakes can be estimated from the difference between the mean epilimnetic rates of plankton respiration and the rates of phytoplankton photosynthesis measured during the summer (Table 1); the estimated respiratory $CO_2$ production in the epilimnion ranges from 11 to 60 mmol $CO_2$ $m^{-2}$ $d^{-1}$, depending on lake trophy and DOC concentration. These estimates are within the range of $CO_2$ fluxes from lakes to the atmosphere that have been measured in arctic lakes, 5 to 45 mmol $CO_2$ $m^{-2}$ $d^{-1}$ (Coyne and Kelley 1974, Kling et al. 1992), and in Canadian Shield lakes, 5 to 59 mmol $CO_2$ $m^{-2}$ $d^{-1}$ (Bower and McCorkle 1980, Hesslein et al. 1980).

Our results indicate that planktonic metabolism of allochthonous DOC probably constitutes a major source of $CO_2$ in lakes. The total $CO_2$ flux from these lakes is still unknown, because the metabolism of the hypolimnion and sediments, and production by littoral flora were not considered. Rates of $CO_2$ production in the hypolimnion have been measured in almost half of the Quebec lakes sampled in the present study, and range from 30 to 217 mg C $m^{-2}$ $d^{-1}$ (Schallenberg 1992). Summer respiration rates for the whole water column, calculated as the sum of areal epilimnetic and hypolimnetic rates of respiration (which include sediment respiration), result in water column P/R ratios that are 20 to 70% lower than those reported in the present study for the epilimnion, depending on the hypolimnetic depth. Littoral primary production could

potentially reverse the patterns for whole-lake P/R ratios, but these data are not available.

**Impact of DOC on planktonic P/R ratios:** DOC plays a key role in plankton metabolism, because external inputs of organic carbon enter planktonic food webs through bacterial uptake of the dissolved organic compounds; yet DOC had a relatively small statistical effect on the patterns in planktonic P/R ratios in lakes. The variation in DOC concentrations across the lakes we studied was small (threefold) when compared to the variation in chlorophyll or nutrient concentrations (fortyfold). Thus, phytoplankton photosynthesis has a much greater potential to increase across these lakes than the metabolism supported by external inputs of carbon. Because of this much larger range in phytoplankton photosynthesis, compared to the rather invariant external inputs of organic matter, it is the potential for phytoplankton photosynthesis that determines planktonic P/R ratios in lakes. Planktonic P/R ratios are thus strongly correlated to measures of lake trophy, such as chlorophyll or TP, and only weakly correlated to DOC or water color.

There is further evidence that it is not the absolute amount of DOC that is relevant to plankton metabolism, but rather the fraction that may be utilized by bacteria. Our results suggest that the amount of biologically labile carbon may not differ substantially across our study lakes, in spite of a threefold variation in total DOC. The constancy of the absolute amount of labile DOC across lakes would explain the lack of statistical effect of DOC on rates of plankton respiration. This hypothesis implies that the fraction of the DOC pool that can be effectively taken up by bacteria should decrease as DOC concentrations increase, so that increases in concentration are balanced by decreases in the proportion of the DOC that is bioavailable. The net result of this pattern, which has to be further tested, is that rates of plankton respiration

supported by bacterial uptake of DOC would remain almost constant across gradients of DOC ( in the range of 2.5 to 8 mgC $l^{-1}$).

**Implications for planktonic food web structure**: Our results indicate that scaling plankton processes to phytoplankton photosynthesis, as has traditionally been done in limnology, is not appropriate for most freshwater plankton communities. Only the most eutrophic lakes appear to conform to the traditional phytoplankton-based food web. In oligotrophic temperate lakes, phytoplankton-derived carbon was often a minor fraction of the total amount of organic carbon consumed by the plankton community. In agreement with these reports, bacteria and small heterotrophic protists have been shown to dominate the metabolism in many oligotrophic freshwater (Hessen 1992, Jones 1992, del Giorgio and Peters 1993), estuarine (Findlay et al. 1992) and marine systems (Hopkinson et al. 1989). This evidence is further supported by studies of planktonic ETS (electron transport system) activity in these same southern Québec lakes (del Giorgio 1992), which also indicate that the contribution of heterotrophs (bacteria + zooplankton) to community metabolism is highest in oligotrophic lakes with low P/R ratios, and declines systematically along gradients of enrichment.

Whereas the evidence for external carbon utilization by the plankton is strong, the fate of this organic carbon is still unclear. The bulk of plankton community respiration in oligotrophic lakes probably corresponds to bacterial utilization of both autochthonous and allochthonous DOC (Jones 1992, del Giorgio and Peters 1993). The extent to which this carbon is effectively converted into bacterial biomass and utilized higher up in the food web is a matter of contention. Hessen (1992) has argued that a substantial portion of bacterial respiration in oligotrophic lakes reflects organic carbon taken up and not incorporated into biomass due to low nutrient availability. Other reports, however, have shown that DOC, mediated by bacteria and

microheterotrophs, is important in the nutrition of zooplankton, in both humic and clear lakes (Salonen and Hammar 1986, Kankaala 1988). These reports agree with evidence of very high relative bacterial, micro- and macrozooplankton biomass in most of the oligotrophic Québec lakes that we studied (del Giorgio and Gasol submitted), suggesting that these systems are not only dominated by heterotrophic activity, but also by the biomass of heterotrophs, presumably supported by external inputs of particulate and dissolved organic carbon.

## ACKNOWLEDGEMENTS

We thank W. Everett for his assistance in the field, and three anonymous reviewers for helpful discussions and comments. This work was supported by federal NSERC and provincial FCAR grants, and it is a contribution of the Limnology Research Centre of McGill, and the Groupe de Récherche Inter-universitaire en Limnologie (GRIL). P.D.G was supported by a Vineberg Family Fellowship.

# REFERENCES

Ahrens, M. A., and R. H. Peters. 1991. Plankton community respiration: relationships with size distribution and lake trophy. Hydrobiologia 224: 77-87.

Baines, S. B., and M. L. Pace. 1994. Relationship between suspended particulate matter and sinking flux along a trophic gradient and implications for the fate of primary production. Can. J. Fish. Aquat. Sci. 51 (in press).

Barica, J., and J. A. Mathias. 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. J. Fish. Res. Board Can. 36: 80-986.

Beaver, J. R., and T. L. Crisman. 1991. Importance of latitude and organic color on phytoplankton primary productivity in Florida lakes. Can. J. Fish. Aquat. Sci. 48: 1145-1150.

Bergmann, M., and R. H. Peters. 1980. A simple reflectance method for the measurement of particulate pigments in lake water and its application to phosphorus-chlorophyll-seston relationships. Can. J. Fish. Aquat. Sci. 37: 111-114.

Birge, E. A., and C. Juday. 1927. The organic content of the water of small lakes. Proc. Amer. Phil. Soc. 66: 357-372.

Bower, P., and D. McCorkle. 1980. Gas exchange, photosynthetic uptake, and carbon budget for a radiocarbon addition to a small enclosure in a stratified lake. Can. J. Fish. Aquat. Sci. 37: 464-471.

Chambers, P. A., and J. Kalff. 1985. Depth distribution and biomass of submersed macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

Cole, J. J., N. F. Caraco, D. L. Strayer, C. Ochs, and S. Nolan. 1989. A detailed organic carbon budget as an ecosystem-level calibration of bacterial respiration in an oligotrophic lake during midsummer. Limnol. Oceanogr. 34: 286-296.

Coyne, P. I., and J. J. Kelley. 1974. Carbon dioxide partial pressures in arctic surface waters. Limnol. Oceanogr. 19: 928-938.

Cuthbert, I. D., and P. A. del Giorgio. 1992. Toward a standard method of measuring color in freshwater. Limnol. Oceanogr. 37: 1319-1326.

De Haan, H. 1992. Impacts of environmental changes on the geochemistry of aquatic humic substances. Hydrobiologia 229: 59-71.

del Giorgio, P. A. 1992. The relationship between ETS (electron transport system) activity and oxygen consumption in lake plankton: a cross-system calibration. J. Plankton Res. 14: 1723-1741.

del Giorgio, P. A., and J. M. Gasol. Biomass allocation in freshwater plankton communities. Submitted to The American Naturalist.

del Giorgio, P. A., and R. H. Peters. 1993. The balance between phytoplankton production and plankton respiration in lakes. Can. J. Fish. Aquat. Sci. 50: 282-289.

Devol, A. H. 1979. Zooplankton respiration and its relation to plankton dynamics in two lakes of contrasting trophic state. Limnol. Oceanogr. 24: 893-905.

Eckhardt, B. W., and T. R. Moore. 1990. Controls of dissolved organic carbon concentrations in streams, southern Québec. Can. J. Fish. Aquat. Sci. 47: 1537-1544.

Energy, Mines and Resources Canada. 1974. National Atlas of Canada. McMillan Publ., Ottawa, Can.

Engstrom, D. R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can. J. Fish. Aquat. Sci. 44: 1306-1314.

Fee, E. J. 1978. Studies of hypolimnion chlorophyll peaks in the experimental Lakes Area, northwestern Ontario. Can. Fish. Mar. Serv. Tech. Rep. 752: iv + 21 pp.

Fee, E. J. 1979. A predictive relation between lake morphometry and primary productivity and its use in interpreting whole lake eutrophication experiments. Limnol. Oceanogr. 24: 401-416.

Fee, E. J. 1990. Computer programs for calculating *in situ* phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. 1740: v + 27 p.

Findlay, S., M. L. Pace, D. Lints, and K. Howe. 1992. Bacterial metabolism of organic carbon in the tidal freshwater Hudson Estuary. Mar. Ecol. Prog. Ser. 89: 147-153.

Gasit A. 1974. Allochthonous organic matter and organic matter dynamics in Lake Wingra, Wisconsin. Ph.D Thesis, University of Wisconsin, Madison. 209 pp.

Gasol, J. M., and C. Pedrós-Alió. 1991. On the origin of deep algal maxima: the case of lake Cisó. Verh. int. Ver. Limnol. 24: 1024-1028.

Golterman, H. L., R. S. Clymo, and M. A. M. Ohnstad. 1978. Methods for physical and chemical analysis of freshwaters. IBP 8, Blackwell, London.

Griesbach, S. J., and R. H. Peters. 1991. The effects of analytical variations on estimates of phosphorus concentration in surface waters. Lake Res. Manag. 7: 97-106.

Harris, G. P. 1984. Phytoplankton productivity and growth measurements: past, present and future. J. Plankton Res. 6: 219-237.

Hessen, D. O. 1992. Dissolved organic carbon in a humic lake: effects on bacterial production and respiration. Hydrobiologia 229: 115-123.

Herczeg, A. L. 1987. A stable carbon isotope study of dissolved inorganic carbon cycling in a softwater lake. Biogeochemistry 4: 231-263.

Hesslein, R. H., W. S. Broecker, P. D. Quay, and D. W. Schindler. 1980. Whole-lake radiocarbon experiment in an oligotrophic lake at the experimental lakes area, Northwestern Ontario. Can. J. Fish. Aquat. Sci. 37: 454-463.

Hopkinson Jr., C. S., B. Sherr, and W. J. Wiebe. 1989. Size fractioned metabolism of coastal microbial plankton. Mar. Ecol. Prog. Ser. 51: 155-166.

Jackson, T. A., and R. E. Hecky. 1980. Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37: 2300-2317.

Kankaala, P. 1988. The relative importance of algae and bacteria as food for Daphnia longispina (Cladocera) in a polyhumic lake. Freshwat. Biol. 19: 285-296.

Kling, G. W., G. W. Kipphut, and M. C. Miller. 1991. Arctic lakes and streams as gas conduits to the atmosphere: implications for tundra carbon budgets. Science 251: 298-301.

Kling, G. W., G. W. Kipphut, and M. C. Miller. 1992. The flux of $CO_2$ and $CH_4$ from lakes and rivers in arctic Alaska. Hydrobiologia 240: 23-36.

Jones, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73-91.

Laird, G. A., and D. Scavia. 1990. Distribution of labile dissolved organic carbon in Lake Michigan. Limnol. Oceanogr. 35: 443-447.

Likens, G. E., and F. H. Bormann. 1979. The role of watershed and airshed in lake metabolism. Arch. Hydrobiol. 13: 195-211.

Mathias, J. A., and J. Barica. 1980. Factors controlling oxygen depletion in ice-covered lakes. Can. J. Fish. Aquat. Sci. 37: 185-194.

McArdle, B. H. 1988. The structural relationship: regression in biology. Can. J. Zool. 66: 2329-2339.

Meili, M. 1992. Sources, concentrations and characteristics of organic matter in softwater lakes and streams of the Swedish forest region. Hydrobiologia 229: 23-41.

Odum, W. E., and R. T. Prentki. 1978. Analysis of five North American lake ecosystems IV. Allochthonous organic inputs. Verh. int. Ver. Limnol. 20: 574-580.

Pick, F. R., C. Nalewajko, and D. R. S. Lean. 1984. The origin of a metalimnetic chrysophyte peak. Limnol. Oceanogr. 29: 125-134.

Radheyshyam, and D. R. Naik. 1992. Seasonal dynamics of planktonic community metabolism in newly constructed tropical ponds in a swampy area. Int. Revue ges. Hydrobiol. 77: 303-313.

Rask, M., L. Arvola, and K. Salonen. 1993. Effects of catchment deforestation and burning on the limnology of a small forest lake in southern Finland. Verh. int. Ver. Limnol. 25: 525-528.

Rask, M., A. Heinänen, K. Salonen, L. Arvola, I. Bergström, M. Liukkonen, and A. Ojala. 1986. The limnology of a small, naturally acidic, highly humic lake. Arch. Hydrobiol. 106: 351-371.

Rasmussen, J. B., L. Godbout, and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. Limnol. Oceanogr. 34: 1336-1343.

Reynolds, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.

Rich, P. H. 1984. Further analysis of respiration in a North American lake ecosystem. Verh. int. Ver. Limnol. 22: 542-548.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

Salonen, K., and T. Hammar. 1986. On the importance of dissolved organic matter in the nutrition of zooplankton in some lake waters. Oecologia 68: 246-253.

Salonen, K., T. Kairesalo, and R. I. Jones (eds). 1992. Dissolved organic matter in lacustrine ecosystems: energy source and system regulator. Hydrobiologia 229, 291 pp.

Salonen, K., K. Kononen, and L. Arvola. 1983. Respiration of plankton in two small, polyhumic lakes. Hydrobiologia 101: 65-70.

Salonen, K. and T. Tulonen. 1990. Photochemical and biological transformations of dissolved humic substances. (Abstract). Verh. int. Ver. Limnol. 24: 294.

Sarvala, J., V. Ilmavirta, L. Paasivirta, and K. Salonen. 1981. The ecosystem of the oligotrophic Lake Pääjärvi 3. Secondary production and an ecological energy budget of the lake. Verh. int. Ver. Limnol. 21: 422-427.

Scavia, D., and G. A. Laird. 1987. Bacterioplankton in Lake Michigan: Dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. 32: 1017-1033.

Schallenberg, M. 1992. The ecology of sediment bacteria and hypolimnetic catabolism in lakes. Ph.D thesis, McGill University, Montreal, Québec.

Schwaerter, S., M. Søndergaard, B. Riemann, and L. M. Jensen. 1988. Respiration in eutrophic lakes: the contribution of bacterioplankton and bacterial growth yield. J. Plankton Res. 10: 515-531.

Smith, V. H. 1979. Nutrient dependence of primary productivity in lakes. Limnol. Oceanogr. 24: 1051-1064.

Thomas, W. H., B. C. Cho, and F. Azam. 1991. Phytoplankton and bacterial production and biomass in subalpine Eastern Brook Lake, Sierra Nevada, California. I. Seasonal interrelationships between the two biotic groups. Arctic Alpine Res. 23: 287-295.

Tranvik, K. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

Verduin, J. 1956. Energy fixation and utilization by natural communities in western Lake Erie. Ecology 37: 40-50.

Welch, H. E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. 19: 65-73.

Welch, H. E., and M. A. Bergmann. 1985. Winter respiration of lakes at Saqvaqjuac, N. W. T. Can. J. Fish. Aquat. Sci. 42: 521-528.

Welch, H. E., P. J. Dillon, and A. Sreedharan. 1976. Factors affecting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809-1815.

Wetzel, R. G. 1992. Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. Hydrobiologia 229: 181-198.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses. Second edition, Springer-Verlag, New York.

Wetzel, R. G., and J. E. Richey. 1978. Analysis of five North American lake ecosystems VII. Control mechanisms and regulation. Vehr. int. Ver. Limnol. 20: 605-608.

Williams, P. J. leB. 1984. A review of measurements of respiration rates of marine plankton populations, p. 357-389. In J. E. Hobbie and P. J. leB. Williams (eds), Heterotrophic activity in the sea. Plenum Press.

Chapter 5

# HETEROTROPHIC DOMINANCE IN THE PLANKTON OF UNPRODUCTIVE TEMPERATE LAKES

## ABSTRACT

Temperate and boreal lakes are often supersaturated with $CO_2$ and outgas during the growing season. This outflux of $CO_2$ may represent a substantial loss of organic carbon from surrounding terrestrial systems. Here we present data on lake plankton structure and metabolism that support the hypothesis that excess $CO_2$ in lakes originates from the breakdown of terrestrial organic carbon by planktonic organisms. In unproductive temperate lakes, which are typically supersaturated with $CO_2$, the plankton is characteristically dominated by heterotrophic biomass and activity, and community P/R ratios are low. The opposite trends characterize the most productive lakes.

## INTRODUCTION

Increasing biogeochemical evidence shows that many temperate and boreal lakes are supersaturated with $CO_2$, and therefore outgas during the ice-free period (1). Measured $CO_2$ fluxes from lakes to the atmosphere are not trivial (2), and suggest that the significance of lake processes to global carbon cycles should be reassessed. One of the principal mechanisms thought to cause the $CO_2$ imbalance in lakes is the biological degradation of land-derived organic matter (3). If respiratory $CO_2$ within lakes is one of the causes of the high partial pressures of $CO_2$, it follows that lake communities should exhibit low ratios of primary production to respiration (P/R ratios). Such low P/R ratios would imply that heterotrophs dominate community activity and probably community biomass as well.

Although lake sediments have repeatedly been shown to be an important source of respiratory $CO_2$ and methane (4), lake plankton are usually regarded as approximately self-sufficient systems fueled mostly by phytoplankton production. As a consequence of this perception, the possibility that freshwater plankton may function as a net heterotrophic system, and therefore as a source of respiratory $CO_2$ to the water column, has seldom been explicitly investigated. Recent empirical studies, however, have revealed trends in freshwater plankton community structure or metabolism which are inconsistent with the notion of freshwater plankton as predominantly autotrophic systems (5). The combination of these independent empirical models support the hypothesis that excess $CO_2$ in lakes results from biological processes within the water column of lakes. These different trends in biomass and metabolism have seldom been studied in the same set of lakes, so the degree to which they co-occur is uncertain.

To test the hypothetical predominance of heterotrophic pathways in the plankton of unproductive lakes, we measured the biomass of autotrophs (phytoplankton) and heterotrophs (bacteria and zooplankton) in a set of 20 temperate lakes spanning a broad range in primary production (6). We then compared these data with simultaneous measurements of phytoplankton production, plankton community respiration and planktonic electron transport system (ETS) activity from these same lakes (7). The patterns in plankton biomass and metabolism that emerge are coherent, and suggest that planktonic communities in the most unproductive lakes are predominantly heterotrophic, and that the plankton becomes increasingly self-sufficient as lakes become enriched in nutrients.

## RESULTS AND DISCUSSION

The biomass of both planktonic heterotrophs (8) and autotrophs (9) increased systematically with mean total phosphorus in the 20 Québec lakes that we studied (fig. 1a). Phytoplankton biomass, however, increased much more rapidly (slope of 1.57) than total heterotrophic biomass (slope of 0.75), and these two log-log slopes were significantly different ($p < 0.05$). Thus, the ratio of total heterotrophic to autotrophic biomass was not constant across lakes, but declined steeply, with a log-log slope of -0.78, along the gradient of increasing phosphorus concentration (fig 1b). The ratios for bacteria:autotrophs, microzooplankton:autotrophs and macrozooplankton:autotrophs also declined with increasing TP concentrations, with slopes significantly below 0 ($p < 0.05$, fig. 1b). The most unproductive lakes were characterized by such high heterotrophic biomass relative to total plankton biomass, that total heterotrophic biomass often exceeded that of phytoplankton.

Figure 1. Mean summer total autotrophic biomass (A, μgC $l^{-1}$) and total heterotrophic biomass (H, μgC $l^{-1}$) as functions of total phosphorus (TP, μg $l^{-1}$) in 20 southern Québec lakes (fig.1a). The regression equations are: log A = 0.38 + 1.54 log TP, n = 20, $r^2 = 0.88$, $p < 0.01$, and log H = 1.09 + 0.75 log TP, n = 20, $r^2 = 0.77$, $p < 0.01$. Total heterotrophic biomass is the sum of bacteria, microzooplankton (< 150 μm) and macrozooplankton (> 150 μm). Figure 1b: the mean summer ratio of total heterotrophic biomass to total autotrophic biomass (H/A ratio) as a function of total phosphorus concentration. The regression equation is log H/A = 0.71 - 0.78 log TP, n = 20, $r^2 = 0.61$, $p < 0.01$. The lines for the ratio of individual component biomass bacteria, micro (microzooplankton) and macro (macrozooplankton), to total autotrophic biomass (A) are also shown. All variables are log-transformed.

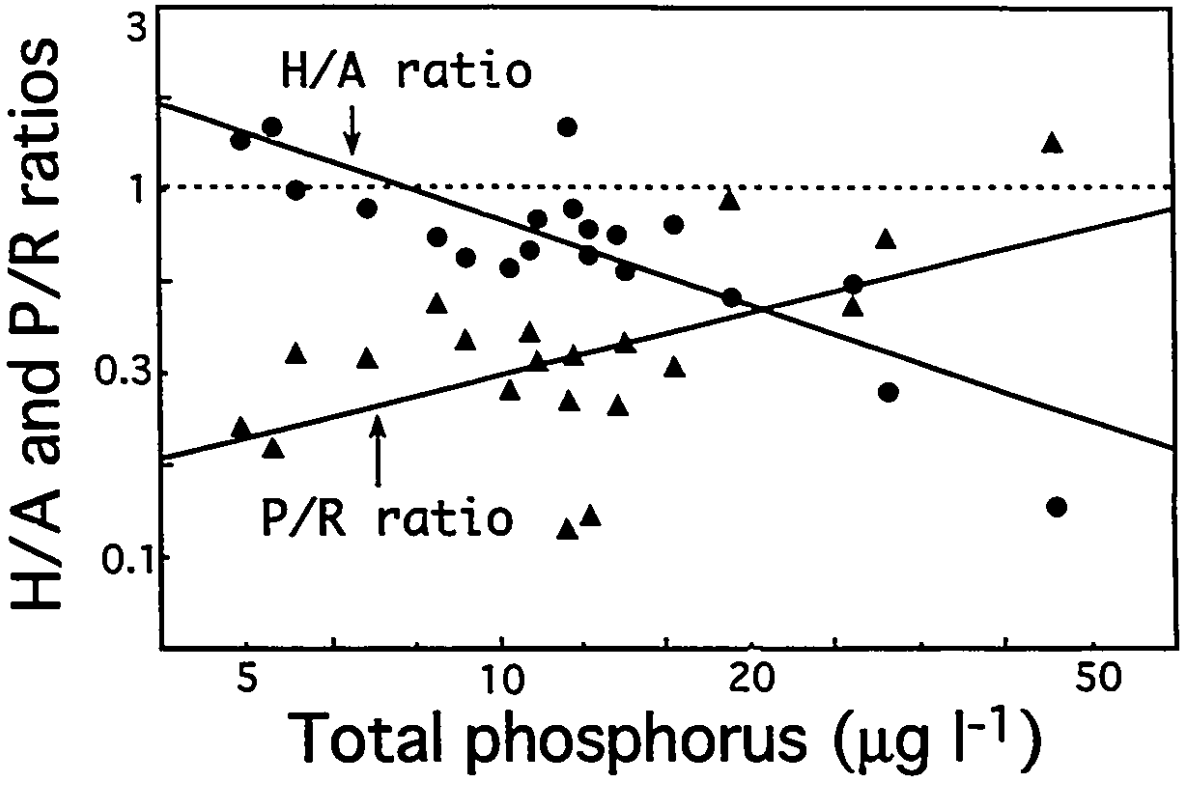
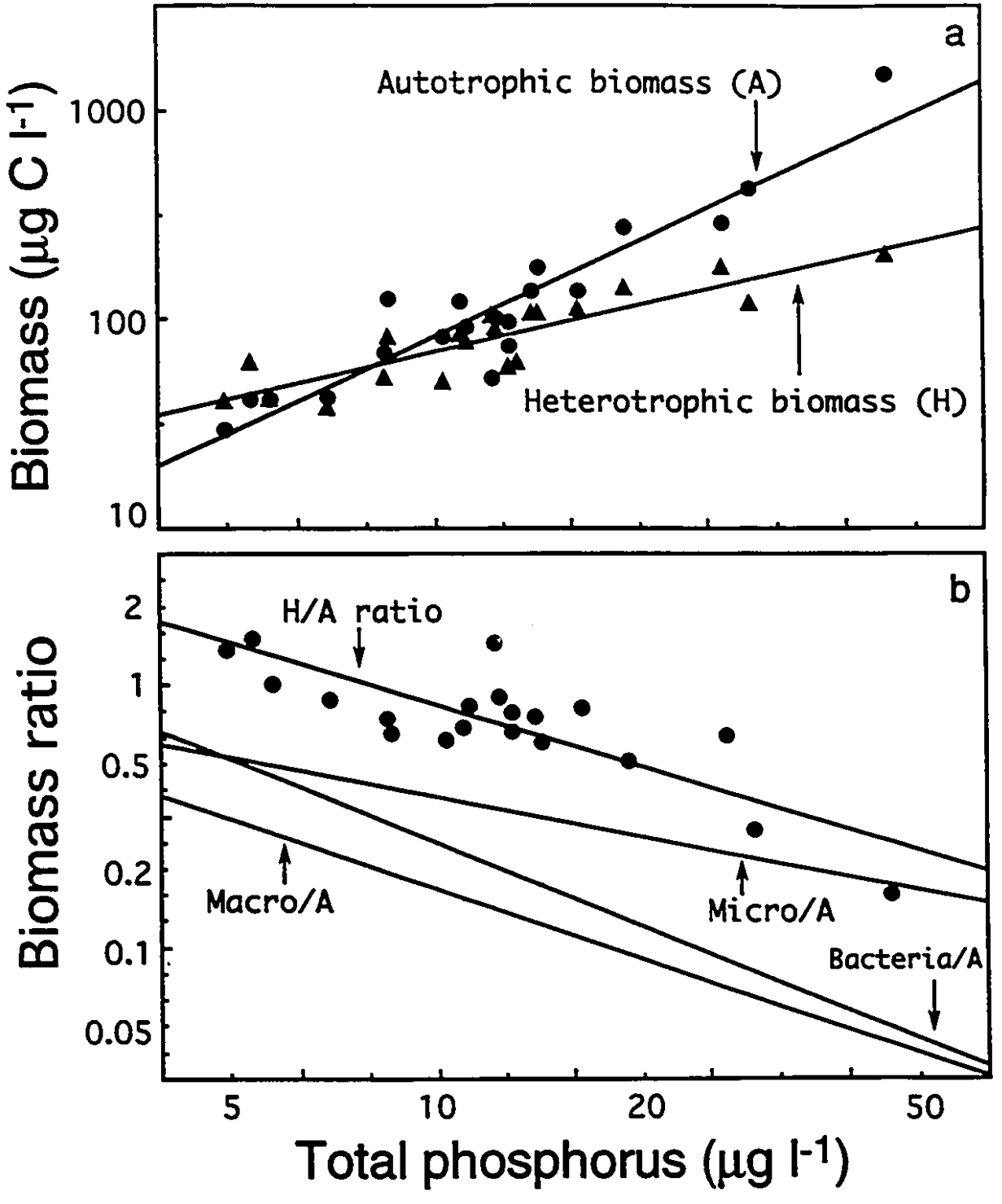

H/A and P/R ratios
3
1
0.3
0.1
H/A ratio
P/R ratio
5
10
20
50
Total phosphorus (μg l-1)

Figure 2. The mean summer ratio of total heterotrophic to total autotrophic biomass (H/A ratio), and the mean summer ratio of phytoplankton production to plankton community respiration (P/R ratio), as functions of the mean summer total phosphorus concentration (TP). The regression equations are: log H/A = 0.71 - 0.78 log TP, n = 20, $r^2 = 0.61$, $p < 0.01$, and log P/R = -1.07 + 0.57 log TP, n = 20, $r^2 = 0.27$, $p < 0.05$. All variables are log-transformed.


a
Autotrophic biomass (A)
Heterotrophic biomass (H)
Biomass (µg C l-1)
1000
100
10
b
H/A ratio
Macro/A
Micro/A
Bacteria/A
Biomass ratio
2
1
0.5
0.2
0.1
0.05
5
10
20
50
Total phosphorus (µg l-1)

When the ratio of heterotrophic to autotrophic biomass was compared to that between phytoplankton production and community respiration (P/R ratio) for the same plankton communities (10), the two ratios displayed contrasting trends along gradients of enrichment (fig. 2). The H/A ratio tended to peak in unproductive lakes and decline with enrichment, but the P/R ratios tended to be low in unproductive lakes and to increase with lake enrichment. Thus, the most unproductive lakes were characterized by relatively high heterotrophic biomass and P/R ratios that were well below unity. P/R ratios approached or exceeded one only in the most productive lakes, where phytoplankton dominated the community biomass.

The low planktonic P/R ratios encountered in lakes with low to medium productivity further suggest the utilization of sources of organic carbon other than phytoplankton. Most lakes, regardless of their productivity, receive considerable amounts of organic carbon from their drainage basins (11). The high relative heterotrophic biomass encountered in many oligotrophic lakes probably reflects the greater impact of these carbon subsidies on the plankton structure and metabolism of systems where phytoplankton production is low. Contrary to our expectations, we found no significant correlation between dissolved organic carbon (DOC) and water color, a surrogate measure of DOC (17) with total heterotrophic biomass, once the effect of TP had been removed. For any given TP concentration, clear-water and colored lakes had similar total heterotrophic biomasses.

Although DOC did not seem to influence the total amount of heterotrophic biomass, there are strong qualitative changes in the composition of the heterotrophic biomass along gradients of humic color in lakes. Microzooplankton greatly increased their contribution to total heterotrophic biomass as water color increases, from less than 40% in the clearest lakes (DOC < than 3.5 mgC $l^{-1}$) to more than 60% in the more

colored lakes (DOC > 6.5 mgC $l^{-1}$, fig. 3). The microzooplankton fraction (< 150 μm) is dominated by rotifers, ciliates, and flagellated protozoans, which with bacteria, form the microbial loop within planktonic food webs. Thus, an increasing supply of external organic carbon may increase the relative importance of microbial pathways.

Terrestrially derived DOC is usually of low nutritional value. Bacteria assimilate this DOC with low efficiency (12), and carbon transfer efficiency within the microbial loop is also low (13). Both processes result in high respiratory losses (14). Bacteria and microheterotrophs comprise the bulk of total heterotrophic biomass in unproductive colored lakes (DOC > 5 mgC $l^{-1}$). In clear-water, oligotrophic lakes (DOC < than 3.5 mgC $l^{-1}$) macrozooplankton, like cladocerans, comprise a relatively large percentage of the total heterotrophic biomass (up to 40%), and the importance of microheterotrophs declines. Although oligotrophic clear-water and colored lakes share similarly low P/R ratios and high H/A ratios, the carbon pathways seem to differ between these two types of systems. In colored lakes, more organic carbon is channeled through microbial pathways, and the low contribution of macrozoplankton to total biomass suggests that this organic carbon is not effectively transmitted up the food web. In contrast, the contribution of macrozooplankton to total biomass is high in clear-water lakes, suggesting that the microbial loop is less important and that the link between bacteria and the larger heterotrophs is more direct.

Regardless of the differences in the patterns of carbon flow across systems, the plankton communities of oligotrophic temperate lakes appear to be dominated by the activity of heterotrophs. Measurements of electron transport system (ETS) activity, taken simultaneously with biomass, respiration and production, provide further evidence of the large contribution of planktonic heterotrophs to community metabolism in unproductive lakes. The ETS method was originally proposed as an indirect

measurement of marine plankton respiration, based on the enzymatic reduction of a tetrazolium salt, INT, in plankton homogenates (15). Several studies have shown that the ratio of respiration (oxygen consumption) to ETS activity (R/ETS ratio) varies substantially, so that different types of planktonic organisms have characteristic R/ETS ratios (16). Zooplankton have the highest R/ETS ratios (range 0.3 to 0.6), followed by bacteria (range 0.2 to 0.4), whereas algae usually exhibit extremely low R/ETS ratios (range 0.04 to 0.16), presumably because photosynthetic ETS contributes to INT reduction (16). Thus the R/ETS ratio of whole plankton communities may be used as an index of the relative contribution of phytoplankton and planktonic heterotrophs to community respiration.

Our measurements of planktonic ETS show that the R/ETS ratio is highest in unproductive lakes, and declines along gradients of enrichment in lakes (17). A comparison of this pattern to that of the biomass distribution (fig. 4a), indicates that when plankton communities are dominated by heterotrophic biomass (high H/A ratios), R/ETS ratios tend to be highest, approaching the values empirically determined for planktonic heterotrophs. In contrast, where the H/A ratios are low, the communities are dominated by the biomass of phytoplankton, and the R/ETS ratios tends to approach the values that characterize pure algal assemblages. Thus, the relatively high heterotrophic biomass in unproductive lakes appears to contribute actively to community metabolism. The link between relatively high heterotrophic biomass and low P/R ratios in plankton communities of unproductive lakes is further strengthened by the consistent trends in planktonic P/R and R/ETS ratios (fig. 4b). Plankton communities characterized by low P/R ratios also exhibit R/ETS ratios which approach those of planktonic heterotrophs, suggesting that the metabolism of these communities is dominated by bacteria and zooplankton. As P/R ratios approach or exceed one, the R/ETS ratios decline to values which are characteristic of

Figure 3. The relative contribution (%) of microzooplankton (< 150 μm) and macrozooplankton (> 150 μm) to total heterotrophic biomass (H), as functions of water color, measured as absorbance at 440 nm in a 1 cm cell. All variables are log-transformed.

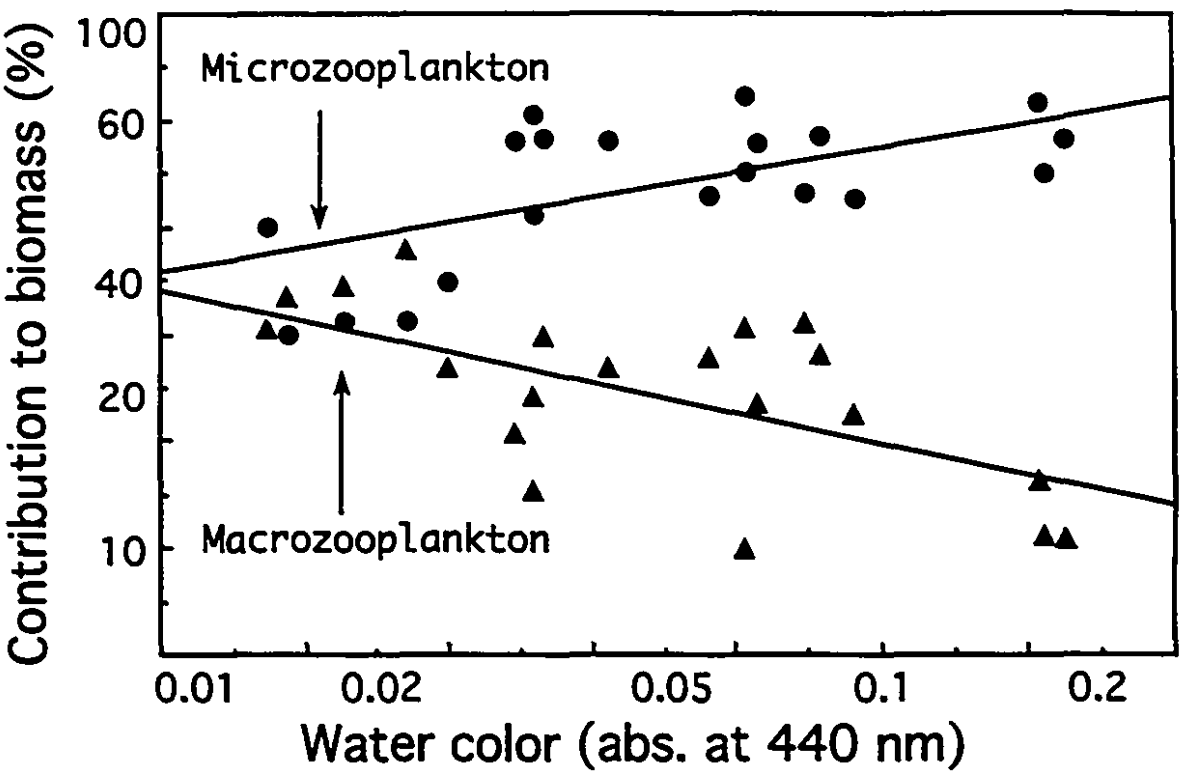
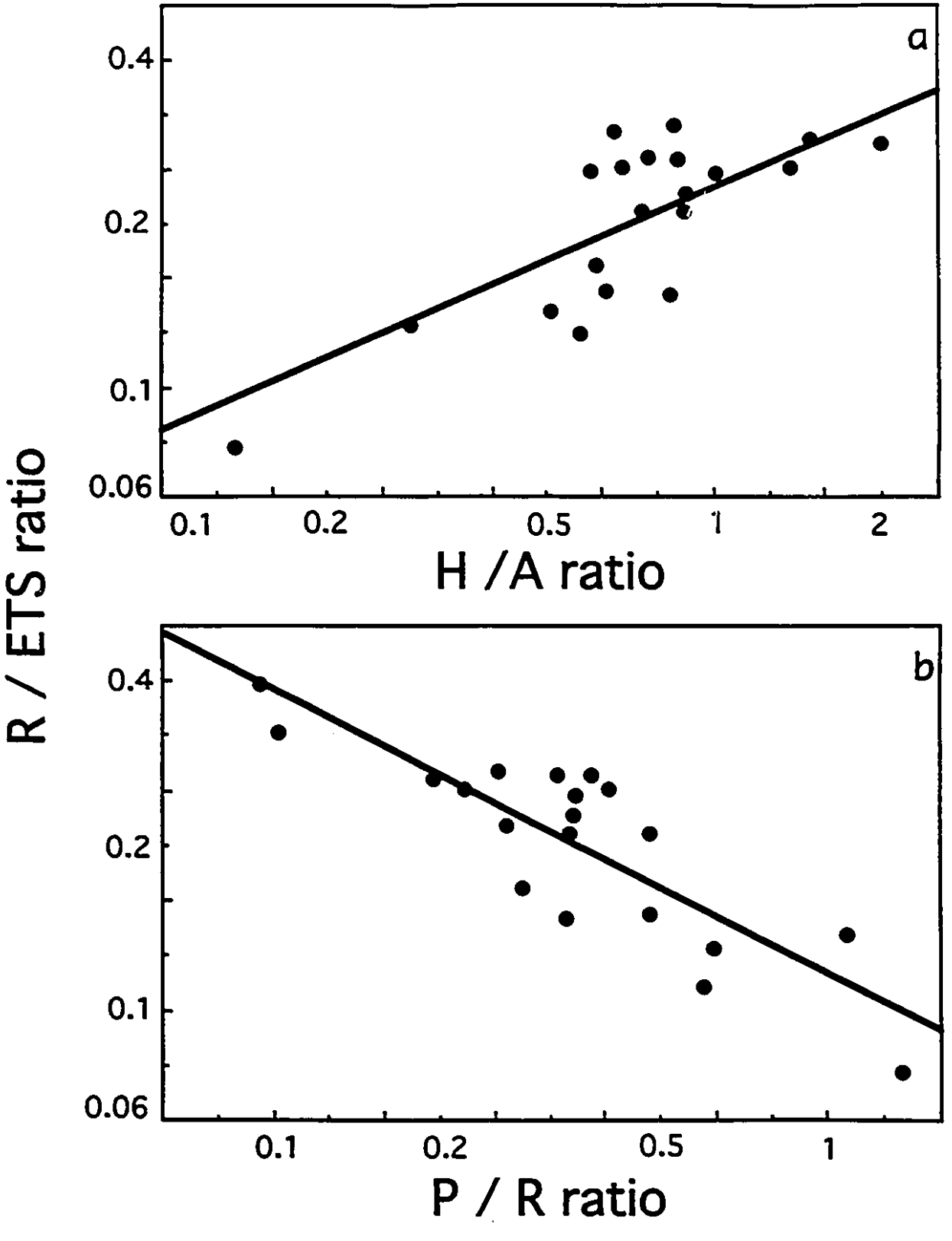

Contribution to biomass (%)
100
60
40
20
10
Microzooplankton
Macrozooplankton
0.01
0.02
0.05
0.1
0.2
Water color (abs. at 440 nm)

Figure 4. The ratio of plankton respiration to ETS activity (R/ETS ratio) as a function of (a) the ratio of total heterotrophic to total autotrophic biomass (H/A ratio), and (b) the ratio of phytoplankton production to plankton respiration (P/R ratio) (fig. 4b). The regression equations are: log R/ETS = 0.63 + 0.45 log H/A, $n = 20$, $r^2 = 0.71$, $p < 0.05$, and log R/ETS = -0.93 - 0.52 log P/R, $n = 20$, $r^2 = 0.71$, $p < 0.01$. All variables are log-transformed.


a
0.4
0.2
0.1
0.06
0.1
0.2
0.5
1
2
H /A ratio
R / ETS ratio
b
0.4
0.2
0.1
0.06
0.1
0.2
0.5
1
P / R ratio

phytoplankton. The contribution of heterotrophs to community metabolism in the most productive lakes appears to be relatively small.

We conclude that plankton communities of oligotrophic temperate lakes are predominantly heterotrophic and dominated by the biomass and activity of planktonic heterotrophs. As lakes become more productive, phytoplankton overwhelmingly dominate community biomass and metabolism. These broad patterns suggest that pelagial communities of most oligotrophic lakes are not energetically self-sufficient and extensively utilize external sources of carbon, presumably of terrestrial origin, even in clear-water lakes with relatively low concentrations of dissolved organic carbon. In northern North America, freshwaters cover 1/6 of the total surface, including over 5 million lakes. Most of these temperate, boreal and arctic lakes are oligotrophic and many have substantial amounts of dissolved organic carbon derived from their drainage basins. According to the empirical models that we present here, heterotrophs are likely to dominate many of these lakes, most likely fueled by terrestrial inputs of dissolved organic carbon. The resulting excess plankton respiration is an extension of the process of mineralization of terrestrial plant material.

Plankton respiration in excess of phytoplankton production ranged from 18 to 107 gC $m^{-2}$ of lake surface for a period of 150 days, from the beginning of May to the end of September. When expressed per unit area of the drainage basin, the average loss of carbon through excess plankton respiration was 6.5 gC $m^{-2}$ for the same period of 150 days. Net ecosystem production (NEP) for temperate and boreal forests ranges from 50 to over 200 gC $m^{-2}$ $y^{-1}$ (18). Assuming that most of the excess plankton respiration is fueled by terrestrial inputs of DOC, up to 10% of NEP could be remineralized by the plankton in lakes and returned to the atmosphere as $CO_2$. Organic carbon accumulation in northern temperate and boreal terrestrial systems

may thus be significantly underestimated if this component of the cycle of terrestrial organic matter is neglected.

**ACKNOWLEDGEMENTS**

We thank W. Everett and S. Clinton for their assistance in collecting and preparing samples, and J. Cole and S. Baines for helpful comments on the manuscript. This research was supported by federal NSERC and provincial FCAR grants, and is a contribution of the McGill Limnology Research Center and the Groupe de Récherche Inter-universitaire en Limnologie (GRIL).

## REFERENCES

1. P. I. Coyne and J. J. Kelly, Limnol. Oceanogr. 19, 928 (1972); S. Emerson, Limnol. Oceanogr. 20, 754 (1975); P. Bower and D. McCorckle, Can. J. Fish. Aquat. Sci. 37, 464 (1980); R. H. Hesslein, W. S. Broecker and P. D. Quay, Can. J. Fish. Aquat. Sci. 37, 454 (1980); G. W. Kling, G. W. Kipphut and M. C. Miller, Science 251, 298 (1991).

2. G. W. Kling, G. W. Kipphut and M. C. Miller, Hydrobiologia 240, 23 (1992).

3. G. W. Kling, G. W. Kipphut and M. C. Miller, Science 251, 298 (1991).

4. M. Schallenberg, Ph.D Thesis, McGill University (1992); B. T. Hargrave, J. Fish. Res. Board Can. 30, 1317 (1973).

5. R. I. Jones, Hydrobiologia 229, 73 (1992); P. A. del Giorgio and J. M. Gasol, Am Nat (submitted); P. A. del Giorgio and R. H. Peters, Can. J. Fish. Aquat. Sci. 50, 282 (1993).

6. The study lakes are located in southern Québec, Canada (45° N, 72° W). The morphometry of these lakes is diverse: mean depth = 2.9 to 48 m, lake area = 0.3 to 47 $km^2$, and water retention times = 0.3 to 11 years. These lakes also vary widely in trophic status, total phosphorus (4.9 to 46 mg $l^{-1}$) and chlorophyll (0.7 to 37 mg $l^{-1}$). Mean summer phytoplankton production varies from 13 to 380 mgC $m^{-3}$ $d^{-1}$. Because of large differences in the ratio of basin area to lake area (3.2 to 30.5), humic color varies thirteen-fold (0.014 to 0.180, absorbance at 440 nm) and dissolved organic carbon (DOC) varies from 2.7 to 8.0 mgC $l^{-1}$.

7. These data are measurements of total heterotrophic and autotrophic biomass, phytoplankton production, plankton respiration and ETS activity taken simultaneously from May to September of 1991. The ETS data has already been presented in Chapter 3 and the data on planktonic P/R ratios has been presented in Chapter 4. The complete data sets for ETS and P/R ratios appear in Appendix 3. All the plankton biomass data used in Chapter 5 appear in Appendix 4 (bacteria), Appendix 5 (microzooplankton) and Appendix 6 (macrozooplankton and phytoplankton), together with details of the methods.

8. Total heterotrophic biomass is the sum of the biomasses of bacteria, microzooplankton and macrozooplankton in epilimnetic water samples taken monthly from May to September of 1991. Bacterial density was determined following K. Porter and Y. S. Feig, Limnol. Oceanogr. 25, 943 (1980); counts were converted to biomass ($\mu gC\ l^{-1}$) following P. K. Bjørnsen, Appl. Environ. Microbiol. 51, 1199 (1986). Quantitative macro- and microzooplankton samples were collected from two serial screens of 150 and 40 μm mesh size, respectively. Microzooplankton (nauplii, rotifers, ciliates, and heterotrophic protozoans, size < 150 μm) were counted and sized in a standard microscope at 125X. Macrozooplankton (copepods, *Daphnia,* bosminids, nauplii, ciliates and rotifers, length > 150 μm) were counted and measured in settling chambers under 125X with an inverted microscope. Size was converted to biomass following K. Y. Børsheim and G. Bratbak, Mar. Ecol. Progr. Ser. 36, 171 (1987); M. A. Gates et al., Oecologia 55, 145 (1982) for flagellates and ciliates, and E. McCauley, in Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters, J. A. Downing and F. Rigler, Eds. (IBP Handbook 17, Blackwell, Oxford, 1984), p. for rotifers, ciliates and crustacean zooplankton. Total microzooplankton biomass was corrected for heterotrophs smaller than 40 μm, using correction factors determined in earlier studies of these same lakes (P. A del Giorgio and J. M. Gasol, submitted). All

the biomass data presented here are arithmetic means of four to six samples taken during the sampling period, and the complete data sets appear in Appendices 4, 5 and 6 of this thesis.

9. Total autotrophic biomass was estimated from chlorophyll a concentrations, using a conversion factor of 1 µg chlorophyll = 40 µg C. A full discussion of the problems associated with a constant conversion factor from chlorophyll to carbon can be found in Chapter 2.

10. Plankton respiration was measured as the consumption of oxygen in bottles incubated at *in situ* temperature. Phytoplankton production was measured as $^{14}C$ uptake during 3 h incubations. The complete data sets and details of the methods appear in Chapter 4 and Appendix 3 of this thesis.

11. M. Meili, Hydrobiologia 229, 23 (1992); R. G. Wetzel, Hydrobiologia 229, 23 (1992)

12. E. A. S. Linley, and R.C. Newell, Bull. Mar. Sci. 35, 409 (1984).

13. L. J. Tranvik, Hydrobiologia 229, 107 (1992).

14. D. O. Hessen, Hydrobiologia 229, 115 (1992).

15. T. T. Packard, J. Mar. Res. 29, 235 (1991).

16. T. T. Packard, Adv. Aquat. Microbiol. 3, 207 (1985).

17. The complete data sets and details of the methods used for ETS analyses appear in Chapter 3 and Appendix 3 of this thesis.

18. N. T. Edwards, H. H. Sugart, Jr., S. B. McLaughlin, W. F. Harris and D. E. Reichle, in Dynamic Properties of Ecosystems, D. E. Reichle, Ed. (Cambridge University Press, New York, 1981), p. 499; R. H. Whittaker et al., Ecology 60, 203 (1979); D. E. Reichle, R. V. O'Neill and W. F. Harris, in Unifying Concepts in Ecology, W. H. van Dobben and R. H. Lowe-McConnell, Eds. W. Junk, The Hague, 1975), p. 27.

# GENERAL CONCLUSIONS

This thesis has shown that phytoplankton photosynthesis is insufficient to fuel respiration in oligotrophic lakes in Québec (Chapter 4), and that this pattern probably applies to many unproductive lakes in other regions (Chapters 1). Unproductive lakes are characterized by a relatively high contribution of planktonic heterotrophs to community respiration (Chapter 3). The proportion of heterotrophs and autotrophs in the plankton also varies with trophy, and my own measurements of biomass (Chapter 5) confirmed the pattern found in Chapter 2 using literature data and an independent set of measurements for Québec lakes provided by J. M. Gasol. These trends in metabolism and biomass are not independent from each other, but rather, they are different manifestations of the impact of external organic subsidies on freshwater plankton communities. In Chapter 5 I have combined all my field measurements, presented separately in Chapters 3, 4 and in Chapter 5 itself, to show that most of the temperate lakes that I studied are characterized by low planktonic P/R ratios and communities dominated by the biomass and activity of planktonic heterotrophs. The classical paradigm of phytoplankton-based plankton food webs does not apply to these, and presumably to other lakes of similar characteristics, because neither community metabolism nor biomass scale down to algal photosynthesis.

This research, in turn, has generated several questions regarding the origin, processing and fate of external carbon subsidies to plankton communities, and among these questions there are two that I consider of particular importance: the first concerns the effectiveness of relating plankton metabolism to total DOC, and the second concerns the fate of external organic carbon supplements within planktonic food webs.

One of the underlying assumptions of this thesis, and of similar research elsewhere (Hessen et al. 1990; Tranvik 1992; Meili 1992; Jones 1992), has been that bacterial uptake of DOC supports heterotrophic activity in the plankton of lakes, in addition to the direct consumption of phytoplankton by grazers. It was thus expected that DOC would influence the patterns in metabolism and biomass structure of the plankton.This key role assigned to DOC, however, is not entirely evident in the present results. DOC was shown to have a depressing effect on rates of phytoplankton production (Chapter 4), and to stimulate the respiration of planktonic heterotrophs relative to phytoplankton (Chapter 3). There were also qualitative effects of DOC on the composition of the total heterotrophic biomass (Chapter 5). Overall, however, the effect of DOC on plankton metabolism and biomass was weak, compared to effect of nutrient enrichment. Thus, heterotrophy in lake plankton appears to be driven mostly by the potential for phytoplankton production rather than by external inputs of organic carbon. Odum and Prentki (1978) reached the same conclusion for the degree of heterotrophy in lakes, based on whole-lake organic carbon budgets.

The most unexpected result of this thesis was probably the lack of statistical effect of DOC on rates of plankton respiration, which were comparable in clear-water and colored lakes of similar trophic status (Chapter 4). Although DOC varied only threefold in my study lakes, this variation represents a substantial amount of organic carbon when compared to the overall organic pool of these lakes. This apparent lack of influence of DOC on plankton respiration does not necessarily mean that dissolved organic carbon, from both internal and external sources, is not a major substrate for plankton metabolism. Rather, it suggests that it may not be the absolute amount of DOC that is relevant to plankton metabolism, but only the fraction that may be effectively used by bacteria, and hence by other planktonic heterotrophs. The present evidence has led me to hypothesize (Chapter 4) that the amount of organic carbon that

is bioavailable did not vary substantially across these lakes, in spite of a threefold variation in the total amount of DOC. This hypothesis requires that the fraction of the DOC that may be readily utilized by bacteria should decline with increasing DOC concentrations, so that an increase in the total amount of carbon would be balanced by a decrease in the proportion of the carbon that can be taken up by bacteria, and thus respired or transferred to other planktonic heterotrophs.

A relatively uniform amount of bioavailable DOC across lakes would explain the lack of statistical effect of total DOC on plankton respiration. There is scattered evidence in the literature to support a decline in the quality of DOC (Tranvik 1988; de Haan 1992), but the hypothesis has yet to be explicitly tested. If confirmed, our approach to the effect of DOC on plankton and whole-lake function will have to be modified, to incorporate these qualitative variations in bioavailability. In studies of plankton metabolism across lakes, total DOC may have to be replaced by a more meaningful estimate involving the biologically reactive fraction.

The second major question that emerges from this thesis is the fate of the external organic subsidies that enter planktonic food webs. Bacteria take up DOC, part of this carbon is respired and the remainder converted into biomass which may be utilized by other planktonic heterotrophs. The pathways that lead from bacteria to the larger zooplankton are complex and often indirect, involving the passage of carbon through flagellated protozoans, rotifers and ciliates. Each one of these trophic transfers represents major losses of carbon through respiration, and the low P/R ratios reported in this thesis are likely the result of a high contribution of heterotrophs to the respiration term of the ratio.

Because of these high respiratory losses (Hessen 1992), it is uncertain what proportion of the external organic carbon taken up by bacteria reaches the macrozooplankton. In highly humic lakes, allochthonous organic matter often comprises a large portion of the diet of zooplankton (Salonen and Hammar 1986; Hessen 1992), but similar measurements are lacking for clear-water lakes, where phytoplankton have traditionally been regarded as the major source of organic carbon. This thesis has not attempted to directly quantify the proportion of allochthonous organic carbon utilized by the zooplankton of the study lakes, but Chapter 5 shows that crustacean zooplankton attain the highest biomass relative to phytoplankton in oligotrophic lakes, where the imbalance between photosynthesis and respiration is greatest. This pattern suggests that organic carbon supplements effectively reach the macrozooplankton, in addition to carbon derived from algal photosynthesis. Whether the high relative biomass of crustacean zooplankton found in both clear-water and colored oligotrophic lakes results from the tranfer of allochthonous organic carbon up the food web remains to be explicitly tested, however; using methods that can trace the flow of carbon through planktonic food webs, such as the measurement of stable isotope ratios of carbon and nitrogen.

## REFERENCES

De Haan, H. 1992. Impacts of environmental changes on the biogeochemistry of aquatic humic substances. Hydrobiologia 229: 59-71.

Jones, R. i. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73-91.

Hessen, D. O. 1992. Dissolved organic carbon in a humic lake: effects on bacterial production and respiration. Hydrobiologia 229: 115-123.

Hessen, D. O., T. Andersen and A. Lyche. 1990. Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. Limnol. Oceanogr. 35: 84-99.

Meili, M. 1992. Sources, concentrations and characteristics of organic matter in softwater lakes and streams of the Swedish forest region. Hydrobiologia 229: 23-41.

Odum, W. E. and R. T. Prentki. 1978. Analysis of five North American lake ecosystems. IV. Allochthonous carbon inputs. Verh. int. Ver. Limnol. 20: 574-580.

Salonen, K., and T. Hammar. 1986. On the importance of dissolved organic matter in the nutrition of zooplankton in some lake waters. Oecologia 68: 246-253.

Tranvik, L. J. 1988. Availability of dissolved organic carbon for planktonic bacteria in oligotrophic lakes of different humic content. Microb. Ecol. 16: 311-322.

Tranvik, L. J. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

# Appendix 1

Literature data on phytoplankton production (mg C $m^{-3}$ $d^{-1}$) and chlorophyll concentration (mg $m^{-3}$) used in Chapter 1. Full citation for the sources appear in the Reference section of Chapter 1. Comments refer to differences in integration depth, sampling period and analytical techniques.

| Source | Lake | CHA | PP | Comments |
|---|---|---|---|---|
| Belay & Wood 1984 | Awassa (Ethiopia) | 40 | 1001.1 | Areal data divided by $Z_{eu}$ |
| | Abiata | 65 | 1300 | PQ=1 used to convert $O_2$ to $CO_2$ |
| | Zwei | 91 | 5044 | |
| Stockner & Shortreed 1985 | Bonilla (Canada) | 5.3 | 81.8 | Unspecified itegration depth |
| | | 6.6 | 58.3 | |
| | | 4.5 | 53.3 | |
| | | 4.3 | 62.9 | |
| | Curtis | 3.7 | 30.8 | |
| | | 4.2 | 27.6 | |
| | | 5.1 | 67.9 | |
| | | 3.1 | 15.2 | |
| | Devon | 4.67 | 26.2 | |
| | Kennedy ClayoquotArm | 3.1 | 29.3 | |
| | | 11.2 | 110.2 | |
| | | 5.7 | 34.7 | |
| | | 3.8 | 30 | |
| | Kennedy Main Arm | 2.0 | 16.2 | |
| | | 1.5 | 10.5 | |
| | | 1.1 | 4.9 | |

| | | | | |
|---|---|---|---|---|
| | | 1.1 | 9.2 | |
| | Long | 2.6 | 10.6 | |
| | | 1.9 | 8.6 | |
| | Lowe | 1.8 | 10.4 | |
| | Sproat-1 | 0 5 | 3.5 | |
| | Sproat-2 | 0.5 | 3.0 | |
| Bayne et al. 1990 | West Point (USA) | 13.6 | 84.6 | Integrated over $Z_{eu}$. Average of cool and warm seasons. |
| | | 9.7 | 140 | |
| | | 10.7 | 169 | |
| | | 8.8 | 145 | |
| | | 11.8 | 127 | |
| | | 13.6 | 111 | |
| | | 8.9 | 176 | |
| | | 6.9 | 199 | |
| | | 7.7 | 202 | |
| | | 19.7 | 316 | |
| Tolstoy 1988 | Vanern (Sweden) | 1.4 | 8.7 | Integrated over $Z_{eu}$ |
| | Vattern | 1.5 | 5.8 | |
| | Ekolm Bay | 10.9 | 54.3 | |
| | | 6.7 | 52.2 | |
| | Lilla Ullfjarden | 9.5 | 27.4 | |
| | | 14.6 | 37 | |
| Jackson & Hecky 1980 | Notigi (Canada) | 4.2 | 131 | Unspecified depth of integration. |

| | | | | |
|---|---|---|---|---|
| | Kettle | 6.0 | 81 | |
| | | 6.7 | 158 | |
| | Kelsey | 4.7 | 149 | |
| | | 5.0 | 151 | |
| | Southern Indian | 1.9 | 39 | |
| | | 1.7 | 43 | |
| | | 2.3 | 31 | |
| | | 4.7 | 174 | |
| Beaver & Crisman 1991 | Anderson (Florida, USA) | 5.2 | 54.5 | Unspecified depth of integration. |
| | | 3.2 | 14.9 | Data compiled from the literature |
| | Adaho | 5.3 | 93.7 | |
| | Alice | 4.4 | 98.6 | |
| | Altho | 5.9 | 150.3 | |
| | Annie | 2.6 | 25.0 | |
| | Apopka | 60.4 | 4182.3 | |
| | | 45.8 | 2500.1 | |
| | Arbuckle | 25.6 | 709.7 | |
| | Beauclair | 93.2 | 4130.9 | |
| | Brooklyn | 1.9 | 9.9 | |
| | Burnt | 29.0 | 3299.3 | |
| | Bevilles Pond | 23.7 | 22.8 | |
| | Bivens Arm | 56.0 | 3299.3 | |
| | Calf Pond | 23.5 | 165.1 | |
| | Clay | 9.5 | 409.6 | |
| | Clear | 26.4 | 1140.3 | |

| | | |
|---|---|---|
| Clearwater | 2.3 | 5.9 |
| Conway | 4.4 | 284.6 |
| Cooter Pond | 22.6 | 368.1 |
| Cowpen | 1.6 | 4.7 |
| Dora | 50.4 | 3891.9 |
| | 76.0 | 2487.1 |
| Elisabeth | 8.0 | 80.9 |
| Eustis | 23.8 | 1174.8 |
| | 25.0 | 1315.7 |
| Francis | 18.1 | 193.8 |
| Galilee | 1.9 | 23.4 |
| Geneva | 1.4 | 32.8 |
| Griffin | 47.3 | 2755.1 |
| | 45.6 | 2741.9 |
| Harris | 14.5 | 349.7 |
| Hawthorne | 56.8 | 1207.1 |
| Hickory Pond | 7.6 | 48.5 |
| Istokpoga | 15.7 | 314.1 |
| | 18.6 | 1115.3 |
| Jeggord | 7.0 | 82.9 |
| Josephine | 20.6 | 345.4 |
| June-in-Winter | 9.2 | 299.4 |
| Kingsley | 1.8 | 34.5 |
| Kanapaha | 42.7 | 2064.4 |
| Lochloosa | 23.3 | 265.0 |
| Long | 1.4 | 3.5 |
| Long Pond | 12.6 | 18.9 |

| | | | |
|---|---|---|---|
| Little Orange | 9.8 | 270.0 | |
| Little Santa Fe | 4.5 | 23.0 | |
| Magnolia | 1.5 | 11.8 | |
| McCloud | 7.2 | 71.5 | |
| | 2.4 | 9.9 | |
| Meta | 3.3 | 27.9 | |
| Mize | 33.9 | 137.3 | |
| Moss Lee | 8.0 | 306.8 | |
| Newnans | 47.4 | 1271.7 | Newnans 1980 data excluded |
| Okeechobee | 14.4 | 1322.5 | |
| Orange | 15.6 | 338.3 | |
| Placid | 6.3 | 193.9 | |
| Palatka | 15.6 | 109.8 | |
| Reedy | 42.6 | 737.5 | |
| Sand Hill | 1.3 | 9.0 | |
| Santa Fe | 5.6 | 117.7 | |
| Santa Rosa | 1.7 | 7.2 | |
| Still Ford | 3.1 | 5.5 | |
| Suggs | 3.4 | 84.2 | |
| Swam | 1.6 | 39.6 | |
| Ten | 12.6 | 216.4 | |
| Thonotosassa | 63.8 | 624.7 | |
| Tuscawilla | 11.3 | 379.3 | |
| Twenty | 92.8 | 3142.6 | |
| Twenty-five | 3.5 | 29.9 | |
| Twenty-seven | 30.1 | 15.6 | |

| | | | | |
|---|---|---|---|---|
| | Wall | 5.1 | 84.1 | |
| | Wauberg | 37.3 | 1299.0 | Wauberg 1980 data excluded |
| | Weir | 6.4 | 151.1 | |
| | Winnott | 2.6 | 16.6 | |
| | Watermelon | 9.0 | 226.1 | |
| Carmouze et al. 1983 | Chad (Africa) | 90 | 1078 | Data integrated over mixed layer |
| Malueg et al. 1972 | Tahoe (USA) | 0.5 | 1.9 | Data integrated over top 20 m |
| Beuchamp & Kerekes 1989 | Beaverskin (Canada) | 1.2 | 37.5 | Data integrated over $Z_{eu}$ |
| | | 1.1 | 34.8 | |
| | Kejimkujik | 1.2 | 11.6 | |
| | | 0.9 | 13.6 | |
| | Peblelogitch | 1.2 | 23.3 | |
| | | 1.7 | 36.9 | |
| Lafond et al. 1990 | Achigan (Canada) | 1.0 | 54.0 | Data integrated over the mixed layer |
| | Al'ours | 2.3 | 101.9 | |
| | Connelly | 1.5 | 17.4 | |
| | Croche | 1.6 | 64.9 | |
| | Cromwell | 8.6 | 138.7 | |
| | Echo | 2.1 | 76.3 | |
| | En Coeur A | 1.3 | 30.4 | |
| | En Coeur B | 1.5 | 27.4 | |
| | Pin Rouge | 2.7 | 53.4 | |

| | | | | |
|---|---|---|---|---|
| | Thibault | 5.5 | 176.2 | |
| | Triton | 3.5 | 119.2 | |
| Kifle & Belay 1990 | Awasa (Ethiopia) | 35.1 | 935 | Data integrated over $Z_{eu}$ |
| Dubinsky et al. 1984 | Constance (Germany) | 1.7 | 28.6 | Data integrated over top 15 m |
| Adams et al. 1990 | Crystal (USA) | 1.6 | 38 | Data integrated over epilimnion |
| | | 1.8 | 38 | |
| | Sparkling | 2.3 | 43 | |
| | | 3.1 | 46 | |
| | | 2.1 | 44 | |
| | Trout | 2.6 | 48 | |
| | | 3.2 | 50 | |
| | | 2.7 | 59 | |
| Heyman 1983 | Botjarn (Sweden) | 0.5 | 14.2 | Data integrated over mixed layer |
| | Erken | 4.0 | 45.4 | |
| | Sigeforesjon | 1.4 | 28.3 | |
| | Vitalampa | 0.8 | 18.3 | |
| Riggiu & Mosello 1984 | Garda (Italy) | 1.7 | 14 | Data integrated over $Z_{eu}$ |
| | Maggiore | 5.1 | 58 | |
| | Como | 6.4 | 126 | |
| | Iseo | 9.4 | 80 | |
| | Lugano | 24 | 353 | |

# Appendix 2

Literature data on plankton community respiration (mg C $m^{-3}$ $d^{-1}$) and chlorophyll concentration (mg $m^{-3}$) used in Chapter 1. Full citations for the sources appear in Reference section of Chapter 1. Comments refer to integration depth, sampling period and analytical techniques.

| Source | Lake | CHA | Resp | Comments |
|---|---|---|---|---|
| Jones 1977 | Neagh, Kinnego Bay (N. Ireland) | 106 | 2071 | Average over $Z_{eu}$ |
| Kravtsova et al. 1988 | Proletarshoye (USSR) | 100 | 2160 | CHA calcualated from wet weight using 1g ww = 4 mg CHA |
| | Veselov | 50 | 2309 | same as above |
| Talling et al. 1973 | Kilotes (Ethiopia) | 334 | 4800 | Data averaged over entire depth |
| | Aranguadi | 1387 | 8400 | same as above |
| Chenard 1980 | Dolly (Canadian Arctic) | 0.3 | 34.3 | same as above |
| Hunding 1979 | Myavatn (Iceland) | 13.2 | 1339 | Summer average |
| Caron 1976 | Meretta (Canada) | 4 | 456 | Summer average |
| Northcote et al. 1985 | Titicaca (Peru) | 3.5 | 792 | |
| Barica 1975 | 885 (Canada) | 283 | 6408 | Maximum values reported |
| Fontaine & Carter Ewel 1981 | Little Lake Conway (Florida, USA) | 5.4 | 1061 | Annual daily mean integrated over depth; CHA calcualated from TP |

| | | | | |
|---|---|---|---|---|
| Grobbelaar & Soeder 1985 | Receway ponds | 5700 | 57744 | CHA calculated from dry weight using dry w:CHA of 75 |
| Ahrens & Peters 1991 | Orford (Quebec, Canada) | 1.6 | 66.5 | Summer mean |
| | Stukely | 2.2 | 93.6 | same as above |
| | Lyster | 1.6 | 156 | same as above |
| | North | 1.6 | 193 | same as above |
| | Baldwin | 2 | 187 | same as above |
| | Central | 1.2 | 295 | same as above |
| | Cerises | 6.3 | 182 | same as above |
| | South | 3.5 | 155 | same as above |
| | Newport | 4.1 | 234 | same as above |
| | Pond | 3.8 | 319 | same as above |
| | Magog | 9 | 408 | same as above |
| | Waterloo | 28.9 | 1286 | same as above |
| Gibson 1975 | Neagh (N. Ireland) | 49.2 | 703 | Annual mean |
| Kamp-Nielsen 1981 | Esrom (Denmark) | 16.8 | 854 | Resp corrected with a $Q_{10} = 2.5$ |
| Jackson 1969 | Onondaga (N.Y., USA) | 167 | 8424 | Summer mean; CHA calculated from dry weight:CHA of 75 |
| Ganf 1974 | George (Uganda) | 288 | 4128 | |
| CSIR 1985 | Hartbeespoort (S. Africa) | 53 | 1344 | Annual average |
| | | 1810 | 49440 | Maximum values |

| | | | | |
|---|---|---|---|---|
| Markager & Sand-Jensen 1989 | Outdoor ponds (Norway) | 325 | 3120 | Average august, september and october |
| Pick 1984 | Jacks (Ontario, Canada) | 5 | 468 | Data integrated over epilimnion |
| Salonen et al. 1983 | Nimeton (Finland) | 2.2 | 173 | Summer average. CHA calculated from 1 g wet weight = 4 mg CHA |
| Alimov & Winberg 1972 | Krivoe (Arctic, USSR) | 0.3 | 39.1 | Data in kcal converted to C using 10 kcal = 1 g C, and C:CHA of 30 |
| Spurr 1975 | Bird Pond (Antarctica) | 1688 | 14040 | Summer average |
| Mitchell & Burns 1979 | Hayes (New Zealand) | 11.6 | 420 | CHA calculated from 1 g wet weight = 4 mg CHA |
| Serruya & Serruya 1972 | Kinneret (Israel) | 35 | 1800 | Annual average |
| | | 280 | 6000 | Maximum values |

# Appendix 3

Raw monthly data used in chapters 3 and 4

Variables are:

TP = total phosphorus ($\mu g\ l^{-1}$)

CHL = chlorophyll a concentration ($\mu g\ l^{-1}$)

DOC = dissolved organic carbon concentration ($mg\ l^{-1}$)

COL = water color (absorbance at 440 nm in a 1 cm cell)

TEMP = water temperature ($^oC$)

RESP = plankton community respiration ($mg\ O_2\ m^{-3}\ d^{-1}$)

ETS = electron transport system activity ($mg\ O_2\ m^{-3}\ d^{-1}$)

PHOT = phytoplankton photosynthesis ($mg\ C\ m^{-3}\ d^{-1}$)

$Z_{int}$ = depth of integration (m)

Month: May 1991

| Lake | TP | CHL | DOC | COL | Temp | RESP | PHOT | ETS | $Z_{int}$ |
|---|---|---|---|---|---|---|---|---|---|
| Nicolet | 6.71 | 0.48 | 3.27 | 0.025 | 10.5 | 271 | 9.7 | - | 9 |
| Bowker | 4.10 | 1.24 | 2.48 | 0.009 | 11.0 | 301 | 19.6 | - | 8 |
| Lyster | 5.67 | 0.78 | 3.62 | 0.022 | 8.4 | 68 | 14.9 | - | 9 |
| Orford | 5.03 | 1.01 | 3.14 | 0.013 | 15.8 | 275 | 31.2 | - | 7 |
| Baldwin | 7.94 | 0.87 | 3.89 | 0.033 | 13.0 | 81 | 10.7 | - | 4 |
| Truite | 6.02 | 2.68 | 4.78 | 0.085 | 17.9 | 217 | 39.4 | - | 6 |
| Brompton | 7.25 | 2.39 | 5.65 | 0.111 | 13.2 | 172 | 28.7 | - | 8 |
| Massawippi | 13.31 | 1.14 | 4.18 | 0.036 | 6.7 | 467 | 24.9 | - | 8 |
| Stukely | 7.45 | 3.44 | 4.90 | 0.046 | 13.5 | 265 | 39.2 | - | 7 |
| Petite Brompton | 9.57 | 1.15 | 5.52 | 0.086 | 14.9 | 231 | 22.1 | - | 6 |
| D'Argent | 11.34 | 1.19 | 4.46 | 0.086 | 15.6 | 161 | 9.4 | - | 5 |
| St. Francoise | 21.25 | 1.73 | 6.78 | 0.177 | 8.1 | 260 | 2.6 | - | 8 |
| Aylmer | 17.85 | 2.87 | 6.64 | 0.210 | 9.6 | 215 | 1.6 | - | 8 |
| Coulombe | 14.10 | 2.17 | 6.96 | 0.169 | 14.8 | 445 | 6.0 | - | 4 |
| Lovering | 20.71 | 4.30 | 6.01 | 0.097 | 11.5 | 170 | 39.6 | - | 7 |
| Central | 19.92 | 3.16 | 4.38 | 0.037 | 8.6 | 403 | 54.5 | - | 9 |
| Brome | 21.70 | 7.67 | 3.82 | 0.031 | 15.0 | 307 | 76.0 | - | 5 |
| Magog | 18.89 | 7.93 | 3.86 | 0.041 | 16.0 | 489 | 88.8 | - | 7 |
| Yamaska | 33.09 | 11.48 | 4.34 | 0.068 | 14.6 | 970 | 177.8 | - | 5 |
| Waterloo | 33.58 | 8.52 | 4.66 | 0.059 | 15.8 | 897 | 172.7 | - | 4 |

Month: June 1991

| Lake | TP | CHL | DOC | COL | Temp | RESP | PHOT | ETS | $Z_{int}$ |
|---|---|---|---|---|---|---|---|---|---|
| Nicolet | 3.88 | 0.63 | 3.58 | 0.026 | 18.2 | 191 | 9.3 | 395 | 7 |
| Bowker | 5.07 | 0.75 | 3.10 | 0.015 | 18.8 | 132 | 7.3 | 580 | 7 |
| Lyster | 5.27 | 0.68 | 3.70 | 0.026 | 17.2 | 189 | 16.5 | 619 | 7 |
| Orford | 5.07 | 0.49 | 3.34 | 0.019 | 19.7 | 120 | 17.0 | 735 | 6 |
| Baldwin | 8.21 | 3.06 | 3.70 | 0.031 | 18.1 | 302 | 34.4 | 1018 | 4 |
| Truite | 10.54 | 3.75 | 5.68 | 0.074 | 21.5 | 400 | 29.5 | 2354 | 4 |
| Brompton | 7.46 | 2.89 | 5.92 | 0.101 | 21.2 | 237 | 15.7 | 1210 | 7 |
| Massawippi | 11.24 | 5.60 | 4.50 | 0.042 | 17.3 | 409 | 62.7 | 1224 | 7 |
| Stukely | 5.12 | 1.60 | 4.03 | 0.046 | 19.9 | 150 | 11.4 | 813 | 7 |
| Petite Brompton | 7.76 | 1.47 | 5.76 | 0.075 | 21.2 | 242 | 18.1 | 1133 | 5 |
| D'Argent | 12.53 | 2.45 | 5.70 | 0.101 | 20.8 | 373 | 41.5 | 1221 | 4 |
| St. Francoise | 11.34 | 1.21 | 7.90 | 0.187 | 16.2 | 228 | 6.1 | 720 | 8 |
| Aylmer | 11.99 | 1.11 | 8.10 | 0.198 | 17.8 | 257 | 6.9 | 778 | 8 |
| Coulombe | 13.48 | 3.34 | 8.11 | 0.191 | 19.2 | 446 | 28.5 | 1006 | 4 |
| Lovering | 13.53 | 5.22 | 5.70 | 0.095 | 18.1 | 393 | 36.6 | 835 | 6 |
| Central | 19.15 | 3.54 | 5.18 | 0.048 | 18.5 | 526 | 42.6 | 2126 | 8 |
| Brome | 15.12 | 4.23 | 4.20 | 0.038 | 20.2 | 402 | 83.7 | 2120 | 5 |
| Magog | 20.79 | 4.12 | 4.98 | 0.039 | 22.0 | 701 | 29.2 | 3821 | 7 |
| Yamaska | 22.08 | 8.29 | 5.60 | 0.068 | 20.5 | 450 | 56.5 | 2189 | 5 |
| Waterloo | 39.49 | 6.75 | 5.35 | 0.069 | 20.7 | 627 | 98.7 | 5395 | 4 |

Month: July 1991

| Lake | TP | CHL | DOC | COL | Temp | RESP | PHOT | ETS | $Z_{int}$ |
|---|---|---|---|---|---|---|---|---|---|
| Nicolet | 6.59 | 0.82 | 2.73 | 0.017 | 22.0 | 143 | 14.6 | 1075 | 7 |
| Bowker | 7.52 | 0.98 | 2.20 | 0.020 | 21.3 | 362 | 11.7 | 1373 | 6 |
| Lyster | 8.12 | 0.87 | 2.93 | 0.016 | 19.3 | 205 | 20.0 | 1209 | 7 |
| Orford | 12.62 | 0.78 | 2.93 | 0.012 | 22.6 | 217 | 25.7 | 1429 | 6 |
| Baldwin | 11.1 | 1.57 | 3.68 | 0.019 | 20.4 | 287 | 44.3 | 1843 | 4 |
| Truite | 9.88 | 1.18 | 4.85 | 0.051 | 23.9 | 240 | 26.0 | 2486 | 4 |
| Brompton | 11.90 | 3.18 | 4.57 | 0.077 | 23.6 | 261 | 15.1 | 2865 | 7 |
| Massawippi | 11.74 | 2.51 | 3.68 | 0.028 | 20.9 | 299 | 49.4 | 1248 | 7 |
| Stukely | 9.93 | 2.79 | 3.66 | 0.035 | 22.6 | 320 | 21.3 | 1143 | 6 |
| Petite Brompton | 10.35 | 1.16 | 4.52 | 0.046 | 23.6 | 317 | 23.0 | 1832 | 5 |
| D'Argent | 13.55 | 3.31 | 4.99 | 0.066 | 23.8 | 358 | 43.2 | 2074 | 4 |
| St. Francoise | 11.23 | 2.01 | 6.75 | 0.161 | 19.5 | 352 | 10.6 | 1080 | 8 |
| Aylmer | 12.95 | 2.72 | 6.61 | 0.167 | 19.9 | 401 | 13.7 | 1325 | 8 |
| Coulombe | 15.22 | 4.28 | 7.59 | 0.155 | 23.7 | 201 | 36.8 | 1686 | 4 |
| Lovering | 11.93 | 3.10 | 5.51 | 0.072 | 21.2 | 292 | 19.1 | 1450 | 7 |
| Central | 12.67 | 1.44 | 3.55 | 0.022 | 22.4 | 362 | 24.8 | 1363 | 8 |
| Brome | 20.74 | 4.84 | 3.35 | 0.028 | 22.2 | 304 | 80.8 | 2776 | 5 |
| Magog | 18.05 | 2.08 | 4.01 | 0.027 | 23.6 | 480 | 56.1 | 3109 | 7 |
| Yamaska | 26.59 | 6.46 | 5.07 | 0.050 | 22.2 | 570 | 47.2 | 5165 | 5 |
| Waterloo | 41.21 | 27.10 | 5.09 | 0.053 | 22.4 | 807 | 264 | 13976 | 4 |

Month: August 1991

| Lake | TP | CHL | DOC | COL | Temp | RESP | PHOT | ETS | $Z_{int}$ |
|---|---|---|---|---|---|---|---|---|---|
| Nicolet | 2.67 | 1.01 | 3.12 | 0.020 | 21.9 | 145 | 16.4 | 1174 | 7 |
| Bowker | 4.89 | 1.10 | 2.47 | 0.013 | 21.2 | 218 | 20.6 | 732 | 7 |
| Lyster | 3.96 | 1.74 | 3.46 | 0.009 | 20.4 | 318 | 31.6 | 1296 | 7 |
| Orford | 5.25 | 1.89 | 3.56 | 0.017 | 22.6 | 322 | 22.4 | 1015 | 6 |
| Baldwin | 6.48 | 1.46 | 3.80 | 0.019 | 20.9 | 221 | 39.6 | 1602 | 4 |
| Truite | 7.87 | 4.76 | 4.78 | 0.061 | 21.8 | 162 | 88.2 | 2592 | 4 |
| Brompton | 14.71 | 2.62 | 4.96 | 0.078 | 22.3 | 246 | 18.4 | 1173 | 7 |
| Massawippi | 7.41 | 2.77 | 4.06 | 0.027 | 22.5 | 266 | 39.6 | 1394 | 7 |
| Stukely | 22.22 | 1.36 | 4.52 | 0.043 | 21.4 | 135 | 16.9 | 1228 | 7 |
| Petite Brompton | 20.77 | 1.40 | 5.11 | 0.054 | 23.0 | 194 | 15.5 | 714 | 5 |
| D'Argent | 11.88 | 2.96 | 5.81 | 0.064 | 23.1 | 261 | 26.9 | 1282 | 4 |
| St. Francoise | 7.56 | 2.51 | 7.1 | 0.147 | 21.2 | 260 | 14.4 | 840 | 8 |
| Aylmer | 8.74 | 2.87 | 7.07 | 0.141 | 21.0 | 392 | 11.9 | 599 | 8 |
| Coulombe | 12.91 | 3.94 | 7.33 | 0.143 | 22.8 | 402 | 43.2 | 1533 | 4 |
| Lovering | 10.60 | 4.82 | 5.96 | 0.067 | 22.3 | 293 | 34.9 | 2496 | 6 |
| Central | 13.12 | 3.47 | 3.52 | 0.026 | 22.5 | 380 | 42.5 | 1324 | 9 |
| Brome | 18.57 | 10.81 | 4.16 | 0.029 | 22.1 | 336 | 197.9 | 3096 | 5 |
| Magog | 48.05 | 13.66 | 4.68 | 0.030 | 21.7 | 563 | 147.4 | 4860 | 7 |
| Yamaska | 34.21 | 15.30 | 5.57 | 0.047 | 22.0 | 705 | 227.3 | 7808 | 5 |
| Waterloo | 68.57 | 106.5 | 6.32 | 0.079 | 21.8 | 1396 | 974.5 | 27256 | 4 |

Month: September 1991

| Lake | TP | CHL | RESP | PHOT | $Z_{int}$ |
|---|---|---|---|---|---|
| Orford | | 2.21 | 190 | 25.1 | 6 |
| Brompton | | 2.14 | 235 | 19.4 | 5 |
| Massawippi | | 6.81 | 214 | 75.6 | 6 |
| Stukely | | 2.50 | 122 | 25.0 | 6 |
| Lovering | | 4.45 | 204 | 29.2 | 6 |
| Central | | 4.2 | 199 | 3402 | 7.5 |
| Magog | | 6.82 | 569 | 76.3 | 5.5 |
| Waterloo | | 9.30 | 622 | 159.6 | 4 |

Month: October 1991

| Lake | TP | CHL | TEMP | RESP | PHOT | $Z_{int}$ |
|---|---|---|---|---|---|---|
| Stukely | 6.94 | 1.81 | 10.1 | 95 | 20.1 | 6.5 |
| Bowker | 9.16 | 1.55 | 11.0 | 35 | 16.5 | 7 |
| Central | 12.45 | 5.72 | 14.5 | 208 | 63.9 | 8 |
| Magog | 21.50 | 4.52 | 11.7 | 234 | 54.2 | 7 |
| Waterloo | 67.84 | 6.86 | 12.1 | 586 | 79.6 | 4 |

# APPENDIX 4

Bacterial biomass data used in Chapter 5. Bacteria were stained with DAPI and counted and measured under epifuorescence at 1250X, following Porter and Feig 1980 (in References, Chapter 5). Bacterial density (in millions per ml) was converted to biomass (in $\mu g\ C\ l^{-1}$) using the mean volume determined for all samples (0.02 $\mu m^3$) and the conversion factor of 354 fg C $\mu m^3$, given by Bjørnsen 1986 (in References, Chapter 5). The data are for May, June, July, August of 1991, and the arithmetic means for the period are also provided.

Bacterial density ($x10^6$ $ml^{-1}$) and biomass ($\mu g$ C $l^{-1}$)

| | May | | June | | July | | August | | Mean | |
|---|---|---|---|---|---|---|---|---|---|---|
| Lake | Density | Biomass | Density | Biomass | Density | Biomass | Density | Biomass0 | Density | Biomass |
| Nicolet | 3.73 | 23.05 | 2.72 | 16.81 | 0.72 | 4.45 | 2.16 | 13.35 | 2.33 | 14.33 |
| Bowker | 2.39 | 14.77 | 3.43 | 21.20 | 0.91 | 5.62 | 3.50 | 21.63 | 2.56 | 15.82 |
| Lyster | 2.39 | 14.77 | 3.62 | 22.37 | 0.49 | 3.02 | 5.68 | 35.10 | 3.04 | 18.79 |
| Orford | 1.85 | 11.43 | 3.40 | 21.01 | 4.45 | 27.50 | 2.55 | 15.76 | 3.06 | 18.91 |
| Baldwin | 3.94 | 24.35 | 3.80 | 23.48 | 4.33 | 26.76 | 3.78 | 23.36 | 3.96 | 24.47 |
| Truite | 3.07 | 18.97 | 3.41 | 21.07 | 3.48 | 21.51 | 2.93 | 18.11 | 3.22 | 19.89 |
| Brompton | 2.79 | 17.24 | 5.33 | 32.94 | 0.64 | 3.95 | 3.38 | 20.89 | 3.03 | 18.72 |
| Massawippi | 2.82 | 17.43 | 3.32 | 20 52 | 3.18 | 19.65 | 2.94 | 18.17 | 3.06 | 18.91 |
| Stukely | 3.57 | 22.06 | 2.84 | 17.55 | 0.96 | 5.93 | 2.87 | 17.74 | 2.56 | 15.82 |
| Petite | 4.11 | 25.40 | 5.64 | 34.85 | 0.48 | 2.97 | 3.58 | 22.12 | 3.45 | 21.32 |
| Brompton | | | | | | | | | | |
| D'Argent | 2.25 | 13.90 | 3.87 | 23.92 | 5.01 | 30.96 | 4.73 | 29.23 | 3.96 | 24.47 |
| St. Francoise | 3.43 | 21.20 | 4.21 | 26.02 | 3.94 | 24.35 | 3.49 | 21.57 | 3.77 | 23.30 |
| Aylmer | 3.33 | 20.58 | 4.52 | 27.94 | 1.01 | 6.24 | 4.09 | 25.28 | 3.24 | 20.02 |
| Coulombe | 2.67 | 16.50 | 4.22 | 26.08 | 1.87 | 11.56 | 3.98 | 24.60 | 3.18 | 19.65 |
| Lovering | 2.44 | 15.08 | 5.76 | 35.60 | 1.43 | 8.84 | 2.79 | 17.24 | 3.10 | 19.16 |
| Central | 6.16 | 38.07 | 4.20 | 25.96 | 6.22 | 38.44 | 10.99 | 67.92 | 6.89 | 45.80 |
| Brome | 6.28 | 38.81 | 4.16 | 25.71 | 2.56 | 15.82 | 5.19 | 32.07 | 4.55 | 28.11 |
| Magog | 5.10 | 31.52 | 3.78 | 23.36 | 4.71 | 29.11 | 6.29 | 38.87 | 4.97 | 30.72 |
| Yamaska | 8.25 | 50.98 | 7.33 | 45.30 | 4.17 | 25.77 | 4.42 | 27.32 | 6.04 | 37.33 |
| Waterloo | 13.30 | 82.19 | 6.78 | 41.90 | 1.47 | 9.08 | 10.10 | 62.42 | 7.91 | 48.88 |

# APPENDIX 6

Macrozooplankton biomass data used in Chapter 5. The following organisms (length > 150 μm) were counted and sized under 150X: Cyclopoids, calanoids, *Daphnia, Bosmina, Holopedium* a, nauplii larvae and rotifers. Length was converted to biomass using the conversion factors in McCauley 1984 (in References, Chapter 5). Biomass data are for May, June, July, August and September, and the arithmetic means for the period are also provided. Biomass is in μg C $l^{-1}$, and total macrozooplankton biomass is the sum of the components mentioned above.

Month: May 1991

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 2.61 | 9.40 | 12.42 | 1.72 | 0 | 0.07 | 0.17 | 26.40 |
| Bowker | 2.64 | 0.82 | 17.51 | 0.17 | 0 | 0.14 | 0.03 | 21.30 |
| Lyster | 1.49 | 2.91 | 0.92 | 0.26 | 0 | 0 | 0.02 | 5.60 |
| Orford | 1.94 | 3.58 | 1.10 | 0 | 0 | 0.03 | 0.29 | 6.93 |
| Baldwin | 1.92 | 1.99 | 0.82 | 0.77 | 1.74 | 0.19 | 0 | 7.43 |
| Truite | 1.94 | 5.79 | 0 | 0.09 | 15.36 | 0.03 | 0.16 | 21.39 |
| Brompton | 3.06 | 1.38 | 8.42 | 0.09 | 0 | 0.07 | 0.15 | 13.17 |
| Massawippi | 2.23 | 0.42 | 4.33 | 0 | 0 | 0 | 0.01 | 6.98 |
| Stukely | 4.12 | 2.44 | 0.72 | 0.11 | 0.24 | 0.07 | 0.69 | 8.41 |
| Petite Brompton | 4.80 | 7.27 | 2.09 | 0 | 0 | 0.06 | 0.43 | 14.65 |
| D'Argent | 3.50 | 9.94 | 0.60 | 0.14 | 0 | 0.06 | 0.025 | 14.28 |
| St. Francoise | 0.05 | 0.36 | 0.18 | 0.41 | 0 | 0.01 | 0.03 | 1.04 |
| Aylmer | 0.06 | 0.42 | 0.21 | 0.29 | 0 | 0.07 | 0.06 | 1.11 |
| Coulombe | 1.78 | 2.98 | 0 | 0.04 | 0.37 | 0.04 | 0.08 | 5.30 |
| Lovering | 2.22 | 7.71 | 2.60 | 2.49 | 0.55 | 0 | 0.36 | 15.94 |
| Central | 6.73 | 2.67 | 0.10 | 0.10 | 0 | 0.05 | 0.25 | 9.91 |
| Brome | 2.05 | 11.51 | 0.29 | 0.34 | 0 | 0.11 | 0.17 | 14.47 |
| Magog | 3.34 | 3.31 | 2.52 | 0.94 | 0 | 0.28 | 0.83 | 11.22 |
| Yamaska | 0.26 | 3.31 | 0.34 | 0.57 | 0.70 | 0.2 | 7.94 | 13.32 |
| Waterloo | 5.38 | 8.85 | 6.71 | 0.76 | 0 | 0.19 | 0.10 | 21.99 |

Month: June 1991

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 0.55 | 0.84 | 14.31 | 1.09 | 3.69 | 0.03 | 0.05 | 20.56 |
| Bowker | 0.11 | 0.40 | 18.37 | 0 | 3.28 | 0.02 | 0.05 | 22.23 |
| Lyster | 1.48 | 1.44 | 11.68 | 0.25 | 0 | 0.03 | 0.30 | 15.19 |
| Orford | 0.82 | 3.01 | 4.55 | 0.16 | 0 | 0.01 | 0.21 | 8.75 |
| Baldwin | 1.97 | 4.25 | 1.48 | 0 | 0 | 0.18 | 0.82 | 8.71 |
| Truite | 0.38 | 2.93 | 2.38 | 0.19 | 0.52 | 0.01 | 0.07 | 6.47 |
| Brompton | 0.93 | 0.05 | 6.13 | 0.84 | 0 | 0.01 | 0.40 | 8.36 |
| Massawippi | 1.46 | 5.92 | 4.67 | 0 | 0 | 0.11 | 0.94 | 13.12 |
| Stukely | 0.44 | 0.70 | 8.94 | 0.13 | 0 | 0.01 | 0.06 | 10.30 |
| Petite Brompton | 0.53 | 0.37 | 2.33 | 0 | 0.85 | 0.01 | 1.03 | 5.11 |
| D'Argent | 5.76 | 9.89 | 9.66 | 2.30 | 0 | 0.26 | 0.20 | 28.07 |
| St. Francoise | 0.70 | 3.89 | 4.58 | 0.97 | 0.36 | 0.07 | 0.18 | 10.76 |
| Aylmer | 0.58 | 3.29 | 6.51 | 1.78 | 0.26 | 0.04 | 0.05 | 12.52 |
| Coulombe | 1.36 | 10.59 | 2.91 | 0.48 | 2.89 | 0 | 0.36 | 18.60 |
| Lovering | 3.78 | 5.17 | 12.55 | 0.30 | 0.28 | 0.14 | 0.10 | 22.32 |
| Central | 1.06 | 1.88 | 19.71 | 1.94 | 1.05 | 0.07 | 0.72 | 26.43 |
| Brome | 0.65 | 4.25 | 1.50 | 0.69 | 0 | 0.15 | 1.59 | 8.82 |
| Magog | 1.69 | 5.84 | 28.64 | 1.78 | 0 | 0.04 | 0.02 | 38.02 |
| Yamaska | 5.18 | 11.62 | 14.56 | 2.27 | 0 | 0.12 | 0 | 33.75 |
| Waterloo | 1.53 | 24.04 | 11.64 | 0.94 | 0 | 0.06 | 0.11 | 38.32 |

Month: July 1991

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 0 | 0 | 0.87 | 0.67 | 0.97 | 0 | 0.97 | 3.49 |
| Bowker | 0 | 0.53 | 8.22 | 0.1 | 0.45 | 0 | 0.08 | 9.38 |
| Lyster | 0.43 | 3.17 | 1.61 | 0.59 | 0.76 | 0.01 | 0.34 | 6.91 |
| Orford | 0.13 | 1.28 | 12.79 | 0.55 | 0 | 0.01 | 0 | 14.75 |
| Baldwin | 0 | 7.71 | 2.21 | 0.25 | 0.80 | 0.04 | 0.27 | 11.28 |
| Truite | 0.30 | 5.02 | 10.84 | 0.76 | 0.29 | 0.03 | 0.15 | 17.39 |
| Brompton | 0.51 | 0.41 | 7.49 | 0.36 | 0 | 0.01 | 0.05 | 8.81 |
| Massawippi | 0.27 | 0 | 1.85 | 0 | 0 | 0.24 | 1.22 | 3.58 |
| Stukely | 0.83 | 1.80 | 9.61 | 0.17 | 0.26 | 0.03 | 0.04 | 12.73 |
| Petite Brompton | 0.23 | 0.51 | 13.93 | 0.18 | 0.46 | 0 | 0.08 | 15.40 |
| D'Argent | 1.65 | 7.67 | 3.24 | 0.46 | 2.92 | 0.03 | 0.11 | 16.07 |
| St. Francoise | 0.90 | 2.28 | 1.84 | 0.26 | 0 | 0.03 | 0.34 | 5.65 |
| Aylmer | 0.83 | 1.67 | 2.18 | 0.26 | 0 | 0.06 | 0.07 | 5.08 |
| Coulombe | 2.45 | 4.24 | 1.05 | 4.10 | 5.71 | 0.07 | 0.42 | 18.05 |
| Lovering | 1.03 | 2.01 | 43.98 | 0.91 | 1.42 | 0.03 | 0.16 | 49.55 |
| Central | 0.34 | 0.64 | 34.97 | 2.83 | 1.45 | 0.02 | 0.19 | 40.43 |
| Brome | 1.49 | 2.35 | 6.75 | 12.95 | 0 | 0.41 | 0.18 | 24.14 |
| Magog | 1.80 | 13.85 | 46.20 | 9.94 | 0 | 0.02 | 0 | 71.81 |
| Yamaska | 2.51 | 15.48 | 11.72 | 3.14 | 0 | 0.06 | 0 | 32.92 |
| Waterloo | 2.39 | 33.52 | 10.14 | 1.69 | 0 | 0.10 | 0.03 | 47.87 |

Month: August 1991

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 0 | 0.21 | 1.65 | 1.30 | 3.69 | 0.01 | 0.17 | 7.03 |
| Bowker | 0.29 | 0.86 | 8.94 | 0.60 | 3.47 | 0.07 | 0.02 | 14.26 |
| Lyster | 0.49 | 8.29 | 5.74 | 2.15 | 0.84 | 0.02 | 0.41 | 17.92 |
| Orford | 0 | 0.20 | 4.11 | 0.39 | 0.06 | 0.01 | 0.01 | 4.78 |
| Baldwin | 1.63 | 4.36 | 10.76 | 0.09 | 0.09 | 0.05 | 0.11 | 17.10 |
| Truite | 0.33 | 4.23 | 3.10 | 1.19 | 1.01 | 0 | 3.75 | 13.62 |
| Brompton | 0.13 | 0.26 | 3.48 | 0.21 | 0.47 | 0 | 0.04 | 4.59 |
| Massawippi | 14.12 | 0.91 | 2.65 | 0.75 | 0 | 0.01 | 0.02 | 18.45 |
| Stukely | 0.46 | 3.01 | 22.11 | 2.05 | 0.55 | 0.03 | 0.69 | 28.90 |
| Petite Brompton | 0.78 | 1.70 | 2.37 | 0.33 | 0.41 | 0.01 | 0.06 | 5.64 |
| D'Argent | 2.43 | 13.28 | 14.46 | 0.60 | 3.37 | 0.03 | 0.06 | 34.23 |
| St. Francoise | 1.48 | 1.40 | 3.65 | 0.20 | 0 | 0.02 | 0.19 | 6.94 |
| Aylmer | 1.59 | 1.42 | 4.01 | 0.19 | 0.29 | 0.03 | 0.19 | 7.72 |
| Coulombe | 1.64 | 6.23 | 1.53 | 0.76 | 2.51 | 0.02 | 0.34 | 13.03 |
| Lovering | 0.97 | 1.06 | 5.76 | 0.38 | 0.24 | 0.02 | 0.17 | 8.60 |
| Central | 3.08 | 4.65 | 13.67 | 0.14 | 0.51 | 0.02 | 0.42 | 22.49 |
| Brome | 5.59 | 3.56 | 33.56 | 0.60 | 0.31 | 0.05 | 0.51 | 44.19 |
| Magog | 2.04 | 8.08 | 63.27 | 1.73 | 0 | 0.02 | 0.07 | 74.61 |
| Yamaska | 2.91 | 4.20 | 16.35 | 1.43 | 0 | 0.07 | 0.07 | 25.03 |
| Waterloo | 11.61 | 39.46 | 13.63 | 10.92 | 0 | 0.02 | 0 | 75.63 |

Month: September 1991

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Bowker | 2.15 | 1.32 | 6.28 | 0.38 | 0.48 | 0.05 | 0.09 | 10.76 |
| Stukely | 0.35 | 1.18 | 17.68 | 1.93 | 1.24 | 0 | 0.04 | 22.43 |
| Central | 1.29 | 1.49 | 0.30 | 0.27 | 0.77 | 0.07 | 0.48 | 4.69 |
| Magog | 5.47 | 9.46 | 4.15 | 4.77 | 0 | 0.05 | 0.18 | 24.09 |
| Waterloo | 10.55 | 19.49 | 24.49 | 18.40 | 0 | 0.14 | 0.18 | 73.25 |

Summer 1991, means

| Lake | Cyclopoids | Calanoids | Daphnids | Bosminids | Holopedium | Nauplii | Rotifers | TOTAL |
|---|---|---|---|---|---|---|---|---|
| Nicolet | 0.79 | 2.61 | 7.31 | 1.19 | 2.09 | 0.03 | 0.34 | 14.36 |
| Bowker | 1.04 | 0.79 | 11.86 | 0.25 | 1.54 | 0.06 | 0.05 | 15.59 |
| Lyster | 0.97 | 3.95 | 4.99 | 0.81 | 0.40 | 0.01 | 0.26 | 11.39 |
| Orford | 0.72 | 2.01 | 5.64 | 0.27 | 0.01 | 0.01 | 0.13 | 8.79 |
| Baldwin | 1.38 | 4.58 | 3.82 | 0.28 | 0.66 | 0.11 | 0.30 | 11.13 |
| Truite | 0.74 | 4.49 | 4.08 | 0.56 | 4.29 | 0.02 | 1.03 | 15.21 |
| Brompton | 1.16 | 0.52 | 6.38 | 0.37 | 0.12 | 0.02 | 0.16 | 8.73 |
| Massawippi | 4.52 | 1.81 | 3.37 | 0.19 | 0 | 0.09 | 0.55 | 10.53 |
| Stukely | 0.58 | 1.83 | 11.81 | 0.89 | 0.46 | 0.03 | 0.30 | 15.90 |
| Petite Brompton | 1.58 | 2.46 | 5.18 | 0.13 | 0.43 | 0.02 | 0.40 | 10.20 |
| D'Argent | 3.33 | 10.19 | 6.99 | 0.87 | 1.57 | 0.09 | 0.10 | 23.14 |
| St. Francoise | 0.78 | 1.98 | 2.56 | 0.46 | 0.09 | 0.03 | 0.18 | 6.08 |
| Aylmer | 0.76 | 1.70 | 3.23 | 0.63 | 0.14 | 0.05 | 0.11 | 6.62 |
| Coulombe | 1.81 | 6.01 | 1.37 | 1.34 | 2.87 | 0.03 | 0.30 | 13.73 |
| Lovering | 2.01 | 3.99 | 16.22 | 1.02 | 0.62 | 0.05 | 0.20 | 24.11 |
| Central | 2.50 | 2.27 | 13.75 | 1.06 | 0.76 | 0.05 | 0.41 | 20.80 |
| Brome | 2.44 | 5.42 | 10.52 | 3.64 | 0.08 | 0.18 | 0.61 | 22.89 |
| Magog | 2.87 | 8.11 | 28.99 | 3.83 | 0 | 0.08 | 0.25 | 44.13 |
| Yamaska | 2.71 | 8.65 | 10.74 | 1.85 | 0.17 | 0.11 | 2.01 | 26.24 |
| Waterloo | 6.29 | 25.07 | 13.32 | 6.54 | 0 | 0.10 | 0.08 | 51.40 |