

THERMODYNAMIC RELATIONSHIPS BETWEEN TROPHIC LEVELS IN
A SMALL LACUSTRINE ECOSYSTEM IN THE CANADIAN ARCTIC

by

PETER VANRIEL

A thesis
presented to the University of Manitoba
in fulfillment of the
thesis requirement for the degree of
MASTER OF SCIENCE
in
DEPARTMENT OF ZOOLOGY

Winnipeg, Manitoba

(c) PETER VANRIEL, 1989



National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-51659-3

THERMODYNAMIC RELATIONSHIPS BETWEEN TROPHIC LEVELS IN
A SMALL LACUSTRINE ECOSYSTEM IN THE CANADIAN ARCTIC

BY

PETER VANRIEL

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

© 1989

Permission has been granted to the LIBRARY OF THE UNIVER-
SITY OF MANITOBA to lend or sell copies of this thesis, to
the NATIONAL LIBRARY OF CANADA to microfilm this
thesis and to lend or sell copies of the film, and UNIVERSITY
MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the
thesis nor extensive extracts from it may be printed or other-
wise reproduced without the author's written permission.

I hereby declare that I am the sole author of this thesis.

I authorize the University of Manitoba to lend this thesis to other institutions or individuals for the purpose of scholarly research.

Peter Vanriel

PETER VANRIEL

I further authorize the University of Manitoba to reproduce this thesis by photocopying or by other means, in total or in part, at the request of other institutions or individuals for the purpose of scholarly research.

Peter Vanriel

PETER VANRIEL

The University of Manitoba requires the signatures of all persons using or photocopying this thesis. Please sign below, and give address and date.

ABSTRACT

Vanriél, P. 1989. Thermodynamic relationships between trophic levels in a small lacustrine ecosystem in the Canadian Arctic.

Theory indicates that within an ecosystem energy density (energy per unit biomass) increases with ascending trophic levels. This appears to be one of the requirements for ecosystem stability; others are increase in life span and increase in size. Together these factors increase "action" (energy density $\times$ biomass $\times$ time). Stability is most apparent in autonomous ecosystems. The present investigation was designed to test the thesis that the steady state or climax represents a condition of minimum energy dissipation (least value of the P/B ratio); to attain this condition energy density increases along the food chain. It was postulated that a highly autonomous ecosystem should display such an increase. For this reason Keyhole Lake, Victoria Island, N.W.T., was selected as the study site. Samples of benthic bacteria and detritus, benthic algae, phytoplankton, benthic invertebrates, zooplankton, and Arctic charr (Salvelinus alpinus) were collected for

energy density determination. Stratified random sampling was selected for biomass estimation of most trophic levels. Arctic charr were captured mainly with multi-mesh gillnets; biomass was estimated by decline in catch per unit of effort. Physical and chemical limnological surveys were conducted. Energy density was determined using microbomb calorimetry on all trophic levels. Taxa within trophic levels were treated individually where separation was possible. Ages of Arctic charr were determined from otoliths. Total energy contained in each trophic level or taxon was calculated. The results verify the hypothesis: energy density increases with each succeeding link along the food chain. It appears that energy density is a major determinant of the direction of energy flow in an ecosystem. Trophic level pyramids of energy density and biomass displayed an inverse relationship. Obscure relationships were disclosed: energy densities of the links along the food chain were highly correlated with the logarithm of biomass and biomass energy. The Arctic charr population recovered in a well-damped manner after a severe depletion. Illumination of the role of energy density contributes to a unified theory of energy relations in ecosystems. These findings support a theory of ecosystem structure and behaviour based on thermodynamic principles.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ix
LIST OF TABLES	xiii
LIST OF FIGURES	xv
INTRODUCTION	1
Study objectives	2
Thermodynamics of ecosystems	3
STUDY AREA	22
Rationale for selecting a study site	22
General description of the area	25
Limnology	32
Morphometry	32
Bottom sediments	33
Ice cover	33
Lake level	34
Precipitation	34
Temperatures	35
Water transparency	38
Water chemistry	40
Lake classification	40
MATERIALS AND METHODS	44
Field work	44
Sampling location selection for biomass estimation	44
Sampling methodology for trophic levels and communities	48
Benthic bacteria and detritus	48
Benthos	49
Phytoplankton, other microseston, and chlorophyll	51
Zooplankton	53
Arctic charr	54
Taxa Identification	57

	Page
Laboratory analysis	59
Biomass analysis	59
Benthic bacteria and detritus	59
Benthos	61
Phytoplankton, other microseston, and chlorophyll	62
Zooplankton	65
Dehydration temperatures	68
Effects of preserving methods on sample weight	69
Calorimetry	70
Benthic bacteria and detritus	74
Benthos	74
Phytoplankton and other microseston	75
Zooplankton	76
Arctic charr	76
Aging technique of Arctic charr	78
Mathematical and statistical treatment of data	79
Biomass estimation	79
Benthic bacteria and detritus, benthos, and zooplankton	79
Phytoplankton, other microseston, and chlorophyll	82
Arctic charr	84
Energy density estimation	90
Biomass energy estimation	94
RESULTS	96
Energy density	96
Comparison between trophic levels	99
Comparison between taxa within and among trophic levels	116
Changes in individual trophic levels over time ..	125
Changes in individual taxa over time	125
Miscellaneous energy density comparisons	128
Arctic charr	135
Population structure	135
Age structure	151
Food class frequency	159
Biomass	159
Estimates of trophic levels and taxa	159
Changes over time	178
Depth distribution of benthic organisms	183
Chlorophyll content	192
Biomass energy	201
Estimates of trophic levels and taxa	201
Changes over time	209
Miscellaneous comparisons	219
Inverse logarithmic relationships	219
Comprehensive trophic level comparisons	224

	Page
DISCUSSION	225
Characteristics of trophic levels and associated taxa	225
Decomposers	225
Primary producers	226
Benthic algae	227
Phytoplankton and other microseston	228
Consumers	229
Benthic invertebrates	229
Zooplankton	232
Arctic charr	234
The trophic system	243
Energy density and ecosystem stability	251
Epilogue	255
NOTE	258
REFERENCES	260
PERSONAL COMMUNICATIONS	303
APPENDIX A. Morphometric formulae and data	304
APPENDIX B. Temperatures—materials and methods, and data	313
APPENDIX C. Water transparency—materials and methods, formulae, and data	321
APPENDIX D. Water chemistry—materials and methods, and discussion	328
APPENDIX E. Taxa identification	341
APPENDIX F. Application of the Leslie-DeLury method of population estimation to the Arctic charr fishery of Keyhole Lake	351
APPENDIX G. Comparison of energy density between different preserving methods	356
APPENDIX H. Biomass estimates of trophic levels and taxa within trophic levels in Keyhole Lake in wet weight, numerical estimates of benthic invertebrates, and wet to dry weight conversion factors	359
APPENDIX I. Comprehensive trophic level comparisons ..	368

ACKNOWLEDGEMENTS

I am extremely grateful to my supervisor, Dr. Lionel Johnson of the Freshwater Institute, Department of Fisheries and Oceans, Winnipeg. He devoted much time to numerous productive discussions and opened my eyes to underlying ecological processes. His invaluable contribution to this study permitted it to develop beyond its incipient stage. Furthermore, Dr. Johnson's presence in the field was a great asset; his Arctic expertise and hard work significantly contributed to the smooth operation and profitability of the three field seasons. His congeniality made the field seasons most enjoyable.

Dr. A.W. Mansfield, Director of the Arctic Biological Station, Department of Fisheries and Oceans, Ste. Anne de Bellevue, Peter Heinermann and Jean-Pierre Parent, both of the Department of Biological Sciences, University of Montreal, Bonnie Burns, and Renée Sauvé provided valuable contributions to the 1985 field season. Brian Levia and Terry Krenz assisted during the 1986 field season. Jean-Pierre Parent and Valérie Bolliet, also of the Department of Biological Sciences, University of Montreal, were a great asset in the 1988 field season. These people

worked long hours, frequently under harsh climatic conditions, sampling the Arctic charr population. I would like to express my sincere thanks to them.

I also thank Peter Heinermann for his permission to use some of the light quanta data that he collected at Keyhole Lake in 1985.

I thank Eric Gyselman of the Freshwater Institute for his help in organizing the field seasons. Gordon McRae assisted in the shipping of supplies. Terry Krenz helped with some of the laboratory work; he sorted most of the benthos samples and read the aging material. For their many contributions I would like to express my sincere appreciation.

I am greatly indebted to Dr. F.J. Ward of the Department of Zoology, University of Manitoba, for his generosity in permitting me to use his microbomb calorimeter and laboratory facilities. I further thank Dr. Ward for reading my research proposal and his valuable comments.

During the planning stage of this study Dr. H. Halvorson of the Department of Microbiology, University of Manitoba, provided valuable suggestions on the microbial component, Dr. W. Warwick, before he left the Freshwater Institute, provided important information on lake sediments, Dr. R.E. Crawford of the Freshwater Institute commented on lake sampling, and Alex Salki, also of the Freshwater

Institute, gave valuable comments on distribution, collecting, preservation, and analysis of zooplankton. I thank them for sharing their knowledge with me.

Dr. B.J. Hann of the Department of Zoology, University of Manitoba, identified the zooplankton, Dr. G.G.C. Robinson of the Department of Botany, University of Manitoba, identified the benthic algae and mosses, Hedi Kling of the Freshwater Institute identified the phytoplankton and protozoa, Donna Giberson, also of the Freshwater Institute, identified the caddisfly larvae. Dr. Robinson and Hedi Kling provided valuable information on distribution, collecting, preservation, and analysis of phytoplankton. I thank them for their contributions.

I thank Mike Stainton, Ron Schade, and other staff members of the Analytical Chemistry Unit at the Freshwater Institute for analysing the many water samples. I further thank Mike Stainton for permitting me to use some of the Analytical Chemistry Unit's laboratory equipment. He also provided many valuable comments on water chemistry.

I especially thank Linda Neden, consultant of the Statistical Advisory Service, University of Manitoba, for her valuable suggestions on statistical procedures and the formulation of many computer programs. She spent innumerable hours, frequently beyond her regular working hours, solving problems for the present study. Her contribution to this study is invaluable.

I express my gratitude to Dr. G.C. Tabisz of the Department of Physics, University of Manitoba, for broadening my understanding of the physics of "action." I thank Andries Blouw of the Freshwater Institute for allowing me to use the graphics computer and sharing his expertise in graphics.

I am deeply indebted to my fiancée, Debbie Hawrysh, for sacrificing uncountable hours; she entered thousands of data sets into the computer, helped with tedious calculations, and typed the manuscript. I am extremely grateful to my parents and Debbie for their patience, understanding, and continuous support throughout this study.

I thank the Freshwater Institute for financial support.

LIST OF TABLES

	Page
Table 1. Summary of chemical analyses of Keyhole Lake water for 1985 and 1986. Means of all samples collected during each field season (95% confidence intervals).....	41
Table 2. Energy density estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $J \cdot g^{-1}$ dry weight unless noted otherwise (95% confidence intervals).....	97
Table 3. Analysis of variance of energy density estimates among trophic levels and taxa within trophic levels. Dry weight energy density comparisons and one-way ANOVA unless noted otherwise.....	100
Table 4. Sex frequency distribution of Arctic charr from Keyhole Lake captured in 1985 and 1986. Percent of male Arctic charr are indicated. Chi-square (X^2) values under the hypothesis of an equal sex ratio.....	147
Table 5. Numbers and weights of Arctic charr removed from Keyhole Lake during the 1985-86 fishery, and estimates of numbers and weights of the total population prior to the 1985 fishery. Upper and lower 95% confidence estimates are represented by $\bar{N}_T$, $\bar{W}_T$ and $\underline{N}_T$, $\underline{W}_T$, respectively.....	149

Table 6.	Biomass estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $\text{kg}\cdot\text{lake}^{-1}$ dry weight unless noted otherwise (95% confidence intervals).....	167
Table 7.	Biomass energy estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $\text{kJ}\cdot\text{lake}^{-1}$ (95% confidence intervals).....	202

LIST OF FIGURES

	Page
Figure 1. Forces acting within ecosystems. Entropy production (S) decreases with ascending trophic levels. Ecosystems over short time periods ("ecological time"), species, and trophic levels tend to assume a state of most action. Biological temperature, which is equivalent to the biomass accumulation ratio (B/P), increases along the food chain. Energy flows (is "pumped") from species of low biological temperature (or low B/P) to species of high biological temperature (or high B/P) (after Johnson in press b).....	16
Figure 2. Map of the Canadian Arctic showing the location of Keyhole Lake.....	26
Figure 3. Bathymetric map of Keyhole Lake. Depth indicated in meters (after Johnson 1983)...	28
Figure 4. Diagram of sedimentation apparatus employed in zooplankton biomass determination.....	66
Figure 5. Energy density estimates of trophic levels during Period I, 1985 (phytoplankton and other microseston during Period I, 1986) (95% confidence intervals).....	106
Figure 6. Energy density estimates of trophic levels during Period II, 1985 (phytoplankton and other microseston during Period II, 1986) (95% confidence intervals).....	108

	Page
Figure 7. Energy density estimates of trophic levels during Period III, 1985 (phytoplankton and other microseston during Period III, 1986) (95% confidence intervals).....	110
Figure 8. Energy density estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).....	112
Figure 9. Energy density estimates of trophic levels along the main food chain representing the means of Periods I, II, and III, 1985 (95% confidence intervals).....	114
Figure 10. Energy density estimates of trophic levels and taxa within trophic levels during Period I, 1985 (phytoplankton and other microseston during Period I, 1986) (95% confidence intervals).....	117
Figure 11. Energy density estimates of trophic levels and taxa within trophic levels during Period II, 1985 (phytoplankton and other microseston during Period II, 1986) (95% confidence intervals).....	119
Figure 12. Energy density estimates of trophic levels and taxa within trophic levels during Period III, 1985 (phytoplankton and other microseston during Period III, 1986) (95% confidence intervals).....	121
Figure 13. Energy density estimates of trophic levels and taxa within trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).....	123

	Page
Figure 14. Energy density changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston in 1986) (95% confidence intervals).....	126
Figure 15. Energy density changes of taxa within trophic levels during the three sampling periods in 1985 (95% confidence intervals).....	129
Figure 16. Energy density comparisons between soft tissue of clams and clams with shells in 1985 (95% confidence intervals).....	131
Figure 17. Energy density comparisons between the larval and pupal stages of chironomids and caddisflies in 1985 (95% confidence intervals except for caddisfly larvae since n = 1).....	133
Figure 18. Length-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1962; (B) 1963; (C) 1965; (D) 1975 (A, B, C after Johnson (1983) compiled from data collected by Hunter (1970); D after Johnson 1976)....	136
Figure 19. Length-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1980 (after Johnson 1983); (B) 1985; (C) 1986; (D) 1985 and 1986 combined.....	138
Figure 20. Estimated length-frequency distribution of the total estimated Arctic charr population in Keyhole Lake prior to the 1985 fishery (top).....	141
Figure 21. Length-frequency distribution of Arctic charr captured in 1988 from Keyhole Lake (bottom, left).....	141

	Page
Figure 22. Length-frequency distribution of Arctic charr captured by electrofishing in 1985 from Keyhole Lake (bottom, right).....	141
Figure 23. Length-frequency distribution by sex of Arctic charr captured in Keyhole Lake; (A) 1985, males; (B) 1985, females; (C) 1986, males; (D) 1986, females.....	144
Figure 24. Age-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1962; (B) 1963; (C) 1965; (D) 1975 (A, B, C after Hunter 1970; D after Johnson 1976).....	152
Figure 25. Age-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1980 (after Johnson 1983); (B) 1985; (C) 1986; (D) 1985 and 1986 combined (ages obtained in the 1986 fishery were reduced by 1 year to approximate 1985 ages).....	154
Figure 26. Age-frequency distribution by sex of Arctic charr captured in Keyhole Lake; (A) 1985, males; (B) 1985, females; (C) 1986, males; (D) 1986 females.....	157
Figure 27. Age-length frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1985; (B) 1986. Frequency is given at age-length intersections.....	160
Figure 28. Frequency of food item incidence in Arctic charr stomachs examined (n = 503) during the 1985-86 Keyhole Lake fishery.....	162
Figure 29. Percentage frequency of food item incidence in stomachs examined (n = 503) in three length ranges of Arctic charr during the 1985-86 Keyhole Lake fishery.....	164

	Page
Figure 30. Biomass estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).....	170
Figure 31. Biomass estimates of taxa comprising benthic algae representing the means of Periods I, II, and III, 1985 (95% confidence intervals).....	172
Figure 32. Biomass estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals). Broken bar represents soft tissue of clams.....	174
Figure 33. Biomass estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals). Clams with shells are excluded.....	176
Figure 34. Biomass changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals)....	179
Figure 35. Biomass changes of taxa comprising benthic algae during the three sampling periods in 1985 (95% confidence intervals).....	181
Figure 36. Biomass changes of taxa comprising benthic invertebrates during the three sampling periods in 1985 (95% confidence intervals).....	184

- Figure 37. Distribution of benthic algae biomass at various depth ranges in 1985 (95% confidence intervals); (A) distribution during Periods I, II, and III; (B) means of Periods I, II, and III..... 186
- Figure 38. Distribution of biomass of taxa within benthic algae at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) globose blue-green algae; (B) filamentous algae..... 188
- Figure 39. Distribution of benthic invertebrate biomass at various depth ranges in 1985 (95% confidence intervals); (A) distribution during Periods I, II, and III; (B) means of Periods I, II, and III... 190
- Figure 40. Distribution of chironomid biomass at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) larvae; (B) pupae..... 193
- Figure 41. Distribution of biomass of taxa within benthic invertebrates at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) Gammarus lacustris; (B) clams..... 195
- Figure 42. Distribution of biomass of taxa within benthic invertebrates at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) caddisfly larvae and pupae; (B) oligochaetes..... 197

	Page
Figure 43. Distribution of free-living nematode biomass at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals) (top).....	199
Figure 44. Chlorophyll- α content of Keyhole Lake water per sampling period (95% confidence intervals) (bottom).....	199
Figure 45. Biomass energy estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).....	205
Figure 46. Biomass energy estimates of taxa comprising benthic algae representing the means of Periods I, II, and III, 1985 (95% confidence intervals).....	207
Figure 47. Biomass energy estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals).....	210
Figure 48. Biomass energy changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston in 1986) (95% confidence intervals).....	212
Figure 49. Biomass energy changes of taxa comprising benthic algae during the three sampling periods in 1985 (95% confidence intervals).....	215

Figure 50.	Biomass energy changes of taxa comprising benthic invertebrates during the three sampling periods in 1985 (95% confidence intervals).....	217
Figure 51.	Relationship between energy density and the common logarithm of biomass of the main food chain in Keyhole Lake.....	220
Figure 52.	Relationship between energy density and the common logarithm of biomass energy of the main food chain in Keyhole Lake.....	222
Figure 53.	Energy and mass flow of the trophic system in Keyhole Lake. Trophic level locations on the Y axis were determined from energy density values representing the means of Periods I, II, and III, 1985 (phytoplankton/microseston during 1986)....	247
Figure 54.	Eltonian Pyramids of energy density, biomass, and biomass energy of the main food chain in Keyhole Lake. Values represent the means of Periods I, II, and III, 1985. Weight of clamshells is excluded from the biomass of benthic invertebrates. Bars are not drawn to scale.....	249

INTRODUCTION

Understanding the fundamental principles governing biological systems is a prerequisite for both theoretical biology and natural resource management. Traditionally, ecosystems are viewed as collections of determinate processes (Hirata and Ulanowicz 1986). Until recently little effort was allocated to determining the fundamental thermodynamic principles governing biological systems. But over the last 24 years apparent correspondences between biological systems and laws of thermodynamics have stimulated the formation of a number of theories (e.g. Trincher 1965; Woolhouse 1967; Wilson 1968; Gladyshev 1978, 1982; Wicken 1979, 1980, 1981, 1983, 1985, 1986, 1988; Gladyshev et al. 1980; Ulanowicz 1980; Feistel and Ebeling 1981; Johnson 1981, 1983, 1988, in press a, b; Gladyshev and Ershov 1982; Wiley and Brooks 1982, 1983; Brooks et al. 1988; Harrison 1988; Schneider 1988; Wiley 1988).

Theory indicates that within a closed ecosystem energy flows from species of low energy density to species of high energy density. This hypothesis was proposed by Ulanowicz (1972), and May (1973), and further developed by Hirata and Fukao (1977), Hirata (1980), and Hirata and

Ulanowicz (1986). They concluded that energy density (which can be expressed as energy per unit biomass or caloric content) must increase with succeeding links along the food chain if the system is to achieve stability.

It is postulated that the dominant species in an autonomous ecosystem seeks a steady state of least energy dissipation. This is manifest by a high degree of stability after the cessation of a perturbation (Johnson 1981, 1983, 1987, 1988, in press a, b).

STUDY OBJECTIVES

The present investigation was designed to test the hypothesis that energy density increases with ascending trophic level within an autonomous ecosystem and to determine the energy relationships between trophic levels. Thermodynamic relationships between the trophic levels were investigated as expressed in the Eltonian Pyramid (Elton 1927). The state of the system was examined following the severe depletion of the dominant species (landlocked Arctic charr, Salvelinus alpinus) in the early 1960's.

Testing was performed by collecting samples of representative organisms of the various trophic levels in the ecosystem and determining the energy density of each. Energy density was determined by microbomb calorimetry. Keyhole Lake, located in Victoria Island, Northwest Territories, was the ecosystem selected. Biomass estimates

for most trophic levels were obtained by stratified random sampling (Crisp 1971; Slack et al. 1973; Elliott 1977). Arctic charr biomass was estimated with multi-mesh gillnets by determining the decline in catch per unit of effort (Leslie and Davies 1939; DeLury 1947, 1951). The stability of the Arctic charr population was primarily assessed by comparing both length-frequency and age-frequency distributions to previous studies at Keyhole Lake (Hunter 1970; Johnson 1976, 1983).

THERMODYNAMICS OF ECOSYSTEMS

Stability concepts of dissipative thermodynamic systems were pioneered by Glansdorff and Prigogine (1971), Prigogine and Nicolis (1971), Prigogine et al. (1972), Prigogine (1973, 1978, 1980), Nicolis and Prigogine (1977), Prigogine and Stengers (1984), and further stimulated by Soodak and Iberall (1978). Johnson (1981, 1983) expanded these concepts to include ecosystems and recently further developed ecosystem stability concepts (1988, in press a, b).

Johnson (in press b) connected the thermodynamics of biological and physical systems as follows:

Beginning with the general properties of ecological systems, an attempt is made to bring biological phenomena into a unified field with physics, chemistry and thermodynamics. The primary thesis is that biological phenomena represent amplification of events occurring at the sub-atomic level, below the threshold of Newtonian physics. It is postulated that a periodic energy input from the sun induces resonance in certain

cyclic activities occurring spontaneously in the vicinity of thermodynamic equilibrium. Electrons in sensitive atoms, are caused to remain for an extended period at higher energy levels, during which time the atoms are more reactive. Energy input from the sun thus stimulates a gradual increase in time-delay, and greater complexity, before the atom returns to the ground state. This trend to energy accumulation in resonant cyclic activities, is counteracted by the system trend to more rapid dissipation as demanded by the general physical principle of Least Action. Organisms therefore originate at the point of intersection of cyclic (energy storing, or reversible) flows, and countervailing, rectilinear (energy dissipative, or irreversible) flows. For continuity, the trend to increasing time-delay must dominate the system behaviour in the short-term, but the principle of least action dominates system behaviour in the longer-term. Out of this antagonism develops hierarchical organization in the short-term and the changes recognized as "evolution" over the long-term. The fundamental physical process involved is the conflict between the tendency of energy to become uniformly distributed within an open but bounded system, and the energy gradient essential to maintenance of the energy flow.

The biosystem (or biological world as a whole) can be considered a closed system functioning within the biosphere boundaries; energy but not biomatter is exchanged with the universe. A whole biosystem is analogous to a communications network that identifies environmental signals. Ecosystems, sub-systems of the biosystem, are partially open systems: both energy and biomatter are exchanged with the rest of the biosystem. The degree of exchange is a function of the autonomy of the ecosystem; highly autonomous ecosystems exchange relatively little energy and biomatter. Whether a biological system is considered "closed" or "open" is simply a matter of scale.

An isolated system, the basic reference system in thermodynamics, in contrast, does not exchange either energy or matter with the external environment (Johnson 1981, 1988, in press b).

In this context entropy is defined as a measure of "disorder" of a system. Johnson (in press b) elucidated disorder by defining it as a measure of the distribution of energy within a system. The more uniform the distribution of energy the greater the entropy. Conversely, a decline in entropy is equivalent to a more orderly energy distribution. These distributions are independent of the system's total energy.

In its statistical interpretation an increase in entropy is equivalent to an increase in the number of microscopic complexions (Johnson in press b). It is theorized that macroscopic ecological and evolutionary properties are an amplification of physical processes occurring at the microscopic level (Johnson 1988, in press a, b).

Principles of energy flow in ecosystems have been formulated by Johnson (in press a, b). He stated that these principles apply only under specific conditions compared to the more general laws of thermodynamics. They are additive to the laws of thermodynamics and function in a time-dependent mode. The principles apply only to a closed

system. The system must contain specific response materials and can operate only over a specific range of energy values.

Johnson (in press b) explains the principles governing energy flow in ecosystems as follows:

1. The Principle of Least Action

Over long time periods ("evolutionary time") the system created by short-term energy inputs is unstable. Stored free energy dissipates at an accelerating rate with a concomitant increase of power. This results in the identification of an increased number of signals. Increases in complexions or species diversity is due to the augmentation in signal identification and coding. This principle is hegemonic over long time periods.

Johnson (in press b) exemplified the role of least action in an autonomous ecosystem with the following analogy:

Energy enters as sunlight . . . , and is dissipated as heat As species assemble within the system, the main energy flow, as represented by the major species' biomass exists along the path of least action . . . , but other species of higher energy content explore the environment to the full extent possible. This provides an explanation for the main energy pathway, or food-chain through a simple, highly constrained system, but allows also for more intricate energy configurations, or food-webs, in which a network of interrelationships develop, exploring the environment to the limits.

In biological systems the principle of least action increases the internal work done by accelerating the energy flow.

2. The Principle of Most Action

Within a closed system, near thermodynamic equilibrium a periodic input of energy may be temporarily stored by the resonant amplification of spontaneously occurring cyclic activity. Resonance is energy storage through the continual exchange of energy in the potential form with energy in the kinetic form (e.g. a pendulum operated by a clockwork mechanism). Interference between cyclic flows (free energy storing) and rectilinear flows (energy dissipating), results in the system assuming a state of most action (least energy dissipation). The sum of instantaneous energies (energy density times biomass) over a specific time period is equivalent to "action." This principle is antagonistic to the principle of least action and over short time periods ("ecological time") governs the behaviour of the system.

Ecosystems over short time periods, species, and trophic levels proceed to a state of least energy dissipation. This is equivalent to most action or the "least value" of the Production/Biomass (P/B) ratio (Margalef 1968; Odum 1969).

A state of least work and least energy dissipation is promoted by the principle of most action in biological systems. This is accomplished by decelerating the energy flow.

3. The Physics of Action

Action is the sum of the difference in kinetic and potential energies at each point in the path (or trajectory) of a particle in a system integrated over time (Watson 1986). Fundamental action can be expressed by Planck's constant in $\text{J}\cdot\text{sec}^{-1}$; this constant is equivalent to "quantum of action" (Johnson pers. comm.). Action consists of energy times time and can be denoted as follows:

$$\begin{aligned} &\text{Action (in J}\cdot\text{sec}^{-1}\text{)} \\ &= \int_{t_0}^{t_1} (\text{KE} - \text{PE}) \, dt, \end{aligned} \quad (1)$$

where KE = kinetic energy, PE = potential energy, and t = time (Feynman 1963).

The foundation for the principle of least action was established by de Fermat in the

seventeenth century and further developed by de Maupertuis during the eighteenth century. Euler and Lagrange, towards the end of the eighteenth century, placed the principle into a proper mathematical form (Watson 1986). This principle is equivalent to an increase in entropy production (or increased energy dissipation) of a system (Johnson in press b).

The principle of least action can be described by Hamilton's principle (Feynman 1963):

$$\delta \int_{t_0}^{t_1} (T - V) dt = 0, \quad (2)$$

where δ = very small changes in alternative paths (Tabisz pers. comm.), T = total kinetic energy, V = total potential energy, and $T - V$ = kinetic potential or the Lagrangian (Page 1958; Pitt 1983). The dynamical (or true) path and alternative paths have the same termini and are described in the same time, thus $dt=0$ (Page 1958). Energy density, depending on the system, can be equivalent to kinetic potential or the Lagrangian (Watson 1986).

Conversely, the principle of most action, developed by Johnson (in press b), is equivalent to minimum entropy production. In ecosystems this principle corresponds to a trend of least energy dissipation. Most action ensures that the greatest energy content in the biomass is maintained over the longest possible time period. This is reflected by the following increases along the food chain: energy density, life span, and size. Action, when applied to biological systems, can be expressed as follows:

Biological Action (in $\text{J} \cdot \text{sec}^{-1}$)

$$= \int_{t_0}^{t_1} (E\rho) (b), \quad (3)$$

where $E\rho$ = energy density of biomass, and b = biomass.

Since energy density is a component of biological action, an increase in energy density per unit biomass can be expected along ascending trophic levels of ecosystems—which are perpetually governed by the principle of most action (Johnson in press b).

The action principles appear to be dynamic counterparts to the laws of thermodynamics. The first law of thermodynamics states that energy is conserved and can neither be created or destroyed. The principle of most action states that free energy may be temporarily stored. A state of least dissipation is equivalent to maximum conservation (Johnson in press b).

The second law of thermodynamics states that an isolated system assumes a state of maximum entropy at thermodynamic equilibrium. The principle of least action forces a system towards a state of greatest entropy production (Johnson in press b).

4. Property of Most Action

Homeokinesis is a physical principle that promotes equal energy distribution among interacting, charged entities (Soodak and Iberall 1978). These entities may range from simple molecules to , as in this context, complex organisms. Homeokinesis, as explained by Johnson (in press b), ensures that "near-uniform entities become more uniform through internal work done in processing information from collisional inputs, and adjusting internal energy levels." Homeokinesis and uniform interaction promotes least dissipation.

The most significant feature biologically of homeokinesis is size distribution: if the dominant species of an ecosystem is of genetically indeterminate size, homeokinesis promotes uniform size distribution of the population members (Johnson 1983, in press b).

5. Onsager's Reciprocal Relations and Most Action

Interference between two energy transport processes (e.g. diffusion and conduction) near thermodynamic equilibrium causes a system to proceed to a state of least energy dissipation (Onsager 1931). Johnson (in press b) noted that the biosystem assumes a state of most action, however, existing far from thermodynamic equilibrium. He resolves this anomaly by assuming that the biosystem developed near thermodynamic equilibrium through the interference between cyclic flows and rectilinear flows. Reversible processes were amplified over an extremely long time period and the system slowly evolved away from thermodynamic equilibrium. This was possible because of the infinitesimally small energy forces operating at the sub-atomic level which are independent of Newtonian physics. These minuscule forces appear to refute the law of conservation of energy for very short time periods and are the foundation for the energy-time uncertainty relation

of quantum physics (Davies 1980). It is thus postulated that biological systems are magnifications of events in the quantum domain.

6. The Principle of Information Coding

Equipotentiality (= least entropy production) is a requirement for information coding among symbols. Individual cyclic events form uniformly charged entities. Symmetrical interaction between these entities equipartition available energy through homeokinesis. A group of symmetrically interacting entities functions as a tabula rasa for the coding of information (environmental signals). Coding of signals results in obligatory asymmetries which require an increase in energy flow.

Johnson (in press b) stated that:

An ecosystem may thus be regarded as a communications network encoding and transmitting environmental information. . . . The biosystem, within the biosphere boundaries, responding to the environment, gradually explores and dissects the total array of signals at each locality, under the influence of a long-term trend toward increasing energy flux [least action].

7. Unification of Biological and Physical Energy Flow Concepts

The energy "concentration" in a species or trophic level can be determined (1) instantaneously,

as in this study, by direct measurement of the energy density, or (2) over time, by measurement of the Production/Biomass (P/B) ratio. This ratio is the production (P), or amount of energy assimilated, relative to the average biomass (B) per unit of time (or 1/life span) (Margalef 1968; Odum 1969). Production in a steady state ecosystem is equivalent to the rate of entropy production (Johnson in press b). The measurements of actual production estimates for each trophic level exceeded the scope of this study. It is generally acknowledged that the value of the Production/Biomass ratio declines as one ascends the trophic ladder of an ecosystem (Winberg 1972; Winberg et al. 1972; Mann and Brylinsky 1975; Brylinsky 1980; Saunders et al. 1980). Energy becomes more "concentrated" in each successive link along the food chain and this is reflected by the increase in energy density (and increases in both life span and size) along the trophic hierarchy (i.e. the energy residence time increases).

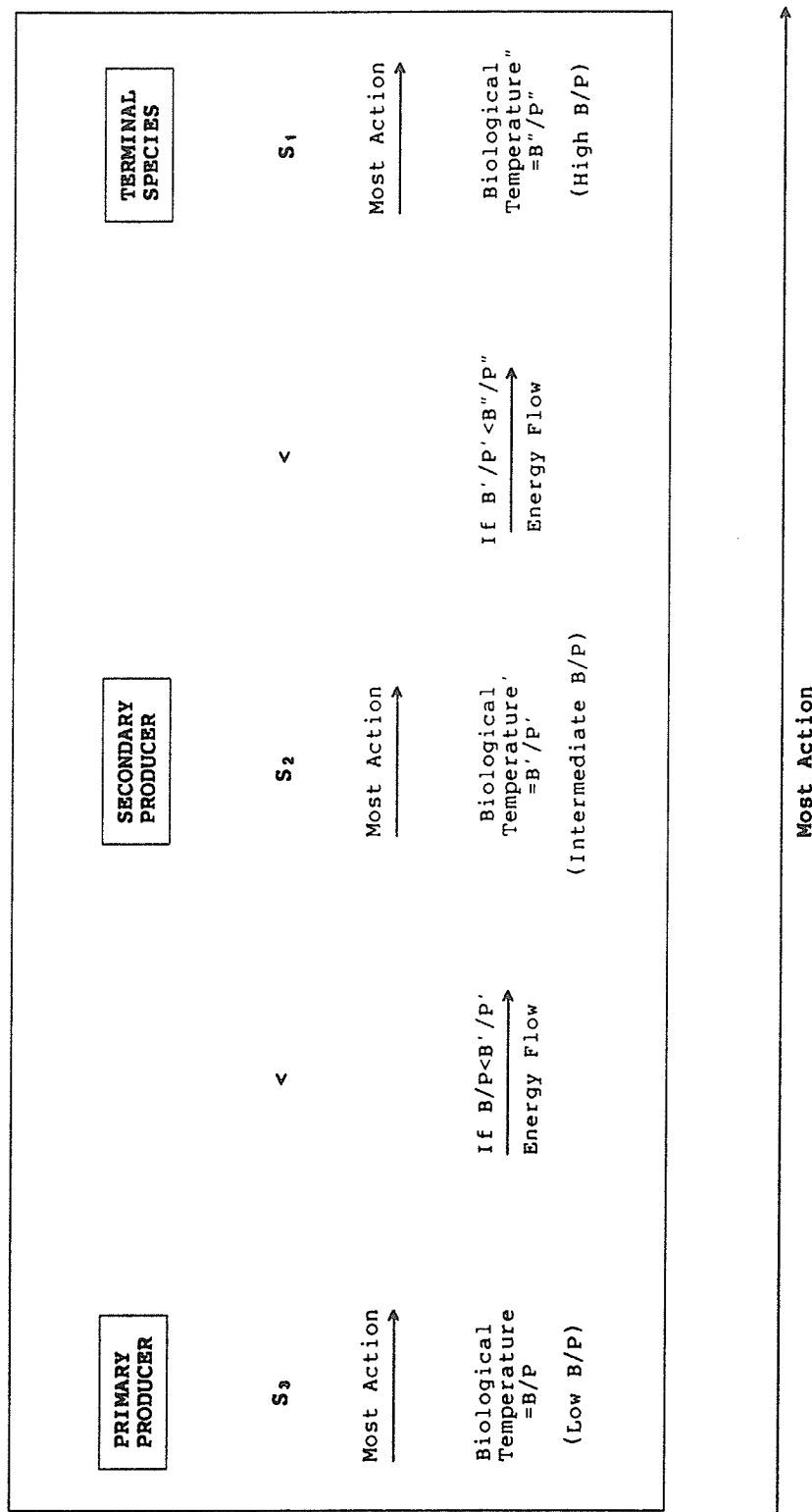
Energy residence time, in terms of the Production/Biomass ratio, is B/P ; the biomass accumulation ratio of Whittaker and Woodwell (1972). Biological temperature, which is measured on a time scale, equals entropy production relative to total energy (see "Note") (Keenan et al. 1974; Johnson

1981). The biomass accumulation ratio is equivalent to biological temperature (Johnson 1981); both are analogous to energy density, except, of course, the time factor is excluded from the latter. The longer the residence time of an energy unit the higher the biological temperature. An increase in energy residence time produces a concomitant increase in energy density. As Johnson (in press b) points out, energy in an ecosystem flows from species of low biological temperature (rapid turnover time) to species of high biological temperature (slow turnover time). Therefore, energy must be "pumped" from primary producer to terminal species. Energy flow is governed by biological temperature, not total energy in a trophic level. The forces acting within ecosystems are summarized in Figure 1.

In the Production/Biomass ratio the numerator represents energy flux and the denominator represents the energy stored in the biomass (Johnson in press b). Energy density times biomass (E_{pb}) is a function of production. The time element of production is missing in E_{pb} . Thus E_{pb} can be considered as a "cross section" through time. When integrated over time biological action is obtained (formula (3)). The relationship between production and E_{pb} can be expressed as follows:

Figure 1. Forces acting within ecosystems. Entropy production (S) decreases with ascending trophic levels. Ecosystems over short time periods ("ecological time"), species, and trophic levels tend to assume a state of most action. Biological temperature, which is equivalent to the biomass accumulation ratio (B/P), increases along the food chain. Energy flows (is "pumped") from species of low biological temperature (or low B/P) to species of high biological temperature (or high B/P) (after Johnson in press b).

ECOSYSTEM



$$P_i = \int_{t_0}^{t_1} E_{TAi} - (E\rho_i) (b_i), \quad (4)$$

where P = production, E_{TA} = total energy assimilated in the system, $E\rho$ = energy density, b = biomass, i = trophic level or organism i , and t = time. The efficiency of energy utilization is measured by formula (4). For example, a "low value" indicates a high degree of efficiency in energy utilization. From formula (4) it follows that the Production/Biomass ratio is:

$$P_i/B_i = \left(\int_{t_0}^{t_1} E_{TAi} - (E\rho_i) (b_i) \right) / B_i, \quad (5)$$

where B = mean biomass of the time interval. Formulae (4) and (5) are only valid from the inception of the system ($t=0$) to the end of the first time interval ($t=1$). These formulae can be applied to succeeding time intervals by adding the energy contained in the biomass of the trophic level or

organism at the beginning of the particular time interval to the integral of E_{TA} . For simplicity, respiration, although important, is omitted from formulae (4) and (5).

A correspondence thus appears to exist between the action of a physical system (formula (1)) and formula (4); E_{TA} (= total energy assimilated in the system) and E_{pb} (= energy density times biomass) can be considered the analogues of kinetic energy and potential energy, respectively. This apparent connection can be extended further:

$$\delta \int_{t_0}^{t_1} (E_{TA} - (E\rho)(b)) dt \geq 0, \quad (6)$$

where δ = very small changes in alternative paths and t = time. A dynamical path in a biological system can be thought of as the mean biomass energy through time of a species, trophic level, or ecosystem. This path is equivalent to the integral of biomass energy through the life span of the individual organisms in the system. In a biological system $dt \geq 0$ since entropy production (energy dissipation) is frequently

reduced (i.e. $dt > 0$); when entropy production is increased $dt = 0$. Ecosystems over short time periods ("ecological time"), and associated sub-systems (i.e. species and trophic levels) tend to assume a state of most action, thus $dt > 0$. However, over long time periods ("evolutionary time") ecosystems are ultimately governed by least action, this dictates that $dt = 0$. Formula (6) appears to correspond to Hamilton's principle (formula (2)). In formula (2) $dt = 0$ since entropy production is increased by least action; this can be reflected by the shortest time a particle takes to traverse a path (Tabisz pers. comm.). The dynamical path of many physical systems occur when $dt = 0$. All the physical theorems of dynamics are derived from Hamilton's principle (Page 1958). It is plausible that this can be extended to include biological dynamics.

Organisms and ecosystems exist at the intersection of cyclic flows (most action) and rectilinear flows (least action). Interference between these flows results in a state of decreased entropy production.

Decreased entropy production in an autonomous ecosystem culminates in the formation of a climax (or stationary) state. The climax state of an ecosystem is assumed to be a constant hierarchy; the dominant species in the hierarchy is characterized by a large organism of

uniform size, with slow turnover rate (Johnson 1981, 1988, in press a, b). The hypothesis states that energy density along the food chain reaches its highest value in the dominant species at the climax state within an autonomous ecosystem.

It was postulated that a simple, highly autonomous ecosystem in a climax state should display most distinctly energy density increase along the food chain. For this reason Keyhole Lake was selected as the study site. Keyhole Lake serves as a basic reference system for biological far-from-equilibrium systems.

STUDY AREA

RATIONALE FOR SELECTING A STUDY SITE

Energy relationships between trophic levels and associated taxa are frequently extremely complex. Platt (1964) indicated that the analysis of complex events should be initiated with the simplest system available which contains all the properties under consideration.

According to the principles governing energy flow in ecosystems a closed system is required for a system to assume a steady state of most action. Only in a closed system do energy (as sunlight) assimilated and energy dissipated as heat approach equality. Highly autonomous ecosystems provide control on energy flow: they form a "free energy sink" from which the energy entering the system is ultimately dissipated mainly as low grade heat (Johnson in press b). These ecosystems, according to the hypothesis, should display energy density increases in ascending trophic levels.

Over a century ago Forbes (1887) recognized the autonomy of many lake ecosystems and described them as:

. . . a little world within itself—a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so

small a scale as to bring it easily within mental grasp.

The understanding of species interactions is more readily acquired in Arctic lakes; species and community compositions are relatively few and simple compared to temperate lakes (Rigler 1975). The complexity of natural variability in temperate and especially tropical lakes is usually so large that it prevents in-depth assessment of the structure and functioning of the system.

Arctic lakes are closed systems for 8 to 11 months per year. During this period a thick ice cover isolates the system; the only energy entering the lake is sunlight, and all energy escapes as heat. During the short open-water period some matter is exchanged with the external world. Matter is removed by the emergence of aquatic insects and piscivorous birds, and is introduced by egg-laying insects and defecating birds (Johnson 1981, 1983, in press b). Johnson (1983) succinctly stated that Arctic lakes probably approach a closed system more closely than any other ecosystem except for permanently ice covered Antarctic lakes. However, the impoverished flora and fauna of perpetually frozen lakes in Antarctica (Goldman 1970) makes them unsuitable for this study.

Keyhole Lake functions as a closed thermodynamic system for approximately 9.5 to 10 months annually. The ice cover may exceed 2 m (Hunter 1970) and prevents any exchange

of matter with the surrounding ecosystems. During the open-water period relatively little matter is removed. Hunter (1970) reported red-throated loons (Gavia stellata) and yellow-billed loons (Gavia adamsii) occasionally feeding on Arctic charr in Keyhole Lake. In the 1985, 1986, and 1988 field seasons Arctic loons (Gavia arctica) and red-throated loons were infrequently observed feeding at Keyhole Lake. Occasionally terns (Sterna sp.) appeared to be feeding on emerging insects.

Keyhole Lake was free of human interference from its inception in the late Pleistocene until 1962 when Hunter (1970) initiated a comprehensive survey on the biological, chemical, and physical components of the lake. This continued intermittently until 1967. During 1962, 1963, and 1965 Hunter (1970) removed approximately 90% of the gillnet catchable Arctic charr population. Johnson (1976, 1983) monitored the recovery of this population in 1975 and 1980, respectively. This extensive background information contributed to the selection of Keyhole Lake. The data indicated that: (1) the trophic relationships in Keyhole Lake are relatively simple and linear, (2) the basin morphology and bottom composition would simplify benthic sampling, (3) the Arctic charr population was non-migratory, and (4) both the size and the age structures of the principal terminal consumer were consistent with those of an autonomous ecosystem in a climax state; the landlocked

Arctic charr population was composed of a dominant mode of old, large fish. This population appeared to have reached a climax state.

GENERAL DESCRIPTION OF THE AREA

Keyhole Lake ($69^{\circ} 22' 39''$ N, $106^{\circ} 13' 38''$ W), named after its configuration, is a small lake (48.6 ha) situated in the south-central coastal lowlands of Victoria Island, Northwest Territories (Figures 2 and 3) (Hunter 1970). Victoria Island is the second largest island in the Canadian Arctic Archipelago. It has a surface area of 216,000 km² and is situated south of Melville Island, west of Prince of Wales Island and King William Island, north of the mainland, and east of Banks Island (Stewart and Bernier 1982, 1983).

Climatic characteristics of south-central Victoria Island resemble those of the nearby mainland. The high degree of continentality is exhibited by a 42°C to 45°C range between the mean temperatures of the coldest winter month (January) and the warmest summer month (July). The fairly massive size of the land areas and the relatively narrow and shallow channel separating the island and mainland contribute to the continental climate (Maxwell 1981).

Mean daily temperatures at south-central Victoria Island range from -35°C to -33°C in January to 8°C to 10°C in July. From the fourth week in August until approximately

Figure 2. Map of the Canadian Arctic showing the location of Keyhole Lake.

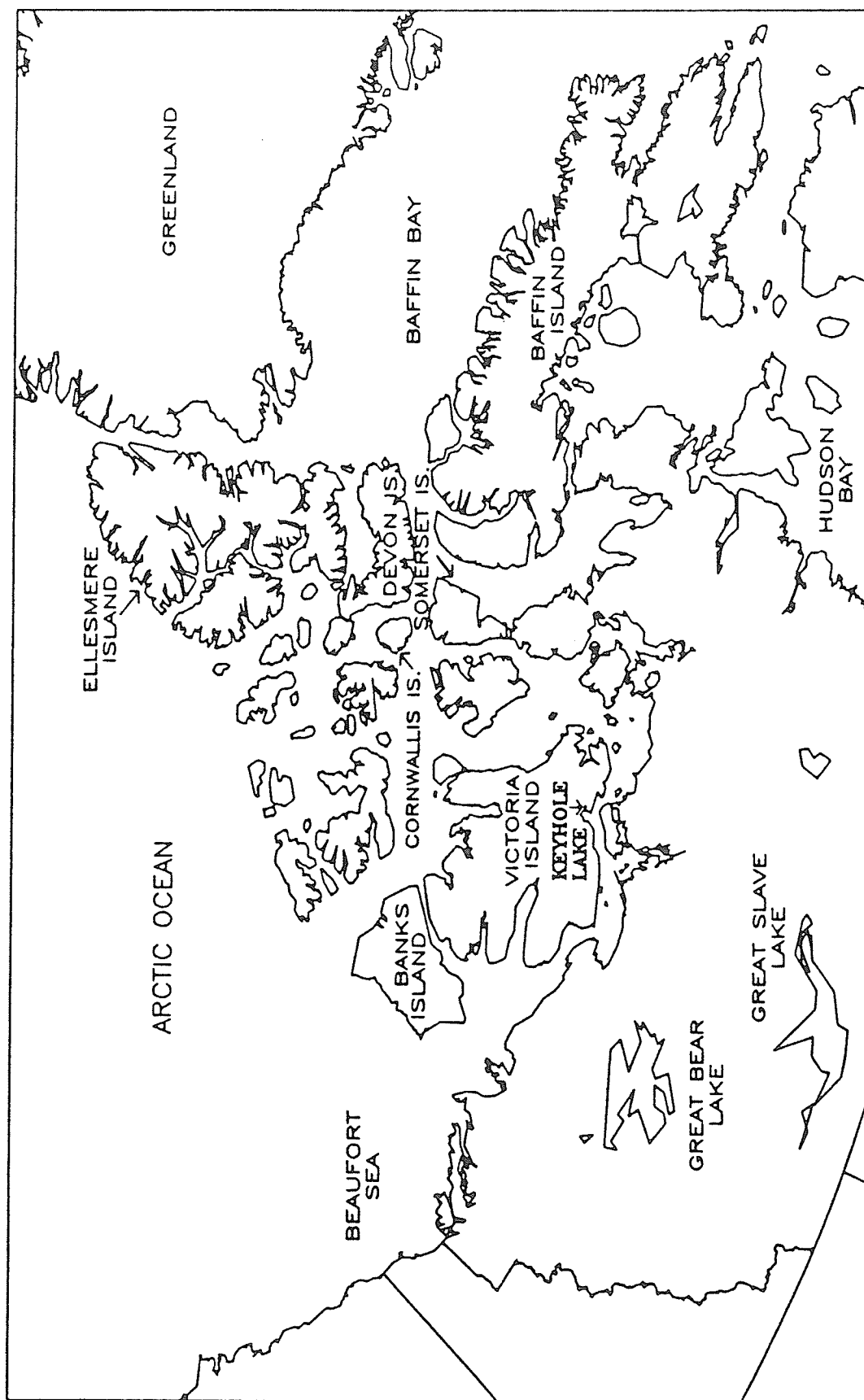
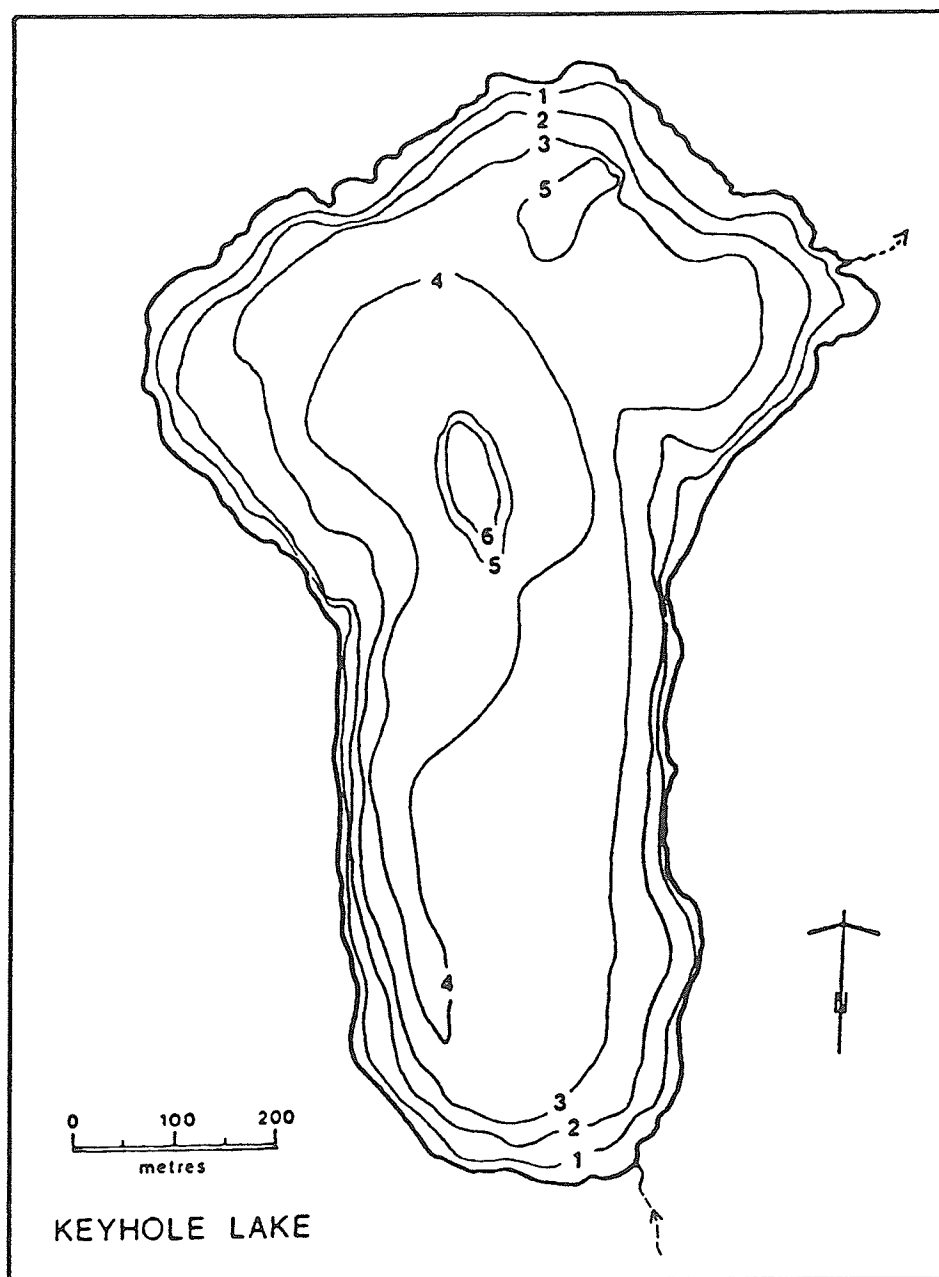


Figure 3. Bathymetric map of Keyhole Lake. Depth indicated in meters (after Johnson 1983).



the second week in June the mean daily temperatures remain below 0°C (Maxwell 1981).

The time of ice breakup varies among water bodies and between years. Ice begins breaking up on rivers in June but many lakes do not become ice-free until the second half of July. Some deep sheltered lakes in the Shaler Mountain Belt and large lakes may remain ice covered until the middle of August. Freeze-up begins in late August and early September but may continue until early October on some rivers and large lakes (Allen 1971; Stewart and Bernier 1982, 1983).

Prevailing anticyclonic conditions result in very low precipitation amounts. South-central Victoria Island receives between 100 to 150 mm annually of which between 50 to 60% falls as rain (Maxwell 1981; Stewart and Bernier 1982, 1983). Mean wind speed is usually 10 to 15 km·h⁻¹, but prevailing wind direction varies with location and season (Stewart and Bernier 1982, 1983).

Victoria Island was covered by the Laurentide Ice Sheet which retreated in a southeasterly direction between 8,500 and 12,500 years B.P. (Prest et al. 1972; Prest 1973; Bird 1980). Due to post-glacial rebound the island has risen from approximately 50 to over 200 m from northwest to southeast, respectively (Andrews 1970, 1972; Bird 1980).

Two physiographic areas divide Victoria Island. These consist of the smaller Shaler Mountain Belt in the northwest and the larger Victoria Lowland covering the remainder of the island (Bostock 1970, 1972).

The Victoria Lowland area is largely underlain by Palaeozoic sedimentary rocks consisting of shales, limestones, sandstones and dolomites (Stewart and Bernier 1983). The Wellington Arch, in south-central Victoria Island, is formed from inliers of Precambrian rock penetrating northward from the mainland (Thorsteinsson and Tozer 1970; Bird 1980). Much of the lowland is covered with glacial drift (Dunbar and Greenaway 1956). The lowland areas are dotted with numerous ponds and lakes ranging in size from a few square meters to Ferguson Lake (740 km²). Lowland elevation is predominantly within 200 m of sea level although some high grounds reach 300 m asl. Drumlins, moraines, eskers, and raised marine beaches dominate local relief ranging in height from a few meters to over 60 m. Low gradients, permafrost and scattering of glacial landforms contribute to the poor drainage of the lowlands (Dunbar and Greenaway 1956; Thorsteinsson and Tozer 1962; Maxwell 1980; Stewart and Bernier 1982, 1983).

Keyhole Lake is located 2.5 km east of Wellington Bay in a low, broad valley at 27.4 m asl. On the west side it borders a fairly steep hill rising to approximately 75 m asl. Drainage into the lake occurs through a small, usually

nearly stagnant creek located at the south end of the lake and along the shores during spring run-off and heavy precipitation. Water also percolates through thawed ground and tundra moss into the lake from a talus slope on the west side and melting subterranean ice (Hunter 1970).

Keyhole Lake discharges through a poorly developed creek at the northeast end of the lake. This creek flows through two small lakes before draining into the outlet of Ferguson Lake 2 km to the north. Near Keyhole Lake this creek supports a prolific growth of predominantly dwarf willows (Salix sp.) and sedges (Family Cypraceae). Except during periods of high discharge this creek is almost indistinguishable from the surrounding wetland (Hunter 1970).

Field work at Keyhole Lake was executed from July 19 to August 31, 1985, July 26 to August 22, 1986, and July 29 to August 6, 1988.

LIMNOLOGY

Morphometry

Keyhole Lake occupies a surface area of 48.6 ha and drains a watershed of approximately 426 ha (Hunter 1970). The maximum length lies in a north-south direction and is 1079 m; maximum breadth is 730 m. The lake has a perimeter of 3246 m and a shoreline development of 1.31. Mean depth is 3.01 m, maximum depth is 6.80 m, and relative depth is

0.86% (Figure 3). Lake volume is estimated at 1,464,132 m³ and volume development is 1.33. The mean slope of the entire lake bottom is 1° 19'. See Appendix A for a description of morphometric formulae (Table A1), a comparison of area, volume, percent volume, and slope between isobaths, at 1 m depth intervals (Table A2), and a percent volume hypsographic curve (Figure A1).

Bottom sediments

Benthic organisms in the sediments of Keyhole Lake were sampled with a Tall Ekman grab (Model 196T—229 cm² sampling surface area) manufactured by the Wildlife Supply Company. Generally regions deeper than 1 to 2 m consisted of soft consolidated clays frequently covered with large patches of attached filamentous algae. The littoral zone was comprised of talus at the central west side and a sandy area in the southeast corner. The remainder of the inshore areas consisted of mud, sand, cobbles, and a few boulders. Most cobbles were less than 15 cm in diameter.

Ice cover

Hunter (1970) measured an ice thickness of 2.12 m on Keyhole Lake on June 18, 1965. Extrapolations from Table A1 and Figure A1 in Appendix A indicate that 62.4% of the lake volume was occupied by ice on the above date.

In 1965 breakup occurred between July 14 and July 24 (Hunter 1970). Some fragmented ice was observed along the

shores when field parties arrived at Keyhole Lake on July 19, 1985 and July 26, 1986. Hunter (1970) noted that ice formation occurred along the shoreline edges in early September of 1963 and 1965. Ice thicknesses were measured at 61 cm on November 5, 1963, and 76 cm on November 25, 1967. In 1985 ice formation was observed along shoreline edges during the last week in August. These data indicate that Keyhole Lake remains ice covered 9.5 to 10 months of the year.

Lake level

Lake levels fluctuated 4 cm between July 25 and August 21, 1985. Hunter (1970) similarly observed only minor water level fluctuations during the summers of 1963 and 1965 at Keyhole Lake. He further noted that discharge rates at the outlet creek after July 15, 1965 were so low and diffuse that reliable estimates were no longer possible.

Precipitation

Precipitation was measured by the Meteorological Station at Cambridge Bay (69° 06' N, 105° 07' W) 56 km southeast of Keyhole Lake. For 1985 precipitation totalled 127.2 mm and of this 51.6 mm fell as rain. In 1986 a total of 130.8 mm was recorded with 39.5 mm falling as rain (Anonymous 1985-86).

Hunter (1970), using an annual precipitation of 170.3 mm, estimated a two year flushing period for Keyhole

Lake. However, he did not correct for evaporation, transpiration, and the melting of subterranean ice. Rare observations of subterranean ice melting in fissures suggests that this process contributes relatively little to the total water influx of Keyhole Lake. Hobbie (1973) noted that in the Peters-Schrader drainage basin, Alaska, 45.8 mm of an annual precipitation of 305 mm was evaporated and the Arctic island of Novaya Zemlya's evaporation was 52.5 mm of its 350 mm of annual precipitation. Brown et al. (in Hobbie 1973) found that evapotranspiration nearly equalled summer precipitation on a drained lake bed near Barrow, Alaska. Roulet and Woo (1986) indicated that evaporation in northern Canada is approximately equal to summer rainfall. Under the assumption of an annual evaporation and transpiration rate at a low of 30 mm during a year of high precipitation (170.3 mm) and a high of 50 mm during a low precipitation year (127.2 mm) the water renewal time approximates 2.5 to 4.5 years.

Temperatures

Maximum and minimum air temperatures were measured by the Meteorological Station at Cambridge Bay. Mean daily temperatures exceeding 0°C were first recorded on May 15 in 1985 and June 17 in 1986, and remained above freezing for 96 and 86 days in the respective years. Minimum and maximum air temperatures for 1985 were -45.6°C on February 26 and 18.8°C on June 26, respectively. In 1986 a minimum air

temperature of -44.9°C was reached on February 24 and a maximum of 22.4°C was recorded on July 11 (Anonymous 1985-86). See Appendix B (Figures B1 and B2) for a graphic description of the regional temperature regime from June 1 to September 30, 1985, and 1986.

The annual surface radiation at Keyhole Lake is unknown. Stewart and Bernier (1982) reported a net annual radiation of $6.28 \times 10^5 \text{ kJ}\cdot\text{m}^{-2}$ at the surface of southwestern Victoria Island. Tundra near Barrow, Alaska (lat. $71^{\circ} 19' \text{ N}$), received $4.98 \times 10^5 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ net surface radiation (Kelley and Weaver 1969). Welch and Kalff (1974) measured a surface radiation of $1.68 \times 10^6 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for Char Lake, Cornwallis Island, Northwest Territories (lat. $74^{\circ} 42' \text{ N}$).

Maximum water temperatures reached 11.0°C on July 28, 1985, and 9.0°C on August 7, 1986. Keyhole Lake was isothermal during the 1985 sampling period and nearly isothermal when occupied in 1986. The less precise recording methodology employed in 1985 may explain the perfectly isothermal conditions recorded during that sampling period. See Appendix B for materials and methods, and water temperature profiles (Figure B3). During ice-free periods isothermal conditions were measured in Char Lake (Schindler et al. 1974a), Greiner Lake, Victoria Island, Northwest Territories (lat. $69^{\circ} 11' \text{ N}$) (Johnson 1962), Imikpuk Lake, Barrow, Alaska (Brewer 1958), and Meretta

Lake, Cornwallis Island, Northwest Territories (lat. $74^{\circ} 42' N$) (Schindler et al. 1974b).

The annual heat budget of Keyhole Lake was calculated according to the procedure outlined in Hutchinson (1957). Minimum temperatures recorded by Hunter (1970) in 1965 were employed. On June 18, 1965 the ice cover was 2.12 m thick; the water temperature was $0.74^{\circ}C$ at 3.0 m and nearly isothermal conditions prevailed from 3.5 m to the bottom. The temperatures at and below 3.5 m ranged from $1.29^{\circ}C$ to $1.33^{\circ}C$ with a mean of $1.31^{\circ}C$. The ice mass temperature was assumed to be $0^{\circ}C$ although the ice surface temperature was probably much lower during the winter (Brewer 1958). However, the insulative qualities of a snow cover most likely prevent the ice surface from approaching minimum ambient air temperatures. The specific heat of ice is relatively low. Just below $0^{\circ}C$ it is approximately half ($2.093 J \cdot g^{-1} \cdot ^{\circ}C^{-1}$) that of water and follows a concomitant decrease as temperature declines (Pick 1969; Wetzel 1983).

At a density of 0.9168 and latent heat of melting of $333.77 J \cdot g^{-1}$ the ice mass required $5.751 \times 10^5 kJ \cdot m^{-2}$ to melt. The annual heat budget for 1985 was estimated at $7.130 \times 10^5 kJ \cdot m^{-2}$ of which 80.7% was used to melt the ice. For 1986 it was estimated at $6.872 \times 10^5 kJ \cdot m^{-2}$ of which 83.7% was absorbed by the latent heat of melting. Heat transfer to bottom sediments in an Arctic lake was studied by Brewer (1958). He concluded that the amount was too

small to be included in the lake's annual heat budget. The preceding annual heat budget estimates are similar to Brewer's (1958) estimate of Imikpuk Lake ($7.536 \times 10^5 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), Hunter's (1970) 1965 estimate for Keyhole Lake ($7.068 \times 10^5 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), and the approximation by Schindler et al. (1974a) of Char Lake (6.699×10^5 to $7.955 \times 10^5 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). All these lakes are characterized by annual heat budgets that have the largest constituent allocated to the latent heat of ice melting rather than water warming. Insolation of the ice-free water surface only begins about one month after the summer solstice.

Water transparency

Water transparency measurements were executed with a Secchi disc (Wildlife Supply Company, Model 59). Readings ranged from 2.30 to 3.40 m in 1985 and 2.95 to 3.20 m in 1986. Hunter (1970) measured a larger variation in Keyhole Lake during the summer of 1965 (2.5 to 6.1 m). Sediment agitation, due to wind induced wave action, appears to be the main agent in reducing water transparency. On July 30, 1985, after 3 days of high winds (up to $59 \text{ km} \cdot \text{h}^{-1}$), Secchi disc readings of only 2.30 m were recorded (see Appendix C, Figure C1). Lack of calm water prevented Secchi disc readings during the latter part of August in 1985 and 1986. Stewart and Bernier (1982, 1983) measured Secchi disc depths from 0.1 to 11 m in eighteen Victoria Island lakes. Schindler et al. (1974a) reported Secchi disc depths from

2.5 to 10 m for Char Lake. Very high Secchi disc readings (17 to 30 m) were measured by Johnson (1964a, 1966, 1975a) in most regions of Great Bear Lake (lat. $64^{\circ} 40'$ to $67^{\circ} 0'$ N), one of the most oligotrophic lakes in the Northwest Territories.

Downwelling visible irradiance above the water surface ranged from 2.276 to $3.835 \times 10^2 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ during a 24 hour period on July 24 to 25, 1985. The mean was $1.189 \times 10^2 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ (or $1.027 \times 10^4 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) and compares well with an approximation of $9.96 \times 10^3 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ for Char Lake during a corresponding period (Schindler et al. 1974a; Welch and Kalff 1974). Both sources noted that the visible spectrum contains approximately 50% of the energy in solar radiation. Just below the water surface of Keyhole Lake downwelling visible irradiance measured from 1.351 to $2.213 \times 10^2 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$; the mean was $7.128 \times 10^1 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ and 59.95% of the surface light energy entered the water. Welch and Kalff (1974) found that on an annual basis 24% of photosynthetically available surface irradiance entered the water of Char Lake. In Keyhole Lake at a depth of 5 m downwelling visible irradiance ranged from 5.196×10^{-2} to $1.019 \times 10^1 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ with a mean of $3.403 \text{ J}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$. Downwelling surface light energy was reduced to an average of 2.86% at 5 m. The mean vertical absorption coefficient from 0 to 5 m over the 24 hour recording period was 0.5996. These data indicate that all depths of Keyhole

Lake are in the euphotic zone. This is consonant with Hunter's (1970) findings that 2% of the incident light reaches the deepest part of Keyhole Lake. See Appendix C for materials and methods.

Water chemistry

Water samples from Keyhole Lake were chemically analysed for the following: dissolved inorganic carbon, dissolved organic carbon, suspended carbon, suspended nitrogen, total dissolved phosphorus, suspended phosphorus, soluble reactive silicon, chloride, sulphate, calcium, iron, magnesium, manganese, potassium, sodium, organic acids, alkalinity, specific conductance, and pH. An annual summary of chemical analyses of Keyhole Lake water samples collected in 1985 and 1986 are listed in Table 1. See Appendix D for materials and methods, and a discussion of the analytical data. Dissolved oxygen concentrations are briefly discussed from the literature.

Lake classification

The classification of Keyhole Lake is polemical. Data compiled by Hunter (1970) indicates that the lake inversely stratifies during the winter and displays vernal circulation. Nearly isothermal conditions exist throughout the summer and are probably maintained, due to frequent strong winds and relative shallowness, as the lake cools in the autumn before a covering of ice is formed. Keyhole Lake does not fit Forel's (1892) categorization of a polar lake;

Table 1. Summary of chemical analyses of Keyhole Lake water for 1985 and 1986. Means of all samples collected during each field season (95% confidence intervals).

Analysis	1985	1986
Dissolved inorganic carbon ($\mu\text{mole}\cdot\text{l}^{-1}$)	1,525 $\pm$ 77	1,201 $\pm$ 38
Dissolved organic carbon ($\mu\text{mole}\cdot\text{l}^{-1}$)	433 $\pm$ 54	331 $\pm$ 26
Suspended carbon ($\mu\text{g}\cdot\text{l}^{-1}$)	838 $\pm$ 294	511 $\pm$ 199
Suspended nitrogen ($\mu\text{g}\cdot\text{l}^{-1}$)	110 $\pm$ 39	53 $\pm$ 16
Total dissolved nitrogen ($\mu\text{g}\cdot\text{l}^{-1}$)	400 $\pm$ 49	309 $\pm$ 40
Total dissolved phosphorus ($\mu\text{g}\cdot\text{l}^{-1}$)	20.2 $\pm$ 6.2	16.3 $\pm$ 2.0
Suspended phosphorus ($\mu\text{g}\cdot\text{l}^{-1}$)	9.2 $\pm$ 2.7	4.5 $\pm$ 0.6
Soluble reactive silicon ($\mu\text{g}\cdot\text{l}^{-1}$)	103 $\pm$ 24	116 $\pm$ 51
Chloride ($\text{mg}\cdot\text{l}^{-1}$)	23.8 $\pm$ 0.8	20.4 $\pm$ 1.3
Sulphate ($\text{mg}\cdot\text{l}^{-1}$)	6.3 $\pm$ 0.5	5.2 $\pm$ 0.2
Calcium ($\text{mg}\cdot\text{l}^{-1}$)	14.1 $\pm$ 0.4	14.4 $\pm$ 0.7
Iron ($\mu\text{g}\cdot\text{l}^{-1}$)	48 $\pm$ 10	60 $\pm$ 18
Magnesium ($\text{mg}\cdot\text{l}^{-1}$)	9.6 $\pm$ 0.3	9.6 $\pm$ 0.7
Manganese ($\mu\text{g}\cdot\text{l}^{-1}$)	<16.7 $\pm$ 3.1	<10.0 $\pm$ 0
Potassium ($\text{mg}\cdot\text{l}^{-1}$)	1.14 $\pm$ 0.04	1.08 $\pm$ 0.06
Sodium ($\text{mg}\cdot\text{l}^{-1}$)	13.1 $\pm$ 0.6	10.2 $\pm$ 0.6
Organic acids ($\mu\text{eq}\cdot\text{l}^{-1}$)	28.9 $\pm$ 12.7	16.0 $\pm$ 13.7
Alkalinity ($\mu\text{eq}\cdot\text{l}^{-1}$)	1,399 $\pm$ 39	1,257 $\pm$ 38
Specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$ at 25°C)	225 $\pm$ 6	199 $\pm$ 6
pH	8.04 $\pm$ 0.06	8.13 $\pm$ 0.03

summer temperatures rise above 4°C. According to Bayly and Williams (1973) this lake may be classified as a warm thereimictic lake. This is defined as a cold monomictic lake with summer holomixis above 4°C. Wetzel (1983) argued that once lake temperatures exceed 4°C the lake is technically dimictic. However, a typical dimictic lake stratifies during the warm months (Cole 1983; Wetzel 1983). Berg (1966) emphasized that dimictic means having two periods of circulation per year. He expanded the definition of a cold monomictic lake by deemphasizing the importance of maximum water density (at approximately 4°C) on lake circulation. This may not, as is probably the case with Keyhole Lake, have any practical effect on autumnal circulation.

MATERIALS AND METHODS

FIELD WORK

Sampling location selection for biomass estimation

Hunter (1970) observed a patchy distribution of filamentous algae attached to the substrate of Keyhole Lake. This strongly indicated a negative binomial distribution (randomly distributed clumps) for benthic organisms (Slack et al. 1973; Elliott 1977). This distribution, according to Slack et al. (1973), is frequently the only model that accurately describes organism distribution patterns in the natural world. The dispersion configuration of randomly distributed clumps may vary greatly among habitats and representative samples should be collected from these different habitats (Slack et al. 1973).

Stratified random sampling was employed in benthic biomass assessments (Crisp 1971; Slack et al. 1973; Elliott 1977). Different depth ranges were assumed to represent various habitats (Warwick pers. comm.). Irradiance and wind induced turbulence declines with increasing depth (Cole 1983; Wetzel 1983) while sedimentation rates are usually higher in deeper regions of a lake (Warwick pers. comm.). Furthermore, the substrate, down to at least 2 m, freezes during the ice cover period.

The entire lake was arbitrarily divided into seven strata and each stratum was sampled independently. A stratum consisted of the area between each set of 1 m contour lines in Figure 3. A region exceeding 5 m in the northern portion of the lake was added to the area bounded by the 5 and 6 m contour lines, and the deepest area of the lake (6.0 to 6.8 m) was designated as a separate stratum.

The locations of sampling stations for the biomass estimates of planktonic organisms were also based on stratified random sampling. Continuous winds may regulate plankton distribution by concentrating organisms towards the leeward side of the lake (Salki pers. comm.). To avoid this possible bias the surface area of Keyhole Lake was subdivided into four approximately equal sections with the axes running north-south and east-west. Each quadrant represented a stratum to which the appropriate sampling effort was allocated.

Sampling stations for benthos and plankton were combined to reduce the overall number of locations. This was accomplished by superimposing the "benthos" strata upon the "plankton" strata (or quadrants). This should not have introduced any significant bias since sampling stations were randomly located within the confines of the strata.

Approximately 25% of the total number of sampling stations were located in each quadrant. With the aid of a

planimeter (Gelman Instrument Company) each "benthos" stratum area was assigned a fractional value of the total quadrant area. Since the "benthos" strata were unequal in area the number of sampling units allocated to each was proportional to the fractional values of each "benthos" stratum; that is, to the total number of sampling units in the quadrant (Slack et al. 1973; Elliott 1977).

The "benthos" strata areas were not corrected for their minimal slope (Appendix A, Table A2). Furthermore, an Ekman grab samples "lake surface area equivalents" under the assumption that the grab maintains a perfectly perpendicular position in relation to lake surface during sampling. This assumption is probably seldom realized in practice.

Elliott (1977) indicated that if the number of samples taken from a population is sufficiently large and the sample means were arranged in a frequency distribution, this distribution would tend to normality regardless of the distribution of each sample mean. He concluded that sample means following non-normal distributions, such as a negative binomial distribution, will approximate normal distributions if the number of sampling units is thirty or larger. Due to time and manpower constraints the recommended minimum of thirty sampling stations were located in Keyhole Lake. However, the collecting or utilization of thirty samples per trophic level or community, in one sampling period, was not always realized and will be noted in the appropriate sections.

Random locations were selected by placing a numbered grid under a transparent bathymetric map of Keyhole Lake. Random numbers from tables in Snedecor and Cochran (1980) were employed to determine intersection points of X and Y axes on the grid. Reference markers were placed at strategic locations along the lake shore. Predetermined distances were measured with a distance meter (Ranging Incorporated, Rangematic Model 610), and by triangulation sampling stations were located and marked with buoys. Station depths ranged from 0.78 to 6.04 m.

Sampling of all trophic levels, except for Arctic charr, was conducted at each station in 1985 during the following periods: July 26 to August 1 (Period I, 1985), August 11 to 15 (Period II, 1985), and August 20 to 24 (Period III, 1985). During 1986 only limited sampling was performed at selected stations; these were occupied on July 27 to 28 (Period I, 1986), August 7 (Period II, 1986), and August 17 (Period III, 1986). The period designations will be referred to in following sections instead of sampling period dates. Collecting dates for chlorophyll samples were identical to those for water samples collected for chemical analyses. The actual dates are given in Appendix D under "Water chemistry—Materials and methods." Multi-period collecting was selected to reduce the effects of population fluctuations and physiological changes of organisms in discerning general patterns (Crisp 1971).

Gillnets were scattered randomly throughout the lake and electrofishing was limited to shallow inshore areas.

Sampling methodology for trophic levels and communities

Benthic bacteria and detritus

Sediment samples were collected during the 1985 field season, with an Ekman grab (described in "Study area" under "Limnology—Bottom sediments"). Subsamples, hereafter referred to as samples, were taken with a modified 50 ml disposable plastic syringe; the bottom section was cut off and the remainder was used as a corer to take sediment samples from the Ekman grab. Duplicate samples were taken: the one for evaluation of organic content (organic dry weight or ash-free dry weight) and the other for energy density determination. Collecting samples in water shallower than 1 m was abandoned because the inability of the modified syringe corer in retaining coarse unconsolidated inshore sediments.

Samples were usually taken to the corer's maximum depth of 12 cm. Ocevski (1966) reported heterotrophic bacteria to a depth of 18 cm in sediments from Balkan lakes. Brinkhurst et al. (1969), in samples from Toronto Harbour, Ontario, found an approximate logarithmic decline in bacteria from the sediment surface downward. Relatively few bacteria were counted below 10 cm. Rheinheimer (1974) stated that the highest number of bacteria is almost always

concentrated in the upper few centimeters of sediments, and especially on the surface; immediately below this the population is usually reduced to a few percent.

Samples were sieved through 500 μ m Nitex to avoid contamination with larger benthic organisms and stored in plastic Nasco Whirlpaks. The samples were fixed with formalin (40% formaldehyde) to a concentration of 10% (Federle and White 1982).

Benthos

Samples of benthic flora and fauna were obtained during the 1985 and 1986 field seasons. Sampling was accomplished with an Ekman grab. The efficiency of an Ekman grab in capturing benthic organisms is controversial. Paterson and Fernando (1971) reported that a core sampler captured more organisms per unit area than an Ekman grab. Brinkhurst et al. (1969) indicated that the KB corer and the Ekman grab gave similar population densities of benthic fauna. Kajak (1963) tested two corers against an Ekman grab and found substantially higher mean chironomid larvae densities in Ekman grab samples.

Ekman grab samples were usually taken to a depth of at least 12 cm. Brinkhurst and Kennedy (1965), and Brinkhurst et al. (1969) reported oligochaetes down to 20 cm in the sediment. However, the vast majority of the worms were found in 0 to 6 cm of sediment depth. In Char Lake

Kirchner (1975) and Rigler (1975) found benthic organism abundance peaking in the first 2 cm of sediment and none were found below 5 cm.

Samples were sieved through 500 μ m Nitex in order to separate sediments from benthic organisms. This mesh size is slightly smaller than the U.S. Standard No. 30 sieve (589 to 595 μ m mesh opening) which is reported to retain most of the biomass (Slack et al. 1973). Heath (1985a, 1985b) recommended the use of a 500 μ m screen for quantitative macrobenthos analysis. The samples were preserved in 5% formalin (Slack et al. 1973) and stored in plastic Nasco Whirlpaks. Periodically duplicate samples were collected.

To ascertain possible effects of formalin preservation on the energy density of organisms additional benthos samples were collected on August 1, 1985, and August 10, 1986. The 1985 samples were sorted, stored in Nasco Whirlpaks, and packed in Dry Ice (solidified carbon dioxide) for shipment to Winnipeg. One half of the samples collected in 1986, consisting of globose blue-green algae, were frozen shortly after collecting while the remaining fraction was preserved in 5% formalin. Frozen samples remained in this state until further analysis.

In 1986 four samples were collected from benthos rich areas and treated identically to samples collected for biomass estimation, with the difference that the sieved

sediments were retained to determine the efficiency of 500 um Nitex in biomass retention. These samples were stored in wide-mouth Nalgene polypropylene jars (4 l) and fixed in 5% formalin.

Phytoplankton, other microseston, and chlorophyll

Water samples for phytoplankton and other microseston, and chlorophyll analyses were obtained with Van Dorn type water-sampling bottles (G.M. Manufacturing, and Instrument Corporation, 6 l capacity, and Wildlife Supply Company, Model 1120) (Saraceni and Ruggiu 1969; Slack et al. 1973). Samples were collected in 1985 and 1986, at a depth of 0.5 m. Due to the complete mixing of the lake during both field seasons sampling depth for phytoplankton was unimportant (Kling pers. comm.). Phytoplankton was probably randomly distributed throughout the water column although some concentrating of planktonic algae, as previously discussed, may have occurred at the leeward side of the lake.

For phytoplankton identification 200 ml water samples were collected and preserved with 2 ml Lugol's solution (Slack et al. 1973) to which 5% formalin was added after 1/2 hour. The formalin prevents pigment degradation and the 1/2 hour delay aids in maintaining cell wall integrity (Kling pers. comm.). Samples were stored in plastic Nasco Whirlpaks.

Water samples for quantitative and energy density evaluations of phytoplankton and other microseston were prefiltered through 153 μm Nitex to eliminate occasional large particles (Slack et al. 1973). The samples were subsequently filtered, with the aid of an electric vacuum pump (set below $4.67 \times 10^4 \text{ N}\cdot\text{m}^{-2}$) and a Millipore filtering system, through Whatman GF/F (0.7 μm) and GF/C (1.2 μm) glass microfiber paper filters (4.25 cm diameter) (Reed and Reed 1970; Slack et al. 1973). Prior to use the filters were ignited in a muffle furnace for 16 hours at 550°C to remove any organic contaminants (Stainton et al. 1977), weighed on a Mettler AE100 balance (0.1 mg accuracy), and individually stored in plastic petri dishes (Slack et al. 1973). Filters were handled with flat-bladed non-serrated forceps (Banse et al. 1963). Filtered water volumes were recorded and each filter was inspected for zooplankton contamination; any visible zooplankters were removed with microforceps. The filters were subsequently air dried (Cummins and Wuycheck 1971) and stored in plastic petri dishes at low ambient temperatures (Slack et al. 1973).

Samples for chlorophyll analysis were treated according to Stainton et al. (1977). Samples were stored in the dark but at approximately 5°C instead of the recommended -10°C . The effects of this is unknown, however, the pigment is reasonably resistant to degradation (Stainton pers. comm.).

Zooplankton

Zooplankton samples for biomass estimation, caloric analysis, and identification were obtained in 1985. Collecting was performed with a pair of 77 μm Nitex Wisconsin nets with a 25 cm mouth diameter, 1 m length, and a filtering area of approximately 2,800 cm^2 . These nets are considered highly efficient due to a non-porous mouth-reducing cone and a filtering area 5.7 times larger than the mouth area (de Bernardi 1984). The nets were attached to a stainless steel cross frame with a central rope connected to the frame by a bridle. Patalas and Salki (1984) stated that this configuration probably significantly reduces zooplankton avoidance of the tow rope by displacing it from the center of the mouth as found in conventional nets. They determined that this net arrangement and the Schindler-Patalas trap are equally efficient in quantitative zooplankton sampling.

A relatively small mesh aperture of 77 μm was selected because of the low zooplankton productivity usually associated with Arctic lakes (Hunter 1970; Kalff 1970; Rigler 1972; Hobbie 1973; Rigler et al. 1974). In lakes with low zooplankton densities the clogging of small mesh nets is minimal and the majority of the biomass is captured (Slack et al. 1973; Salki pers. comm.). However, small nauplii and rotifers may pass through the mesh. Ejsmont-Karabin (1978) reported rotifers passing through mesh apertures down to 10 μm .

Nets were drawn vertically from the lake bottom to the surface to circumvent any non-random zooplankton distributions within the water column. This procedure also simplifies calculations of water volumes filtered through the nets by employing predetermined depths (Tonolli 1971; Slack et al. 1973; de Bernardi 1984). Tests in shallow water indicated that the nets compressed to approximately 10 cm when resting on the bottom; this was subtracted from the measured depth in determining water volumes passing through the nets.

The samples were fixed with formalin at a concentration of 5% (Slack et al. 1973) and stored in plastic Nasco Whirlpaks. On August 1, 1985 some additional zooplankton samples were collected to assess the possible influence of formalin preservation on the energy density of zooplankton. These samples were stored in plastic Nasco Whirlpaks and packed in Dry Ice for transportation to Winnipeg. The samples were stored frozen until analysed.

Arctic charr

Survey type 120 m gillnets, manufactured by Lundgren's of Stockholm, Sweden, were extensively used during the three field seasons. One net type (designated a 10-25 gillnet) consisted of six panels, each 20 m long and 1.8 m deep, of the following mesh sizes (bar measure): 10, 12, 16, 19, 22, and 25 mm. The second net type (designated a 10-60 gillnet), also manufactured from six 20 by 1.8 m

panels, included the following mesh sizes (bar measure): 10, 19, 33, 45, 55, and 60 mm. The nets were of the sinking type and when set as a pair they constituted 1 unit of effort (240 m of net) (Johnson 1976, 1983).

These nets were demonstrated by Johnson (1976, 1983) to encompass catch curves over a wide range of modal lengths (105 to 750 mm). The lower limit catchability is approximately 100 mm, but these nets maintain a high level of efficiency even near the lower limit: in Gavia Lake, Northwest Territories (lat. $68^{\circ} 22' N$), the most abundant length class of Arctic charr was 100 to 110 mm, being effectively captured with gangs of 10-25 and 10-60 nets (Johnson 1983).

Nets were normally set in the afternoon and retrieved the next morning; the average set time was approximately 18.5 hours. A storm on August 23, 1985, postponed net retrieval until the next day. Overnight sets in 1985 usually consisted of 2 units of effort, but were increased, with one exception, to three in the following year. During the 1988 field season 2 and 4 units of effort were employed. A floating 10-25 gillnet was briefly used in 1985 but discontinued after poor catches.

In 1985 a small number of Arctic charr were collected by angling. The smaller stock component was assessed by electrofishing. A Smith-Root Incorporated

Electrofisher (Type VII) was employed along the shoreline in 1985; battery failure and misplacement by a transport company precluded its use during the 1986 and 1988 field seasons, respectively.

All Arctic charr captured were individually weighed to the nearest gram on a Hanson Dietetic Scale (Model 1440) and fork length was measured to the nearest millimeter. Sagittal otoliths were removed for age determination from a randomly selected subsample of the captured population and stored dry in paper envelopes. This subsample was frequently further assessed for sex, maturity level, and stomach contents.

A number of Arctic charr were preserved for energy density analysis. Some specimens were packed in Dry Ice and transported to Winnipeg where they remained frozen until further analysis. Other individuals were initially preserved in 10% formalin (Slack et al. 1973). The body cavities of larger specimens were slit to ensure internal penetration of the preservative. After 7 days the formalin solution was drained and the fish were transported moist in 20 l plastic containers. Upon arrival in the laboratory the specimens were stored in 5% formalin.

To obtain growth information four net caught Arctic charr were tagged in 1985 with plastic "spaghetti" type tags. The survival rate appeared low due to damage

inflicted by netting, measuring, and tagging. Time limitations precluded an extensive tagging program.

Arctic charr data from Keyhole Lake collected by Hunter (1970) and Johnson (1976, 1983) are included in this study to aid in discerning population structure changes from the inception of exploitation in 1962. Hunter (1970) employed a "standard gang" in 1962. This consisted of the following mesh sizes (bar measure): 19.1, 31.8, and 44.5 mm. In 1963 nets of 9.5 and 25.4 mm were added with a further addition of a 17.1 mm net in 1965. Johnson (1976, 1983) used 10-25 and 10-60 sinking gillnets in 1975 and 1980. During the 1975 fishery Arctic charr were also captured by electrofishing but only net caught fish are included in this data. All lengths are given in fork length.

TAXA IDENTIFICATION

Benthic algae and mosses were identified by Dr. G.G.C. Robinson of the Department of Botany, University of Manitoba. The majority of benthic flora biomass consisted of an epipellic filamentous alga, Cladophora sp., which formed large patches in the deeper regions of the lake, exceeding 10 cm in thickness. A large, branched alga, Chara sp., was infrequently found intertwined in these patches. Substantial numbers of a globose blue-green alga (Class Cyanophyceae), Nostoc sp., formed the plocon in areas

generally exceeding 2 m in depth. Inshore regions supported sparse populations of two lithophytic filamentous algae, Stigeoclonium sp. and Vaucheria sp. Small clumps of mosses, Fissidens sp. and Fontinalis sp., inhabited the littoral zone near the outlet creek.

Phytoplankton and Protozoa were identified by H. Kling, Freshwater Institute, Department of Fisheries and Oceans, Winnipeg. She described sixty-seven taxa of phytoplankton and five of Protozoa (see Appendix E, Table E1 and Table E2).

The benthic invertebrate community contained small numbers of free-living Nematoda of the order Dorylaimida (identified from keys in Chitwood and Allen 1959). Significant numbers of Oligochaeta were found in the sediments. With the aid of keys in Brinkhurst and Jamieson (1971), and Brinkhurst (1986) these were identified as belonging to the family Lumbriculidae. Small clams of the family Sphaeriidae commonly inhabited the sediments. Keys in Clarke (1973, 1981) permitted the identification of the following species: Pisidium ferrugineum, Pisidium idahoense, Pisidium lilljeborgi, and Sphaerium nitidum. The amphipod Gammarus lacustris (identified in Johnson 1987, and unpublished) was frequently encountered in benthos samples. The major constituent of benthic invertebrate biomass consisted of midge larvae and pupae (Family Chironomidae). No further identification of the chironomids was attempted

due to the numerous species present and the difficulty in identifying larval stages. One species of caddisfly larvae was found in Keyhole Lake. This was identified by D. Giberson, Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, as Grensia praeterita (Family Limnephilidae).

The identification of zooplankton was accomplished by Dr. B.J. Hann of the Department of Zoology, University of Manitoba (see Appendix E, Table E3). Zooplankton samples infrequently contained hydra (Order Hydroida) and water mites (Hydracarina sp.).

Arctic charr, Salvelinus alpinus, was the only vertebrate present in large numbers. A small population of ninespine sticklebacks, Pungitius pungitius, existed in Keyhole Lake. Their contribution to the total vertebrate biomass was probably negligible.

LABORATORY ANALYSIS

Biomass analysis

Benthic bacteria and detritus

Sediment samples for organic dry weight determination were washed twice to remove most of the formalin. This was accomplished by decanting the preservative and placing the sample in a polypropylene container to which 4 l of distilled water was added. The

sample was briefly agitated and allowed to settle for 24 hours. The distilled water was subsequently decanted and the washing procedure repeated. Federle and White (1982) recorded a formalin concentration reduction of 94% in sediment samples after two washes. These samples were preserved with 10% formalin and the reduction was determined by measuring the fate of radiolabeled formaldehyde.

No attempts were made to separate bacteria from the sediments. White (1983) noted that methods for the removal of microorganisms from a substrate have not proven to be either reproducible or quantitative. Efford and Hall (1975) found bacterial biomass of sediments difficult to estimate; values varied markedly with different techniques.

Weighing, to the nearest 0.01 mg, was accomplished with a Mettler balance (Type H16). This balance was used for all biomass analyses except where noted. Prior to use, aluminum crucibles (5 cm diameter) were placed in a muffle furnace for 16 hours at 550°C, to ensure the removal of any organic contaminants. A subsample of crucibles displayed a mean weight reduction of 0.058% after firing. Sediment samples were placed in tared crucibles and dehydrated at 60°C (maximum oven temperature) for 24 hours in a Blue M Electric Company dry type bacteriological incubator (Model 100A). This oven was employed for the desiccation of all samples in biomass analysis and energy density determination.

After oven drying the sediment samples were cooled to room temperature in a desiccator over anhydrous calcium sulphate (CaSO_4), and weighed (Slack et al. 1973; Heath 1985a, 1985b). The samples were then transferred to a muffle furnace and annealed for 5 hours at 550°C (Rybak 1969; Heath 1985a, 1985b). Samples were cooled in the open air to approximately 80°C , to room temperature in a desiccator then weighed (Heath 1985a, 1985b).

Organic dry weight (or ash-free dry weight) is a reliable estimate of the total organic matter in samples containing mainly soft-bodied organisms (Heath 1985a, 1985b). The organic dry weight was calculated by subtracting ash weight from dry weight; this value represents predominantly the bacteria and particulate detritus in the sediments to a depth of approximately 12 cm. The samples may have contained some Bacillariophyceae (diatoms) (Rigler 1975), benthic protozoa, and minute benthic invertebrates.

Benthos

Prior to sorting, the benthos samples were retained in a 500 μm Nitex sieve and rinsed under a stream of distilled water (Heath 1985a, 1985b). Samples were placed into white trays containing distilled water and sorted with microforceps. The number of faunal organisms in each group was counted. Calcareous shells of clams were mechanically removed and weighed separately from the soft tissue (Crisp 1971; Heath 1985a, 1985b).

Wet weight was determined by blotting specimens with filter paper to remove surface water, prior to weighing in tared aluminum pans (5 cm diameter). Although wet weight is not a reliable measurement of biomass it was included for completeness in this study (Heath 1985a, 1985b). Dry weight was obtained by maintaining samples at 60°C for 24 hours in an oven. After dehydration the benthos samples were placed in a desiccator, cooled to room temperature, and weighed (Heath 1985a, 1985b; Slack et al. 1973). Samples retained for energy density determination were subsequently stored in a desiccator.

Benthos samples collected in 1986 for determining biomass retention efficiency of 500 μ m Nitex were processed identically to those described above. These samples were selected to contain a representative diversity and quantity of benthic organisms. Careful sorting, with the aid of a stereoscopic microscope, through the sieved sediments of these samples failed to produce any visible organisms. Early instars of chironomids (Shiozawa and Barnes 1977), small nematodes, and other diminutive benthic organisms may have escaped detection. However, it appeared that the vast majority of benthic biomass was retained by the Nitex mesh and no correction factor was applied.

Phytoplankton, other microseston, and chlorophyll

Samples of phytoplankton and other microseston on GF/F paper filters were dehydrated at 60°C for 24 hours,

cooled to room temperature in a desiccator, and weighed on a Mettler AE100 balance. The GF/F paper filters (0.7 μm) were selected over the GF/C paper filters (1.2 μm) for quantitative assessments. It was postulated that the finer GF/F paper filter had a higher particulate matter retention capacity per unit water filtered than the coarser GF/C paper filter (used in energy density determination); thereby increasing the accuracy of quantitative assessments. However, the measured difference between the sample means retained on the two filter sizes was not statistically significant ($P > 0.05$) (one-way analysis of variance—e.g. Elliott (1977)).

Organic dry weight of microseston was determined by incinerating the samples for 3 hours at 550°C in a muffle furnace (Cummins and Wuycheck 1971). The samples were cooled in the open air to about 80°C and then placed in a desiccator for further cooling to room temperature (Heath 1985a, 1985b). Organic dry weight was calculated by subtracting ash weight from dry weight. A mean organic dry weight content of only 30.2% was measured suggesting a significant contamination by inorganic particulate matter.

The microseston on the paper filters consisted of phytoplankton, nauplius larvae, protozoa, bacteria, and suspended organic and inorganic particles. This was concluded from water sample analysis for phytoplankton identification. Water samples were placed in a

sedimentation apparatus similar to the type described by Lovegrove (1960). After 24 hours the settled fractions were qualitatively observed with an inverted microscope. This indicated that the samples consisted mainly of phytoplankton. Three species of Bacillariophyceae and one Chrysophyceae frequently dominated the samples (Appendix E, Table E1). Silica frustules of Bacillariophyceae (Lee 1980) may have contributed to the low organic content of the samples. Nauplius larvae, protozoa, and bacteria contributed relatively little to the biomass. Particulate matter was frequently encountered but did not appear quantitatively significant. Reed and Reed (1970) similarly found various planktonic algae dominating the seston sample retained on paper filters.

Microseston samples collected on paper filters during the 1985 field season were damaged in transit. In 1986 forty-eight additional samples were collected; eight per sampling period on each of GF/F and GF/C paper filters.

This paper filter method for quantitatively assessing phytoplankton and other microseston was selected due to time constraints. Reed and Reed (1970) found glass fiber paper filters highly efficient for estimating seston crops; frequently the dry weights of filter catches were approximately twice that of catches determined by centrifugation.

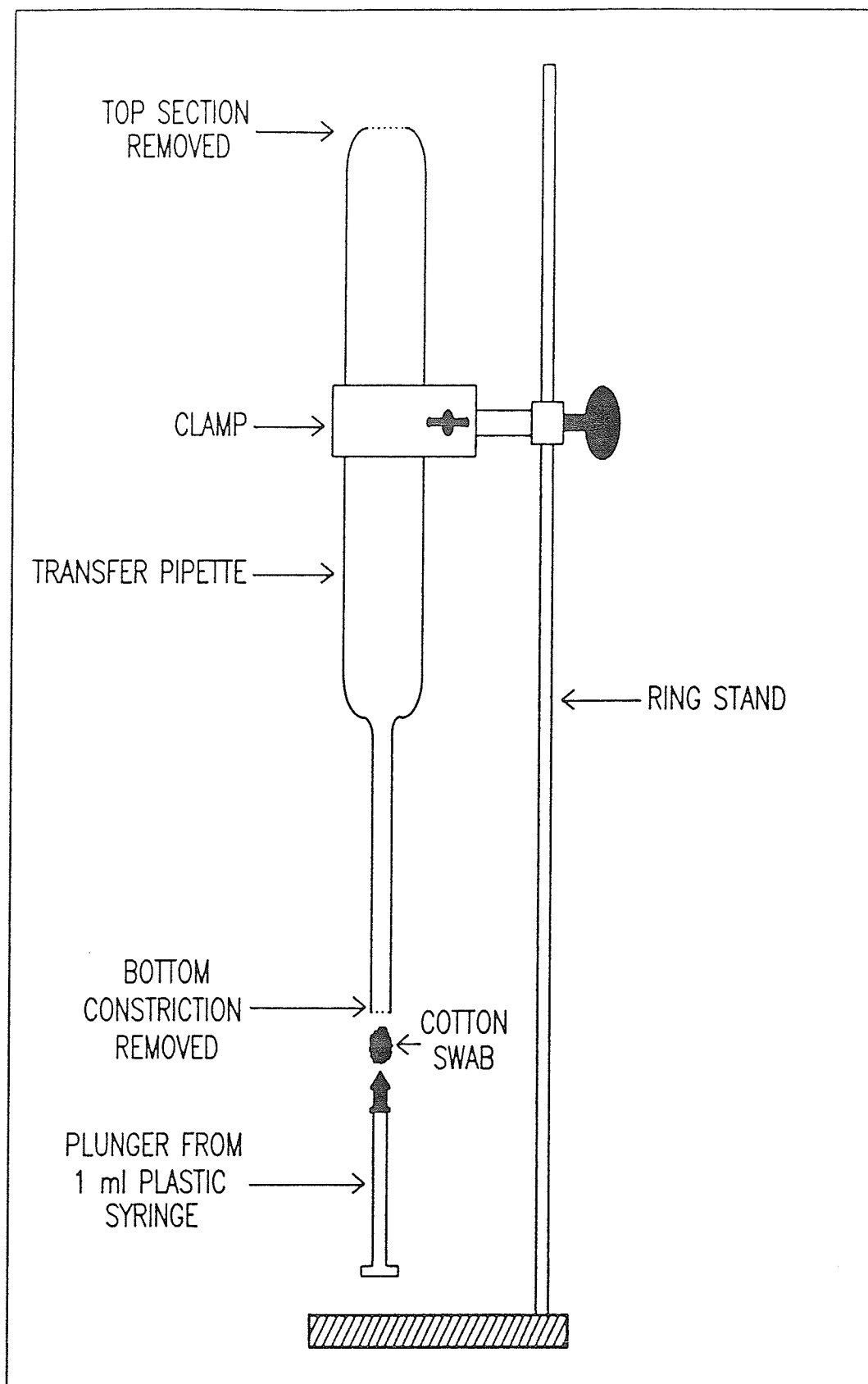
Chlorophyll- α content was determined by the Analytical Chemistry Unit at the Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, mainly according to the procedures outlined in Stainton et al. (1977). A minor deviation was the use of methanol as a solvent instead of acetone (Stainton pers. comm.).

Zooplankton

Zooplankton samples were settled in modified transfer pipettes (50 and 100 ml capacity). These pipettes had the top sections removed to allow easy access to the central expansion. A further modification was the removal of the bottom constriction; this permitted the obstruction of the narrow bottom tube with a plunger from a 1 ml disposable plastic syringe. This sedimentation apparatus was maintained in a vertical position with a laboratory ringstand and clamp (Figure 4).

After 24 hours of settling the preservative was decanted by siphoning. The plunger was removed and the sample was placed in a small aluminum pan containing distilled water. Any visible contaminants were removed with microforceps. Most samples contained little or no debris, however, a few heavily contaminated samples were discarded. This debris was probably due to sediment disturbance by the Wisconsin nets. The sample was returned to the sedimentation apparatus and distilled water was added. The zooplankton was briefly agitated and allowed to settle for

Figure 4. Diagram of sedimentation apparatus employed in zooplankton biomass determination.



24 hours. The water was decanted and the washing procedure was repeated once more.

Wet weight was determined by placing a small cotton swab ahead of the plunger prior to the last washing. After decanting the remaining water was displaced from the settled zooplankton (retained by the cotton swab) by suction created by the removal of the plunger. The sedimentation apparatus was inverted and the cotton swab and sample was pushed through into a tared aluminum pan. The cotton swab was subsequently removed and the sample was weighed.

Dry weight was obtained by placing the sample and pan in an oven for 24 hours at 60°C (Slack et al. 1973). After dehydration the zooplankton samples were placed in a desiccator, cooled to room temperature, and weighed (Heath 1985a, 1985b; Slack et al. 1973). Samples were retained for energy density determination and stored in a desiccator.

Dehydration temperatures

Recommended dehydration temperatures for biological materials vary between materials and among authors. Cummins and Wuycheck (1971) recommended oven drying at 50°C if the material is known to have a high lipid content or to contain in excess of 5% organics volatilized in drying. Slobodkin and Richman (1960) advocated 60°C to prevent losses of volatile, energy rich compounds. Comita and Schindler (1963), and Slack et al. (1973) suggested 60°C for the desiccation of

zooplankton samples. Banse et al. (1963) preferred 70°C for drying seston retained on filters. Heath (1985a, 1985b) recommended 70°C to 100°C for dehydrating macrobenthos. An oven temperature of 80°C produced satisfactory results for Paine (1971) while 100°C was advocated by Crisp (1971), and Atkinson and Wacasey (1983). Ryback (1969) determined dry weights of sediment samples by drying them at 105°C.

Representative samples of sediments, benthos, microseston on paper filters, and zooplankton were maintained at 60°C and weighed at 24, 48, and 72 hours; no appreciable weight change was recorded. These results indicated that a period of 24 hours at 60°C was sufficient for the complete dehydration of small samples; thus permitting accurate dry weight measuring of the sample classes.

Effects of preserving methods on sample weight

The effects of formalin preservation on weights of sediment, benthos, and zooplankton samples are unknown. Howmiller (1972) reported significant losses of organic materials in preserved benthic invertebrates (tubificid worms and chironomid larvae) due to dissolution. Formalin, ethanol, and isopropanol resulted in considerable losses of wet and dry weights. Even freezing induced a significant dry weight loss. The weight losses of specimens maintained in formalin were less than the other preserving methods tested, including freezing. Weight changes in preserved

specimens were found to stabilize after approximately 30 days. On the contrary, Donald and Paterson (1977) found slight wet weight increases in chironomid larvae preserved in formalin. Larvae preserved in formalin with habitat water displayed the least wet weight increase; weights stabilized after 30 days and fluctuated little until the experiment was terminated after 370 days of preservation.

Stanford (1973) concluded that conversion factors for weight loss (or gain), due to preservation, would be difficult to ascertain because weight changes vary among species and depend on the physiological condition of the organisms. This condition maybe influenced by the season and locality from which specimens are collected. Time, manpower, and equipment limitations precluded the sorting and weighing of unpreserved samples in the field. Some weight changes probably occurred in the formalin preserved samples, which were stored for 181 to 314 days.

Calorimetry

Calorimetry is the measurement of energy released from dry substances when they are completely combusted to water and carbon dioxide. Energy units ($\text{cal}\cdot\text{g}^{-1}$ or more recently expressed in $\text{J}\cdot\text{g}^{-1}$) have an identical meaning in all organisms. The energy density (or caloric content) of dry tissue homogenate from whole organisms permits the estimation of energy transfer between trophic levels. Seasonal changes in energy density are frequently induced by

different life-history stages of many organisms (Heath 1985a, 1985b).

All calorimetry was performed with a Gentry-Weigert modification of the Phillipson oxygen microbomb calorimeter manufactured by Gentry Instruments Incorporated. Paine (1971) and Prus (1975) found this instrument entirely adequate for ecological investigations. Detailed operating methods for a similar microbomb calorimeter were covered by Phillipson (1964) and Prus (1975); calorimetry was further reviewed by Crisp (1971), Paine (1971), and Górecki (1975). Output was recorded by a Fisher Recordall (Series 5000) potentiometer manufactured by Houston Instrument.

The calorimeter was calibrated with pelleted samples of calorimetric grade benzoic acid ($\text{C}_6\text{H}_5\text{COOH}$) containing $2.645 \times 10^4 \text{ J}\cdot\text{g}^{-1}$. Operating methods, calibration procedures and frequency, and energy calculations of chart records were according to the operating manual provided by the manufacturer (Gentry Instruments Incorporated, Aiken, South Carolina).

The manufacturer states that the energy density of samples down to 1 mg may be accurately measured. To ensure greater overall accuracy, especially for small samples, the manufacturer's recommendation for determining the heat imparted to the platinum wire from the capacitor discharge was followed. Five separate determinations were carried out

on the platinum wire. The mean of these values was incorporated in calculating energy densities of samples (Gentry Instruments Inc. operating manual).

Schindler et al. (1971) measured reduced accuracy in a calorimeter with standard thermocouples when small samples were employed. To circumvent this possible problem samples in excess of 10 mg were used whenever available, however, this may not have been necessary. To verify the instrument's accuracy over varying sample weight ranges, maximum potential change was plotted against the weights of benzoic acid pellets combusted (range = 3.26-11.00 mg). The maximum potential change was calculated by subtracting the potentiometer reading immediately before igniting the sample from the maximum obtained after ignition and applying the appropriate correction factors (Gentry Instruments Inc. operating manual). A highly correlated linear relationship was found over the benzoic acid pellet weight range ($r^2 = 0.994$, $P < 0.0005$, $n = 12$) (two-tailed t-test for simple linear regression—e.g. Pollard (1977)).

No correction was made for acid formation (HNO_3 and H_2SO_4) during combustion in the calorimeter. Cummins and Wuycheck (1971) noted that the quantities formed are frequently negligible. Craig et al. (1978) found that acid correction changed energy density values obtained by only 1.4%. Determinations were made over the three sampling periods to reduce the effects of periodic energy density

fluctuations that may obscure the interpretation of general trends. All samples for energy density determinations were weighed to the nearest 5 μ g with a Cahn electrobalance (Model Gram). The calorimeter, potentiometer, and electrobalance circuits were activated and allowed to stabilize for 1 hour before use (Schindler et al. 1971). Samples were ground in a small agate mortar, formed into pellets (when sample texture permitted) with a miniature press, then weighed in a tared platinum pan.

Ideally energy density values should be given in both dry weight and organic dry weight. In this study energy density values are generally given in dry weight. The exceptions are noted. Organic dry weight energy density values were not obtainable for many organisms; frequently the limited supply of sample material precluded separate organic content determination. Paine (1971) noted that organic content determination from the residue remaining in a calorimeter after combustion was unacceptable. The combustion of organic materials inside a calorimeter takes place at approximately 1000°C; this temperature is sufficiently high to decompose certain salts (Winberg 1971). In calorimetry for this study the residue was frequently contaminated with molten platinum wire. Cummins and Wuycheck (1971) advocated the expression of energy density values in dry weight.

Benthic bacteria and detritus

To ensure a homogeneous energy distribution per sampling period the sediment samples of each period were consolidated. The washing procedures of sediments for energy density determination were identical to those described in the subsection "Biomass analysis." The samples were subsequently placed in large aluminum pans and dehydrated at 60°C until the weights stabilized; usually between 24 and 72 hours, depending on the sample size. The samples were thoroughly mixed in a Waring blender, reheated to 60°C for 24 hours, and placed in a desiccator for cooling and storage.

After grinding, weighed subsamples (subsequently referred to as samples) were carefully mixed with benzoic acid of predetermined weight (Cummins and Wuycheck 1971) in tared platinum pans. Combustion with this carrier was necessary owing to the low organic content of the sediments. The texture of the sediments prevented the formation of pellets and samples were combusted in an unconsolidated form. Energy per sample was determined by subtracting the known energy of the benzoic acid fraction from the total sample energy.

Benthos

Dehydrated benthos samples, previously preserved in formalin, representing each sampling period were thoroughly mixed to ensure a uniform energy distribution per period.

Ground samples of globose blue-green algae and whole clams could not be formed into pellets and were combusted unconsolidated. Insufficient sample material of nematodes precluded energy density estimates of this phylum.

Frozen samples were thawed and the water was decanted. Desiccation treatment was identical to samples preserved in formalin. No separation of shells from soft tissue was implemented in frozen clams; the sample biomass was insufficient for separate energy density determination of the soft tissue. Samples containing oligochaetes were discarded because the organisms disintegrated after thawing.

Phytoplankton and other microseston

Samples of phytoplankton and other microseston on GF/C paper filters were dehydrated at 60°C for 24 hours, cooled to room temperature in a desiccator, and weighed on a Mettler AE100 balance. The surface layer of the filter was mechanically removed with a scalpel. This layer contained the sample material of predetermined weight and glass fibers from the filter. After grinding, the sample and glass fiber conglomerate was carefully mixed with benzoic acid of premeasured weight (Cummins and Wuycheck 1971) on a tared platinum pan. The glass fiber content of the conglomerate sample precluded ignition without the addition of benzoic acid. Pellet formation was not possible and the mixture was combusted in an unconsolidated form. Energy per net sample was calculated by subtracting the predetermined energy

contained in the benzoic acid fraction from the total sample energy.

The paper filter method of collecting microseston was selected due to the difficulties associated with securing sufficient quantities for calorimetry. The overall higher particulate matter retention capacity of the coarser GF/C paper filters made these more suitable for energy density determination. More sample material was retained on the GF/C paper filters; water volume filtered was double that of the finer GF/F paper filters before the pores clogged.

Zooplankton

Desiccated samples, formerly preserved in formalin, were combined and thoroughly agitated to form three samples, each representing one sampling period. Frozen samples were thawed and the water was immediately decanted by suction from a 50 ml plastic disposable syringe inserted into the Whirlpak. The samples were transferred to aluminum pans and the dehydration treatment was identical to samples preserved in formalin.

Arctic charr

The length-frequency distribution of the subsample of Arctic charr selected for energy density determination represented proportionally the biomass distribution in the different length classes of the whole population. For

example, a larger number of specimens were selected in the adult length classes to sample proportionally the higher biomass contained in Arctic charr 30 cm or larger. This subsample configuration was chosen to reduce bias from possible length dependent energy density relationships. Furthermore, the sex ratio of the subsample was slightly in favour of the males, as in the lake population. Energy density differences between the specimens contained in the subsample were found to be statistically very highly significant ($P < 0.001$) (one-way analysis of variance).

Fourteen Arctic charr, preserved in formalin for 47 to 68 days, were rinsed under a stream of distilled water and preserved wet weight was determined with a Mettler PL3000 balance (0.1 g accuracy). This indicated an average weight reduction of 3.0% from unpreserved wet weight. Whole Arctic charr were individually ground in a Waring blender. The ground specimens were placed in large, tared aluminum pans and desiccated at 60°C until weights stabilized; usually between 24 and 72 hours, depending on specimen size. Samples were re-weighed and percentage dry weight of unpreserved wet weight calculated. Thorough mixing in a Waring blender was repeated with the ground and dehydrated specimens. Samples were returned to an oven and maintained at 60°C for 24 hours followed by cooling and storing in a desiccator.

To ascertain the effects of formalin preservation on the energy density of Arctic charr five frozen specimens, of representative size and sex, were sectioned through the sagittal plane. One half of each individual was placed in 10% formalin for 7 days and transferred to 5% formalin for an additional 30 days. Weight stabilization of formalin preserved benthic invertebrates occurred after approximately 30 days (Howmiller 1972; Donald and Paterson 1977). This procedure was implemented to by-pass energy density differences in individual specimens. The grinding and dehydration methods for formalin preserved and frozen halves were identical to the treatment for whole formalin preserved fish, described in the preceding paragraph.

Aging technique of Arctic charr

Sagittal otoliths were cleared in a 2:1 solution of benzyl benzoate and methyl salicylate followed by reading under a stereoscopic microscope (Johnson 1983). Some otoliths were briefly ground on an abrasive stone to enhance contours between bands.

Bands were read according to Nordeng's (1961) interpretation; a check mark in the nuclear region is believed to be formed in the middle of the first summer after hatching. Data obtained from newly hatched and young Arctic charr parr by Johnson (1983) were consistent with Nordeng's findings. Hunter (1970) followed Grainger's (1953) method of otolith reading; otoliths collected in

Keyhole Lake from 1962 to 1967 were read 1 year older. Age data presented in this study from Hunter (1970) were adjusted downward by 1 year to ensure uniformity in comparing age structures.

MATHEMATICAL AND STATISTICAL TREATMENT OF DATA

Biomass estimation

Benthic bacteria and detritus, benthos, and zooplankton

Mean biomass ($\bar{x}$) estimates of stratified random samples for benthic bacteria and detritus, benthos, and zooplankton were calculated as follows:

$$\bar{x} = \frac{\sum_{i=1}^k n_i \bar{x}_i}{\sum_{i=1}^k n}, \quad (7)$$

where n_i = number of sampling units sampled in the i th stratum, $\bar{x}_i$ = sample mean from these sampling units, and n = number of sampling units sampled from all the strata (Slack et al. 1973; Elliott 1977).

The standard error of the mean ($s_{\bar{x}}$) of the stratified random samples were computed with the following formula:

$$s_{\bar{x}} = \sqrt{\sum_{i=1}^k \left(\frac{N_i}{N} \right)^2 \left(\frac{s_i^2}{n_i} \right) \left(1 - \frac{n_i}{N_i} \right)}, \quad (8)$$

where s_i^2 = sample variance of the i th stratum, N_i = total number of sampling units in the i th stratum, n_i = number of sampling units sampled in the i th stratum, and N = total number of sampling units in all strata ($\sum N_i$) (Slack et al. 1973; Elliott 1977).

Approximate confidence intervals about the mean were calculated according to the formula:

$$\bar{x} \pm (t) (s_{\bar{x}}), \quad (9)$$

where t = Student's t distribution and has $n-1$ degrees of freedom, and $s_{\bar{x}}$ = standard error of the mean given in formula (8) (Slack et al. 1973; Elliott 1977). All confidence intervals are presented at the 95% probability level.

The two "benthos" strata in the deepest region of the lake (5 to 6 m and 6.0 to 6.8 m) were combined to permit the calculation of variance; each stratum contained only one sampling station (see formula (8)). Biomass and confidence

intervals for the whole lake were computed by multiplying formulae (7) and (9) by the number of sampling units contained in the lake, respectively. Trophic level means and confidence intervals were obtained by merging organisms of a particular trophic level into one sample. Means and confidence intervals for combined sampling periods were calculated by consolidating the periods into one. The total number of benthic organisms per lake, mean organism weight, and confidence intervals were also computed with formulae (7) to (9).

Organic dry weight estimates of benthic bacteria and detritus for the whole lake were calculated from estimates of strata exceeding 1 m in depth. The coarse unconsolidated sediments of inshore regions shallower than 1 m probably contributed little to the overall weight of bacteria and detritus. A factor affecting bacteria abundance is the mean grain size of the sediments; microbial biomass generally declines as mean grain size increases (Dale 1974; Rublee and Dornseif 1978). Seyfried and Owen (1979) congruently found bacteria adsorption low in coarse sandy gravel compared to fine-grained sand. During each sampling period in 1985 twenty-seven samples were collected.

Benthos biomass estimates for 1985 were calculated from thirty samples per sampling period. Organisms missing from a sample were recorded as zero.

Distributions of benthic invertebrates at various depth ranges were calculated from formulae (7) and (8). The exclusion of the summation symbol (Σ) from formulae (7) and (8) gave mean biomass ($\bar{x}$) and standard error of the mean ($s_{\bar{x}}$), respectively, of the various strata.

Zooplankton biomass was estimated from 27, 24, and 23 samples collected in 1985 during periods I, II, and III, respectively. During each sampling period thirty samples were collected; a few samples contained large quantities of debris and were discarded.

Phytoplankton, other microseston, and chlorophyll

Total organic dry weight of phytoplankton and other microseston was calculated by assuming simple random sampling (Slack et al. 1973; Elliot 1977). This type of sampling was advocated by Slack et al. (1973) for uniformly distributed organisms, such as phytoplankton, in well-mixed lakes. Sample mean and 95% confidence intervals were computed according to standard statistical procedures described in Slack et al. (1973), Elliott (1977), and most statistics texts (e.g. Snedecor and Cochran 1980; Freund 1981; Huntsberger and Billingsley 1981).

Damage to one sample precluded the use of formulae for stratified random sampling. The omission of this sample resulted in a stratum containing only one sample; formula (8) requires at least two samples per stratum to determine

variance. Two strata (or quadrants) were not combined since this may have negated or even biased the effects, if any, of wind-induced plankton distribution. To ensure consistency in statistical procedures all calculations pertaining to organic dry weight of microseston were performed assuming simple random sampling. The estimates for 1986 were based on eight samples each for sampling periods I and III, and seven for period II.

An organic dry weight to dry weight conversion factor was derived from tables in Cummins and Wuycheck (1971); these tables compared energy densities of dry weights and organic dry weights in twenty-nine taxa of planktonic and benthic algae. This factor was 1.412 and permitted the conversion of organic dry weights of phytoplankton and other microseston to approximate dry weights. The relationship is as follows:

$$\begin{aligned} (\text{organic dry weight in } \text{J} \cdot \text{g}^{-1}) = \\ (\text{dry weight in } \text{J} \cdot \text{g}^{-1}) (K), \end{aligned} \tag{10}$$

hence,

$$\begin{aligned} (\text{dry weight in g}) = \\ (\text{organic dry weight in g}) (K), \end{aligned} \tag{11}$$

where K = conversion factor. This conversion factor is only an approximation since many taxa were not contained in the microseston samples from Keyhole Lake.

The mean and 95% confidence intervals of the sixteen chlorophyll- α samples collected per sampling period were computed according to standard statistical procedures. Correlation between chlorophyll- α content and organic dry weight of phytoplankton and other microseston was evaluated from sixteen sets. Each comparison set was selected from samples collected at the same time and station but different diurnal times and sampling periods were involved among the various sets.

Arctic charr

The Leslie-DeLury method of estimating population size was employed to assess Arctic charr biomass. This technique was developed independently by Leslie and Davies (1939) and DeLury (1947). The non-migratory nature of the Arctic charr population in Keyhole Lake permitted the use of this method. Population size is estimated by calculating a regression over time of an index of current population size on an index of cumulative population decline (Braaten 1969). DeLury (1947, 1951) explains the formula employed as follows:

$$C(t) = kW - kK(t), \quad (12)$$

where (t) = the (t) th interval, $C(t) = c(t)/e(t)$ is the average catch per unit effort during the (t) th interval, $c(t)$ and $e(t)$ = the catch and the effort for the (t) th interval, respectively, $K(t)$ = the total catch up to the (t) th interval (i.e. $K(t) = c(1) + c(2) + \dots + c(t-1)$), $k(t) = k$ (assumed to be a constant) is the "catchability" during the (t) th interval (i.e. the proportion of the population captured by one unit of effort), and $W(t)$ = the weight of the population at the beginning of the (t) th interval. The notation $\hat{W} = W(1)$ is the weight of the population at the beginning of the sampling period based on catch per unit effort. Values for $C(t)$ and $K(t)$ are calculated from catch-effort data and plotted. If the graph is reasonably straight estimates of k and $\hat{W}$ can be computed by the method of least squares:

$$\begin{cases} \hat{k} = -L/M, \\ \hat{k}\hat{W} = [\Sigma C(t) + \hat{k}\Sigma K(t)]/m, \end{cases} \quad (13)$$

$$\begin{cases} L = m\Sigma[C(t) K(t)] - [\Sigma C(t)] [\Sigma K(t)], \\ M = m\Sigma[K(t)]^2 - [\Sigma K(t)]^2, \end{cases} \quad (14)$$

where m = number of samples, and Σ stands for $\sum_{t=1}^m$. The estimate of the population ($\hat{W}$) is calculated by:

$$\hat{W} = \hat{k}\hat{W}/\hat{k}. \quad (15)$$

Confidence intervals for $\hat{W}$ were obtained by the roots of the following quadratic equation (after DeLury 1947, 1951):

$$\hat{W}^2[\hat{k}^2 - t_{\alpha}^2 s^2 c_{22}] - 2\hat{W}[\hat{k}(\hat{k}\hat{W}) - t_{\alpha}^2 s^2 c_{12}] + [\hat{k}\hat{W}^2 - t_{\alpha}^2 s^2 c_{11}] = 0, \quad (16)$$

where t_{α} = the tabulated t-value at the $1-\alpha$ confidence level with $m-2$ degrees of freedom, and

$$\left\{ \begin{array}{l} c_{11} = \Sigma[K(t)]^2/M, \\ c_{12} = \Sigma K(t)/M, \\ c_{22} = m/M, \\ s^2 = \{\Sigma[C(t)]^2 - [\Sigma C(t)]^2/m - L^2/(mM)\}/(m-2). \end{array} \right. \quad (17)$$

Confidence estimates for $\hat{W}$ are given by:

$$\left\{ \begin{array}{l} \bar{W} = \hat{W}X_1, \\ \underline{W} = \hat{W}X_2, \end{array} \right. \quad (18)$$

where $\bar{W}$ = the upper confidence estimate of $\hat{W}$, $\underline{W}$ = the lower confidence estimate of $\hat{W}$, X_1 = the larger solution of formula (16), and X_2 = the smaller solution of formula (16). The confidence intervals were calculated at the 95% probability level.

The estimate of total weight of the Arctic charr population just prior to the 1985 fishery ($\hat{W}_T$) was based on $\hat{W}$ plus the weight of fish captured by methods other than catch per unit of effort (i.e. angling and electrofishing). The latter fraction represented only 2.1% of the estimated total population weight. Confidence estimates were proportionally added to $\hat{W}_T$:

$$\begin{cases} \bar{W}_T = \hat{W}_T X_1, \\ \underline{W}_T = \hat{W}_T X_2, \end{cases} \quad (19)$$

where $\bar{W}_T$ = the upper confidence estimate of $\hat{W}_T$, and $\underline{W}_T$ = the lower confidence estimate of $\hat{W}_T$. Since the weight of Arctic charr captured by methods other than catch per unit effort was relatively small (39.872 kg wet weight) confidence estimates of $\hat{W}_T$ should not have been significantly biased.

Appendix F, Figure F1 displays the results of the Leslie-DeLury procedure applied to the 1985 and 1986 catch weight data. The 1985 data does not follow a distinct straight line. However, estimates of $\hat{W}$ from 1985-86 data

and 1986 data are almost identical; 1880.288 kg wet weight for 1985-86 and 1883.064 kg wet weight for 1986. Thus the 1985-86 catch weight data appeared a reasonable estimator of $\hat{W}$ especially since 1985-86 values were better correlated ($r^2 = 0.667$, $P < 0.0005$, $n = 45$) than 1986 values ($r^2 = 0.504$, $P < 0.0005$, $n = 21$).

An alternative approach was applied in estimating population number (formula (20)). Initial catches consisted predominantly of specimens in the larger length ranges (≥ 30 cm), however, as the population was gradually reduced a shift to smaller individuals occurred. Catch numbers decreased at a slower rate than catch weight. This non-linear relationship resulted in an unreasonably high population number estimate with the Leslie-DeLury method. Furthermore, the decrease in weight per unit of effort displayed better correlation ($r^2 = 0.667$, $P < 0.0005$, $n = 45$) than the decline in numbers per unit of effort ($r^2 = 0.543$, $P < 0.0005$, $n = 45$).

A more acceptable approximation of total population number was obtained by segregating the smaller length classes from the larger length classes at the point of lowest length-frequency (30 cm) and applying formula (12) to the weight per unit of effort of fish ≥ 30 cm (Appendix F, Figure F2). This permitted the development of the following formula:

$$\hat{N}_T = N + \frac{\hat{L}_T - L_C}{\bar{L}} + \frac{\hat{W}_T - \hat{L}_T - S_C}{\bar{S}}, \quad (20)$$

where $\hat{N}_T$ = estimated total number of individuals in the population just prior to the 1985 fishery, N = total number of captured individuals, $\hat{L}_T$ = estimated total weight of individuals ≥ 30 cm in the population just prior to the 1985 fishery, L_C = total weight of captured individuals ≥ 30 cm, $\bar{L}$ = mean weight of captured individuals ≥ 30 cm, $\hat{W}_T$ = estimated total weight of the population just prior to the 1985 fishery, S_C = total weight of captured individuals < 30 cm, and $\bar{S}$ = mean weight of captured individuals < 30 cm. The small fraction of Arctic charr captured by methods other than catch per unit of effort were included in calculating $\hat{N}_T$.

Since $\hat{N}_T$ is proportionally related to $\hat{W}_T$, 95% confidence intervals for $\hat{W}$ from equation (16) were applied to $\hat{N}_T$:

$$\begin{cases} \bar{N}_T = \hat{N}_T X_1, \\ \underline{N}_T = \hat{N}_T X_2, \end{cases} \quad (21)$$

where $\bar{N}_T$ = the upper confidence estimate of $\hat{N}_T$, and $\underline{N}_T$ = the lower confidence estimate of $\hat{N}_T$. Formula (18) discusses the notations X_1 and X_2 . The rationale for applying confidence

intervals obtained from catch per unit effort data to estimates that include other capture methods was discussed in a preceding paragraph in this subsection.

Significance levels for the differences between sex ratios were determined with the chi-square test (Elliott 1977; Snedecor and Cochran 1980; Freund 1981; Huntsberger and Billingsley 1981).

Unpreserved wet weight biomass of Arctic charr and the appropriate confidence intervals were converted to dry weight values by multiplying wet weight values times a conversion factor of 0.2206 (determined in the laboratory).

Energy density estimation

Usually six measurements of energy density per sampling period for each taxon or trophic level were performed. Exceptions were as follows: benthic bacteria and detritus ($n = 4$, Period I, 1985; $n = 3$, Period II, 1985; $n = 4$, Period III, 1985), phytoplankton and other microseston ($n = 7$, Period II, 1986), clams (soft tissue only) ($n = 2$, Period I, 1985; $n = 5$, Period II, 1985; $n = 4$, Period III, 1985); chironomid pupae ($n = 3$, Period I, 1985 only), caddisfly larvae ($n = 3$, Period I, 1985; $n = 1$, Period II, 1985; $n = 1$, Period III, 1985), and caddisfly pupae ($n = 3$, Period III, 1985 only). Frequently insufficient sample material was available for the combustion of six samples and in some instances pupal stages

were not present in the samples from a particular period. Energy densities of Arctic charr were determined by three measurements per specimen (sample $n = 15$, Period I, 1985; sample $n = 42$, Period III, 1985). No individuals were retained in Period II, 1985, for energy density analysis. Standard statistical methods were employed to calculate means and 95% confidence intervals. Estimates of mean energy density for the total period of investigation were obtained by pooling individual values from different sampling periods when the number of samples were equal in each period. If sample numbers were disproportionate among sampling periods then the period mean was used to compute the grand mean. Variances were calculated around this grand mean. This procedure was not required for Arctic charr; the mean of each period was identical. Missing periods were excluded from calculations.

The effects of formalin preservation versus freezing on energy density of organisms collected during the same sampling period are summarized in Appendix G, Figure G1. Only filamentous algae and chironomid larvae did not display statistically significant differences ($P > 0.05$) between the two preserving methods (statistical methods are discussed at the end of this subsection). Similarly, Schindler et al. (1971), and Atkinson and Wacasey (1983) found energy density changes in organisms preserved in formalin compared with fresh and frozen samples. Correction factors were applied

to energy density values of formalin preserved samples of the organisms evaluated in Appendix G, Figure G1. Frozen equivalent energy density estimates were obtained by multiplying formalin preserved values by the following constants: globose blue-green algae 0.9447, filamentous algae 0.9327, clams with shells 0.5426, chironomid larvae 0.9700, Gammarus lacustris 0.8295, zooplankton 1.0932, and Arctic charr 0.9276. These correction factors assume that the effects of formalin preservation are proportionally related to fluctuating energy densities. The foregoing indicates that energy density values of non-corrected formalin preserved samples are probably less accurate than determinations corrected for formalin preservation.

Energy density estimates for the trophic levels designated as benthic algae and benthic invertebrates were computed with formula (7). In this application $\bar{x}$ = energy density of the trophic level, n_i = total biomass of organism i , $\bar{x}_i$ = energy density of organism i , and n = total biomass of all organisms in the trophic level. The standard error of the mean ($s_{\bar{x}}$) was calculated with formula (8). The finite correction factor, $1 - (n_i/N_i)$, was not applicable in this context and omitted (Slack et al. 1973; Elliott 1977). The symbols in formula (8) are subsequently defined as: s_i^2 = sample energy density variance of organism i , N_i = total biomass of organism i , n_i = number of sampling units of organism i , and N = total biomass of all organisms in the

trophic level. Confidence intervals were computed with formula (9). Only energy density values of the soft tissue of clams were included in calculating the energy density of the benthic invertebrate trophic level. The high biomass and low energy density of clams with shells would bias the energy density estimate of this trophic level.

Energy density estimates of the organic dry weight of benthic bacteria and detritus were calculated by applying the appropriate correction factor obtained from the organic content of the sample material. This was ascertained by incinerating some sample material as described in "Biomass analysis—Benthic bacteria and detritus." Energy density estimates of the organic material in microseston were computed by the correction factors obtained in biomass analysis. The organic content of microseston was determined for each sampling period (see "Biomass analysis—Phytoplankton, other microseston, and chlorophyll"). Dry weight energy density values were approximated by the procedure described in "Calorimetry—Phytoplankton and other microseston" (formula (10)). That subsection's criticism of this method applies equally to dry weight energy density estimates.

A one-way analysis of variance was employed for energy density comparisons, except for the comparison between frozen and formalin preserved Arctic charr. The latter required a two-way analysis of variance since energy

density varied among individual Arctic charr and between preserving methods. The one-way analysis of variances were computed according to standard statistical procedures outlined in, for example, Elliott (1977), Snedecor and Cochran (1980), Freund (1981), and Huntsberger and Billingsley (1981). The two-way analysis of variance was calculated by the method described in Elliott (1977).

Biomass energy estimation

An estimate of energy contained in the biomass of a taxon or trophic level in Keyhole Lake was readily calculated by multiplying energy density times biomass. This direct method was not possible with the estimation of variance. Biomass energy variance can not be estimated by combining the variance of energy density with that of biomass. A method called the bootstrap was employed to assess variability.

The technique and application of "bootstrapping", developed by Efron, is well described in the literature (e.g. Efron 1979a, 1979b, 1981a, 1981b, 1984, 1985, 1986; Diaconis and Efron 1983; Efron and Tibshirani 1986). This computer-intensive method involves copying each data set an enormous number of times. The resulting copies of each data set are thoroughly mixed and bootstrap samples are generated by randomly selecting and combining data points from each data set. The distribution of variance for bootstrap samples can be treated as if the variance distribution was

computed from real samples. The variance distribution, when plotted against number of bootstrap samples, becomes asymptotic when sufficient bootstrap samples are generated (Diaconis and Efron 1983). For this study 1,100 to 1,200 bootstrap samples were adequate for reaching the desired results. All confidence intervals were calculated at the 95% probability level.

Energy density values of clams complete with shells were used in calculating the biomass energy in the benthic invertebrate trophic level and this taxon. Some energy was contained in the shells and energy density values corrected for formalin preservation were available for whole clams.

The confidence intervals of the biomass energy in Arctic charr were based on biomass times confidence estimates of energy density. This procedure was employed since biomass variance was based on catch per unit of effort and not on a simple sample variance. The variance would probably be somewhat higher if a technique were to be developed to incorporate catch per unit effort variance in "bootstrapping."

The "bootstrapping" technique was inappropriate for estimating the variance of energy density per trophic level; it would have biased the desired variance by incorporating biomass variance (see "Energy density estimation").

RESULTS

The terms taxa and trophic levels are frequently used in a broad context; some samples may have contained extraneous matter and organisms unrelated to a taxon or trophic level (this was discussed in considerable detail in the preceding chapter under "Laboratory analysis—Biomass analysis"). Period designations represent samples collected in 1985, except for samples of phytoplankton and other microseston which were obtained in 1986.

ENERGY DENSITY

Energy density estimates for different taxa and trophic levels were corrected for formalin preservation except for the following: benthic bacteria and detritus, oligochaetes, clams (soft tissue only), chironomid pupae, caddisfly larvae, and caddisfly pupae (Table 2). Levels of statistical significance for energy density comparisons are as follows unless indicated otherwise (after Elliott 1977):

Not significant	= $P > 0.05$
Significant	= $P < 0.05$
Highly significant	= $P < 0.01$
Very highly significant	= $P < 0.001$

Table 2. Energy density estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $\text{J}\cdot\text{g}^{-1}$ dry weight unless noted otherwise (95% confidence intervals).

Trophic Level	Taxon	Period I	Period II	Period III	Periods $\bar{x}$
Benthic bacteria/detritus (nonadjusted dry weight)* (organic dry weight)		875 $\pm$ 534	940 $\pm$ 261	1,118 $\pm$ 982	978 $\pm$ 271
		10,902 $\pm$ 6,651	11,985 $\pm$ 3,326	13,444 $\pm$ 11,810	12,110 $\pm$ 3,252
Phytoplankton/microseston (organic dry weight)		10,214 $\pm$ 5,010	15,486 $\pm$ 5,311	14,706 $\pm$ 4,697	13,469 $\pm$ 2,562
		14,425 $\pm$ 7,076	21,871 $\pm$ 7,500	20,768 $\pm$ 6,633	19,021 $\pm$ 3,618
Benthic algae	Globose blue-green algae	16,146 $\pm$ 166	15,242 $\pm$ 1,161	16,798 $\pm$ 802	16,062 $\pm$ 490
	Filamentous algae	16,982 $\pm$ 216	15,724 $\pm$ 401	17,092 $\pm$ 396	16,599 $\pm$ 354
Benthic algae $\bar{x}$		16,906 $\pm$ 168	15,674 $\pm$ 324	17,079 $\pm$ 326	16,557 $\pm$ 315
Benthic invertebrates	Chironomid larvae	19,341 $\pm$ 760	18,734 $\pm$ 871	17,909 $\pm$ 884	18,661 $\pm$ 480
	Chironomid pupae	24,179 $\pm$ 822	—	—	24,179 $\pm$ 822
	Gammarus lacustris	19,852 $\pm$ 366	19,212 $\pm$ 258	17,294 $\pm$ 454	18,786 $\pm$ 579
	Clams	—	—	—	—
	(soft tissue only)	21,872 $\pm$ 351	20,582 $\pm$ 1,311	21,098 $\pm$ 843	21,184 $\pm$ 604
	(with shells)	2,741 $\pm$ 185	2,733 $\pm$ 180	2,535 $\pm$ 160	2,670 $\pm$ 92
	Caddisfly larvae	24,373 $\pm$ 789	18,579 $\pm$ —	22,659 $\pm$ —	21,870 $\pm$ 3,426
Benthic invertebrate $\bar{x}$	Caddisfly pupae	—	—	24,964 $\pm$ 537	24,964 $\pm$ 537
	Oligochaetes	21,662 $\pm$ 750	20,938 $\pm$ 1,030	19,934 $\pm$ 625	20,845 $\pm$ 514
		20,508 $\pm$ 318	19,489 $\pm$ 424	18,735 $\pm$ 341	19,604 $\pm$ 270
Zooplankton		26,079 $\pm$ 720	21,976 $\pm$ 874	23,219 $\pm$ 313	23,758 $\pm$ 930
Arctic charr		21,882 $\pm$ 632	—	21,882 $\pm$ 351	21,882 $\pm$ 297

*Includes inorganic contaminants.

Comparison between trophic levels

Periodic energy densities between trophic levels (Figures 5 to 7) and the means of the three sampling periods (Figure 8) indicated a trend: an increase of energy density along ascending trophic levels. Zooplankton energy densities exceeded that of Arctic charr; however, the planktonic fauna appears to represent the terminus of a separate food chain with phytoplankton and other microseston forming the subordinate trophic level. The trophic relationship between benthic bacteria and benthic algae is less clear due to their interaction in a complex detrital cycle; nevertheless, their energy densities were below that of the consumer levels. Separate food chains and detrital cycling are discussed in the following chapter. The main food chain, terminating with Arctic charr, displayed a distinct energy density increase with each succeeding step along the trophic ladder (Figure 9). This energy density hierarchy was also evident in the food chain consisting of phytoplankton and other microseston, and zooplankton (Figures 5 to 8).

No statistically significant differences were found in energy densities of organic dry weight between (1) benthic bacteria and detritus, and (2) phytoplankton and other microseston (Figures 5 to 7), during the three sampling periods (Table 3, Nos. 1 to 3). However, combining the sampling periods (Figure 8) gave highly significant

Table 3. Analysis of variance of energy density estimates among trophic levels and taxa within trophic levels. Dry weight energy density comparisons and one-way ANOVA unless noted otherwise.

No.	Comparison	df	F	Prob>F
1	1; 2a Period I	1,8	0.85	>0.05
2	1; 2a Period II	1,8	4.12	>0.05
3	1; 2a Period III	1,9	2.59	>0.05
4	1; 2a Periods combined	1,29	7.64	<0.01
5	2; 3a*b*; 4a*bc*dfh; 5*; 6* Period I	4,60	66.67	<0.001
6	2; 3a*b*; 4a*c*dfh; 5* Period II	3,45	17.54	<0.001
7	2; 3a*b*; 4a*c*dfgh; 5*; 6* Period III	4,88	30.60	<0.001
8	2; 3a*b*; 4a*bc*dfgh; 5*; 6* Periods combined	4,202	82.84	<0.001
9	3a*b*; 4a*bc*dfgh; 6* Periods combined	2,166	133.05	<0.001
10	2; 5* Periods combined	1,36	55.68	<0.001
11	2; 3a*b*; 4a*c*; 5*; 6* Period I	4,46	78.49	<0.001
12	2; 3a*b*; 4a*c*; 5* Period II	3,33	11.47	<0.001
13	2; 3a*b*; 4a*c*; 5*; 6* Period III	4,74	50.18	<0.001

Continued

No.	Comparison	df	F	Prob>F
14	2; 3a*b*; 4a*c*; 5*; 6* Periods combined	4,162	90.45	<0.001
15	3a*b*; 4a*c*; 6* Periods combined	2,126	325.04	<0.001
16	2; 3a*; 3b*; 4a*; 4b; 4c*; 4d; 4f; 4h; 5*; 6* Period I	10,54	43.26	<0.001
17	2; 3a*; 3b*; 4a*; 4c*; 4d; 4f; 4h; 5* Period II	8,40	6.92	<0.001
18	2; 3a*; 3b*; 4a*; 4c*; 4d; 4f; 4g; 4h; 5*, 6* Period III	10,82	25.28	<0.001
19	2; 3a*; 3b*; 4a*; 4b; 4c*; 4d; 4f; 4g; 4h; 5*; 6* Periods combined	11,195	43.25	<0.001
20	2; 3a*; 3b*; 4a*; 4c*; 5*; 6* Period I	6,44	51.25	<0.001
21	2; 3a*; 3b*; 4a*; 4c*; 5* Period II	5,31	6.55	<0.001
22	2; 3a*; 3b*; 4a*; 4c*; 5*; 6* Period III	6,72	32.84	<0.001
23	2; 3a*; 3b*; 4a*; 4c*; 5*; 6* Periods combined	6,160	59.86	<0.001
24	3a*; 3b* Period I	1,10	62.28	<0.001

Continued

No.	Comparison	df	F	Prob>F
25	3a*; 3b* Period II	1,10	1.02	>0.05
26	3a*; 3b* Period III	1,10	0.72	>0.05
27	3a*; 3b* Periods combined	1,34	3.52	>0.05
28	4a*; 4b; 4c*; 4d; 4f; 4h; Period I	5,20	59.08	<0.001
29	4a*; 4c*; 4d; 4f; 4h Period II	4,19	7.73	<0.001
30	4a*; 4c*; 4d; 4f; 4g; 4h Period III	5,20	85.67	<0.001
31	4a*; 4b; 4c*; 4d; 4f; 4g; 4h Periods combined	6,69	30.98	<0.001
32	4a; 4b Period I	1,7	83.84	<0.001
33	4d; 4e* Periods combined	1,27	7,445.05	<0.001
34	4f; 4g Period III	1,2	85.19	<0.025
35	1 Periods I, II, III	2,8	0.24	>0.05
36	2 Periods I, II, III	2,17	1.86	>0.05
37	3a* Periods I, II, III	2,15	5.99	<0.025
38	3b* Periods I, II, III	2,15	31.46	<0.001

Continued

No.	Comparison	df	F	Prob>F
39	4a* Periods I, II, III	2,15	4.84	<0.025
40	4c* Periods I, II, III	2,15	91.23	<0.001
41	4d Periods I, II, III	2,8	1.84	>0.05
42	4e* Periods I, II, III	2,15	2.92	>0.05
43	4f Periods I, II, III	2,2	125.10	<0.01
44	4h Periods I, II, III	2,15	7.41	<0.01
45	5* Periods I, II, III	2,15	63.59	<0.001
46	6* Periods I, III	1,55	2.88×10^{-6}	>0.05
47	3a Formalin vs. freezing	1,4	19.44	<0.025
48	3b Formalin vs. freezing	1,10	3.73	>0.05
49	4a Formalin vs. freezing	1,10	1.22	>0.05
50	4c Formalin vs. freezing	1,9	93.76	<0.001
51	4e Formalin vs. freezing	1,8	146.32	<0.001
52	5 Formalin vs. freezing	1,10	20.33	<0.005
53	6† Formalin vs. freezing	1,14	107.84	<0.001

Continued

No.	Comparison	df	F	Prob>F
54	6* 19 Specimens compared	18,38	8.18	<0.001

Comparison codes

- 1 = Benthic bacteria/detritus (organic dry weight)
- 2 = Phytoplankton/microseston (organic dry weight adjusted to dry weight)
- 2a = Phytoplankton/microseston (organic dry weight—not formalin preserved)
- 3 = Benthic algae
- 3a = Globose blue-green algae
- 3b = Filamentous algae
- 4 = Benthic invertebrates
- 4a = Chironomid larvae
- 4b = Chironomid pupae
- 4c = Gammarus lacustris
- 4d = Clams (soft tissue only)
- 4e = Clams (with shells)
- 4f = Caddisfly larvae
- 4g = Caddisfly pupae
- 4h = Oligochaetes
- 5 = Zooplankton
- 6 = Arctic charr
- * = Corrected for formalin preservation
- † = Five specimens compared—two-way ANOVA

Figure 5. Energy density estimates of trophic levels during Period I, 1985 (phytoplankton and other microseston during Period I, 1986) (95% confidence intervals).

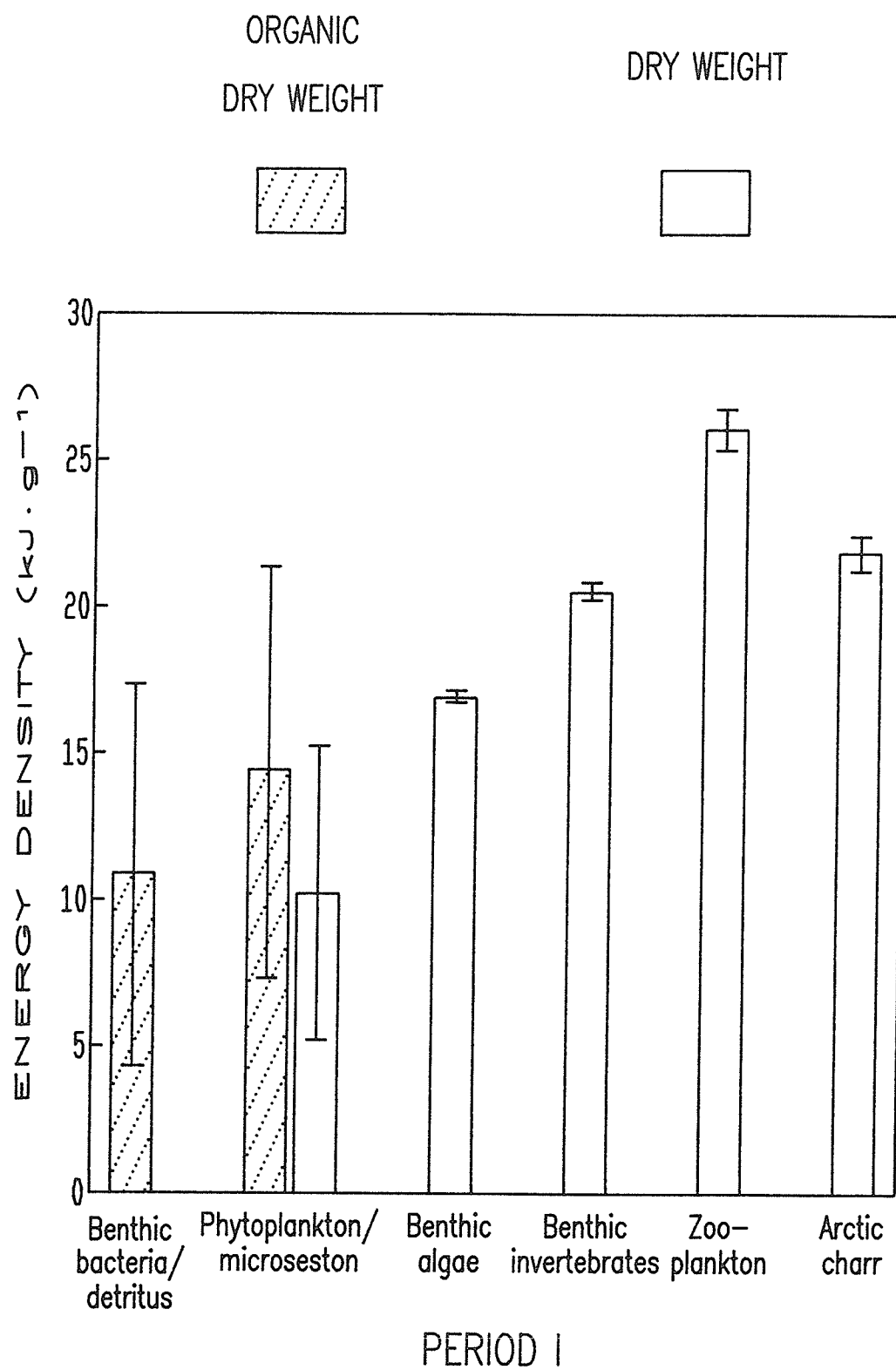


Figure 6. Energy density estimates of trophic levels during Period II, 1985 (phytoplankton and other microseston during Period II, 1986) (95% confidence intervals).

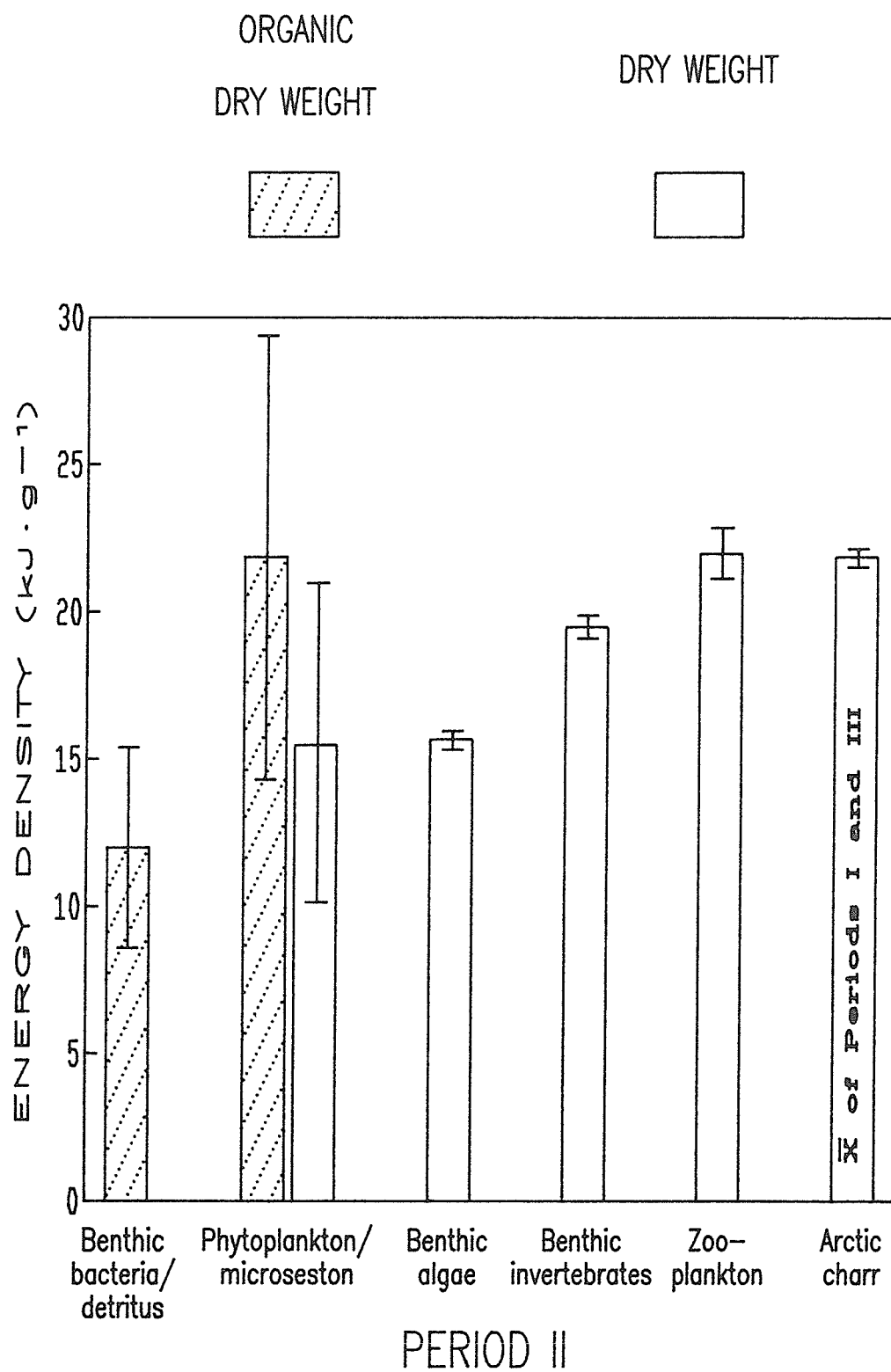


Figure 7. Energy density estimates of trophic levels during Period III, 1985 (phytoplankton and other microseston during Period III, 1986) (95% confidence intervals).

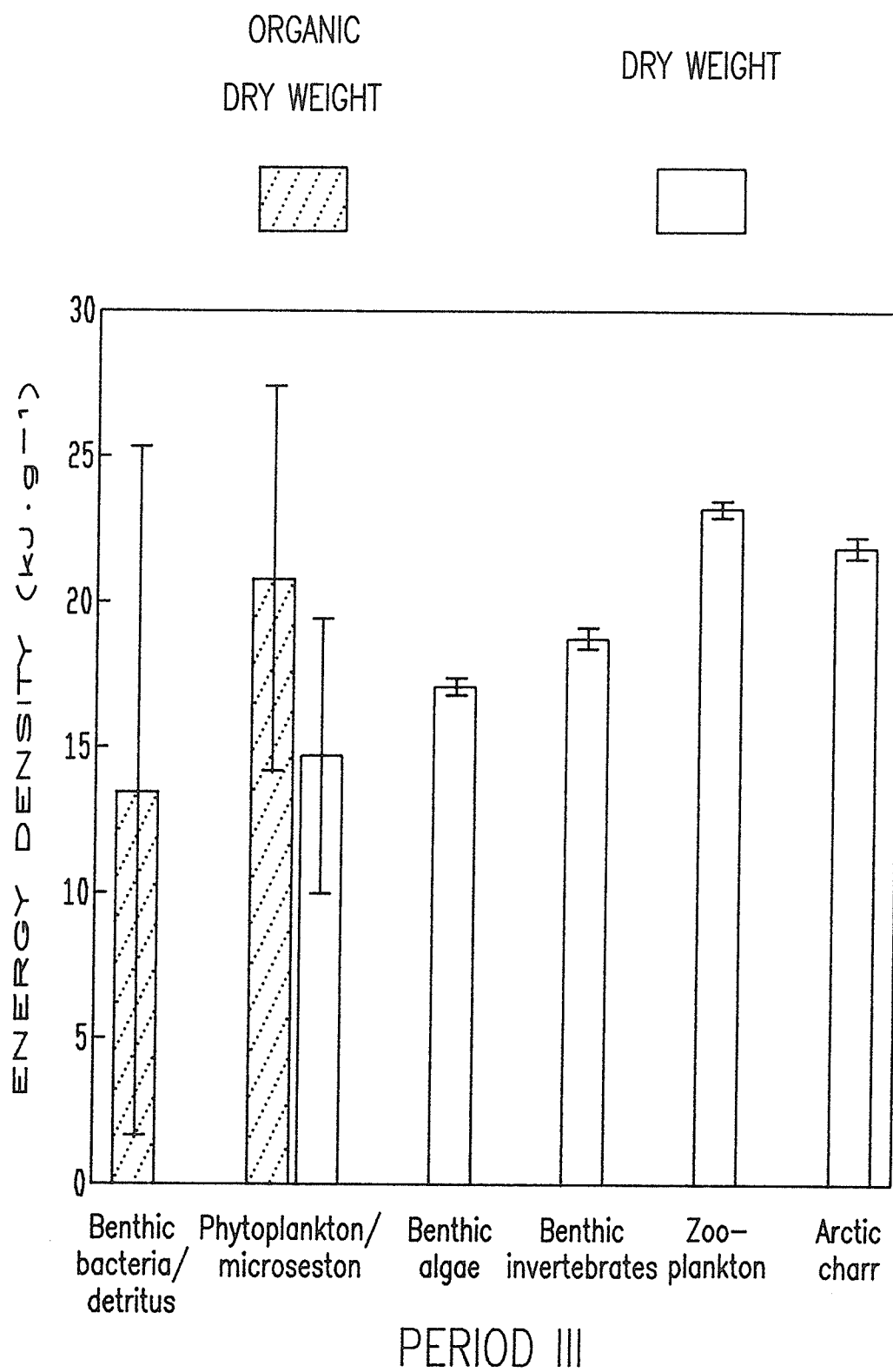


Figure 8. Energy density estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).

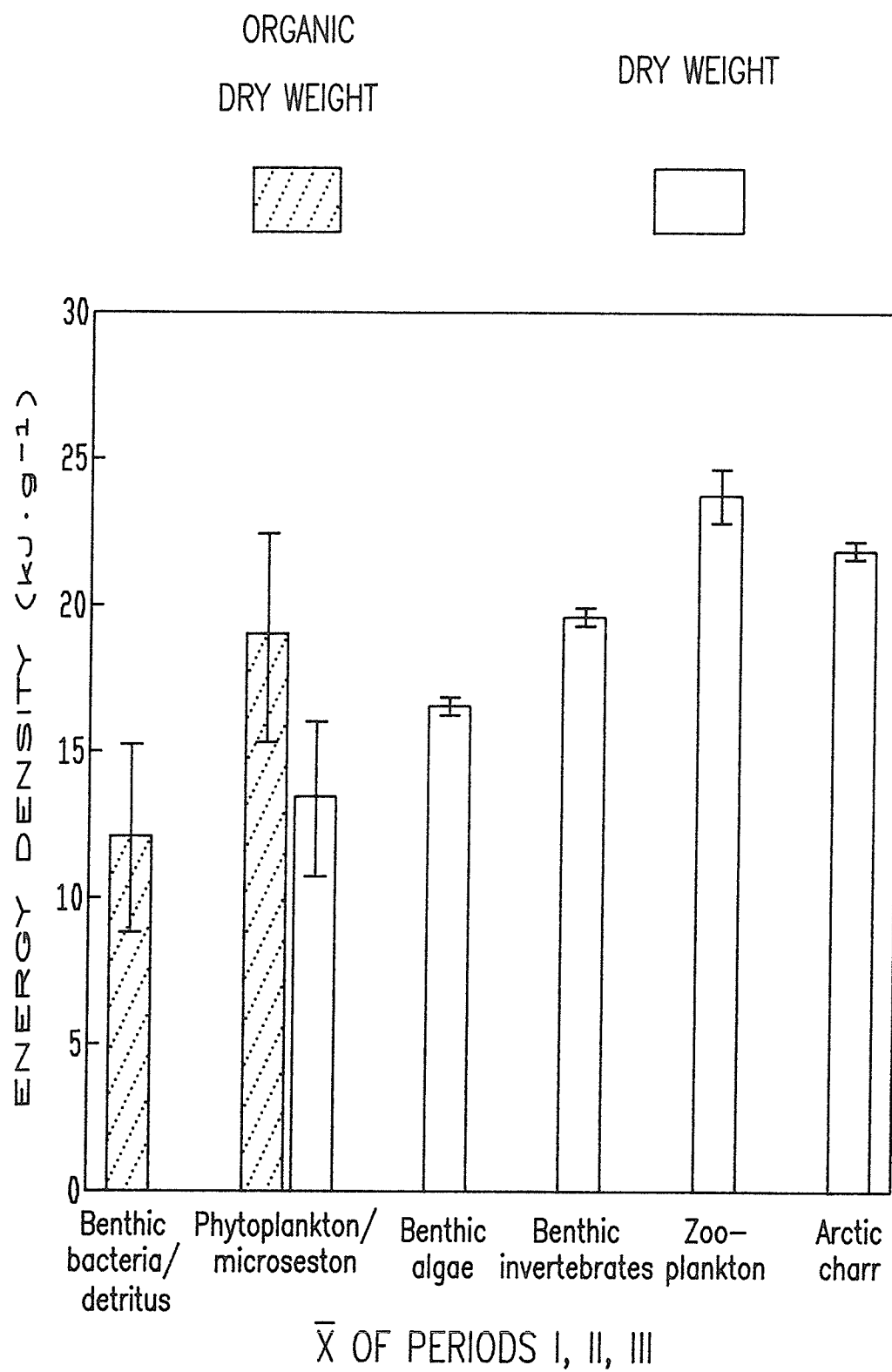
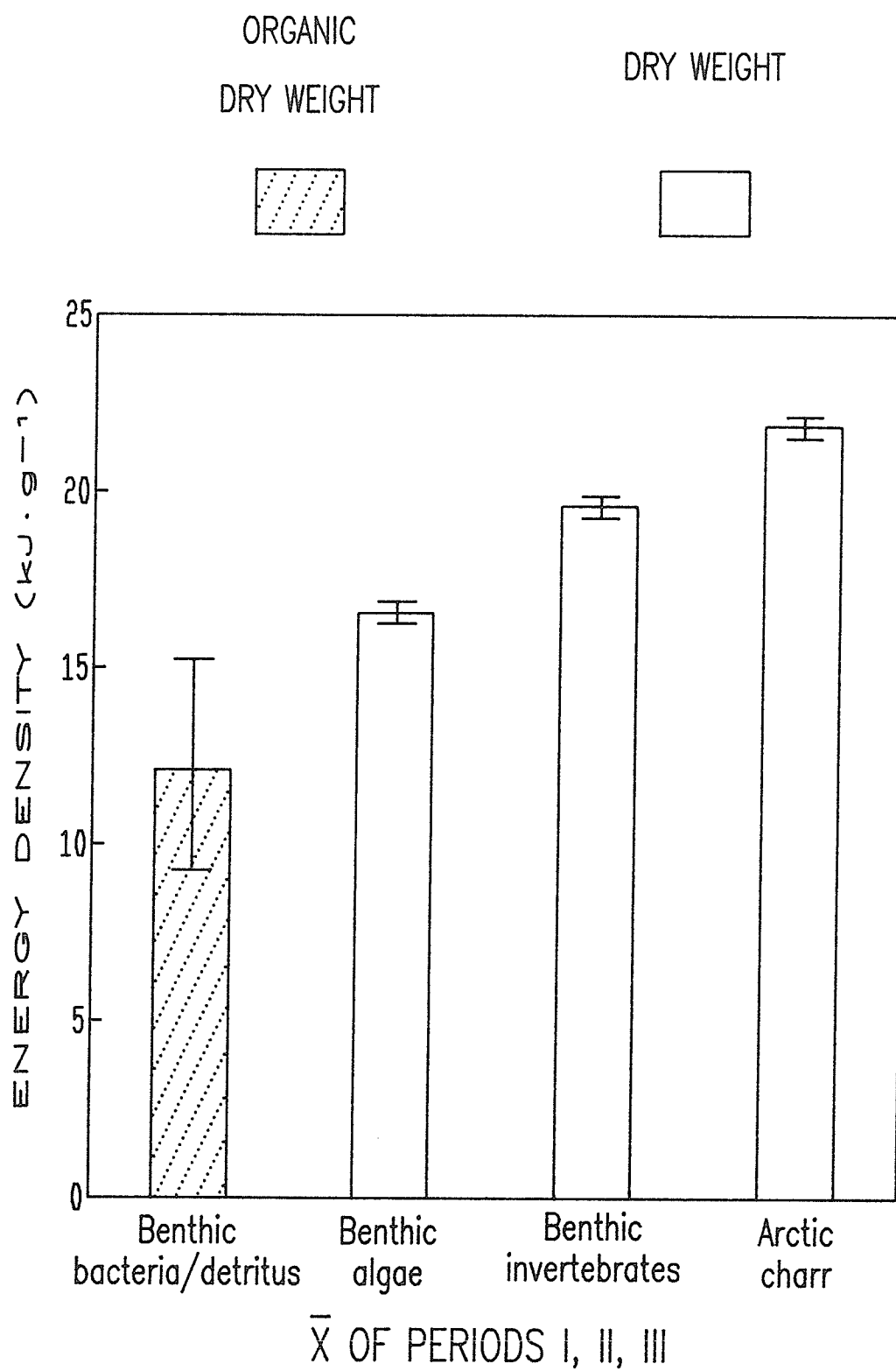


Figure 9. Energy density estimates of trophic levels along the main food chain representing the means of Periods I, II, and III, 1985 (95% confidence intervals).



differences (Table 3, No. 4). Dry weight energy density differences between trophic levels (Figures 5 to 9) were very highly significant (Table 3, Nos. 5 to 10). Very highly significant differences were maintained when formalin preserved values of some benthic invertebrates were excluded from the analysis of variance calculations (Table 3, Nos. 11 to 15).

Comparison between taxa within and among trophic levels

Generally energy density increased from simpler to more complex taxonomic groups. Notable exceptions included pupal stages of chironomids and caddisflies, caddisfly larvae (Periods I and III only), and zooplankton. These displayed higher energy densities when compared with Arctic charr. Also included for comparison are (1) benthic bacteria and detritus, and (2) phytoplankton and other microseston (Figures 10 to 13).

Dry weight energy density differences between all taxa in Figures 10 to 13 were very highly significant (Table 3, Nos. 16 to 19). Very highly significant differences were also found when strictly non-formalin preserved dry weight energy density values (taxa corrected for formalin preservation or actual values) were compared (Table 3, Nos. 20 to 23).

Dry weight energy density differences between globose blue-green algae and filamentous algae were

Figure 10. Energy density estimates of trophic levels and taxa within trophic levels during Period I, 1985 (phytoplankton and other microseston during Period I, 1986) (95% confidence intervals).

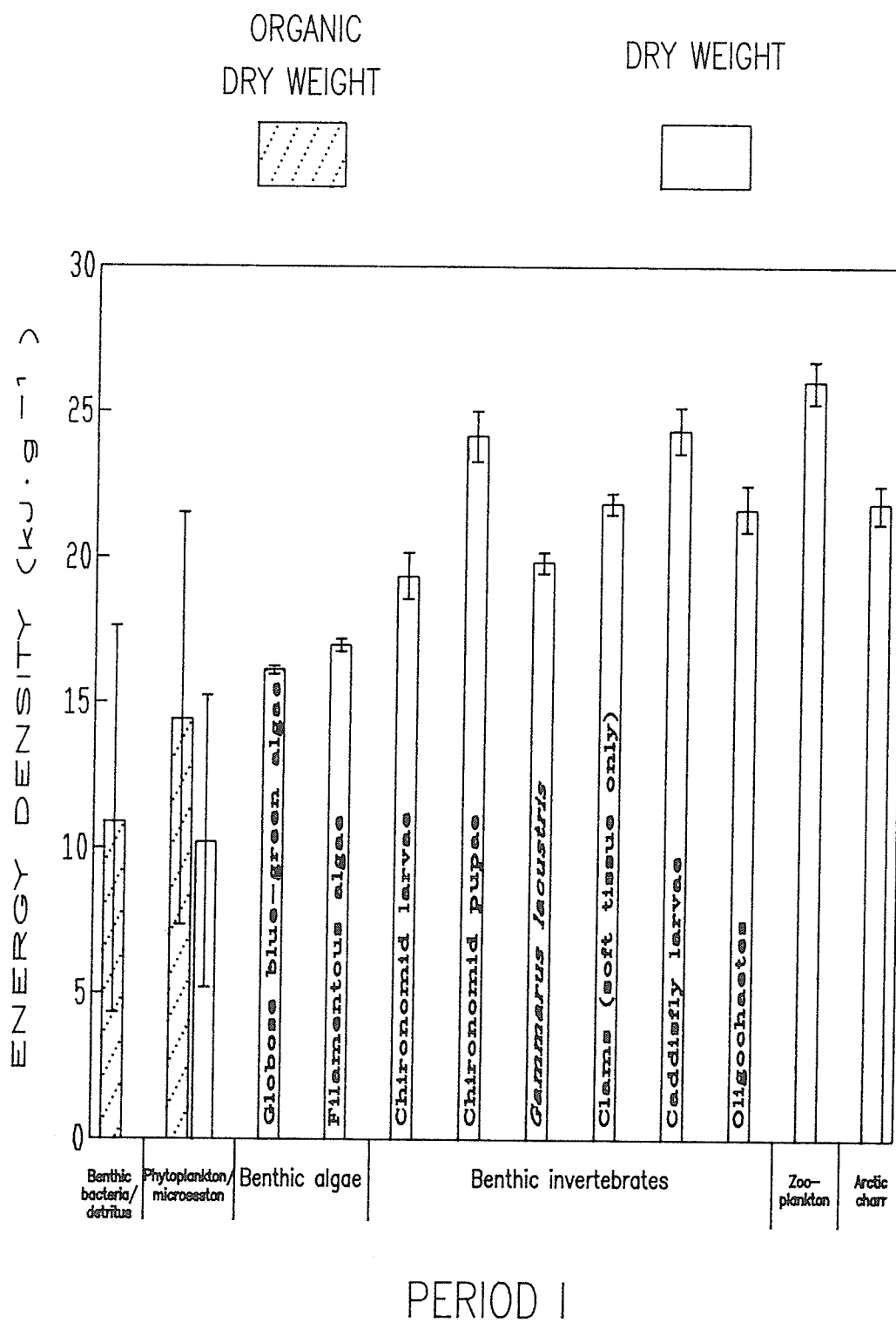


Figure 11. Energy density estimates of trophic levels and taxa within trophic levels during Period II, 1985 (phytoplankton and other microseston during Period II, 1986) (95% confidence intervals).

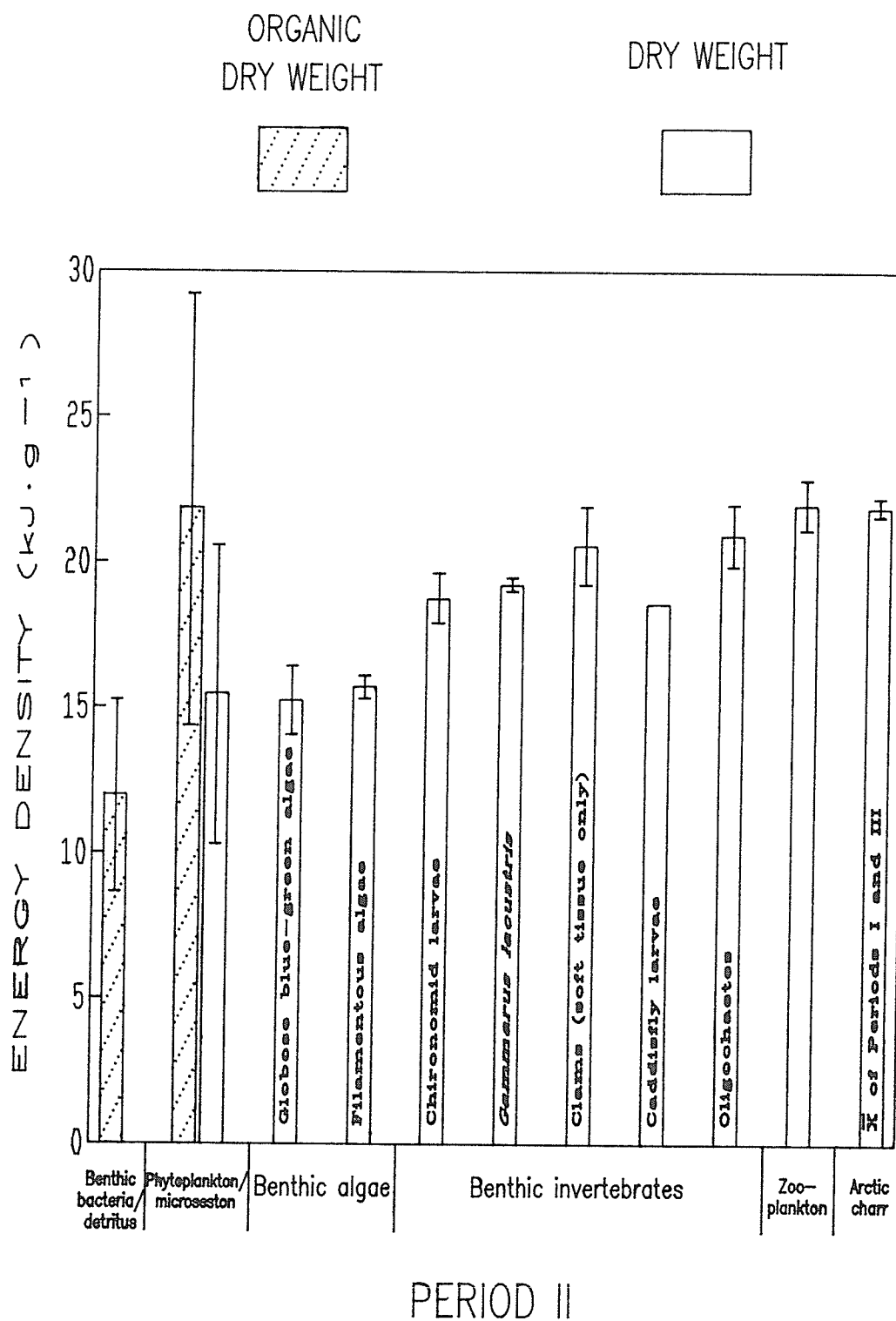
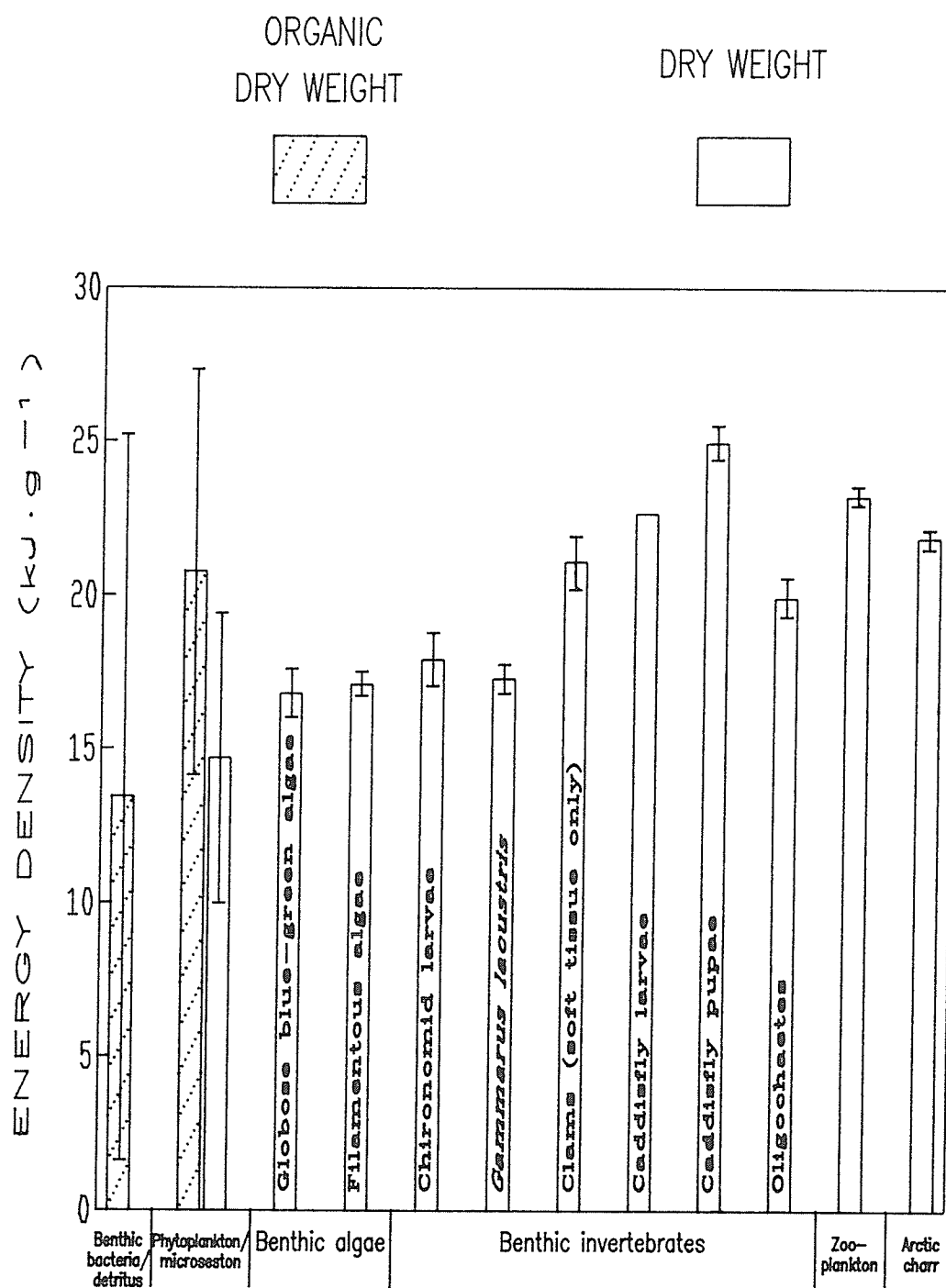
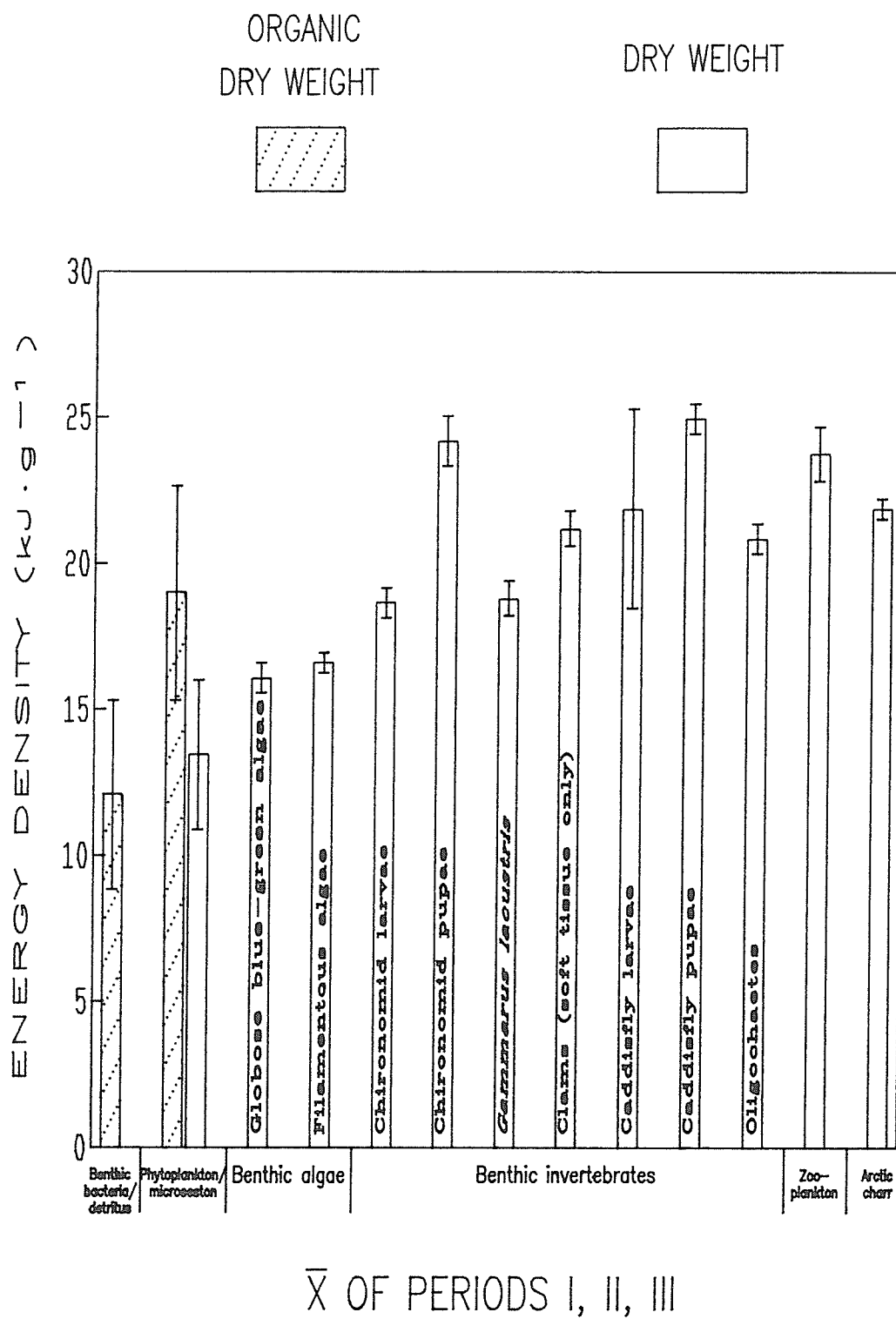


Figure 12. Energy density estimates of trophic levels and taxa within trophic levels during Period III, 1985 (phytoplankton and other microseston during Period III, 1986) (95% confidence intervals).



PERIOD III

Figure 13. Energy density estimates of trophic levels and taxa within trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals.



generally not significant, except for Period I when the difference was very highly significant (Table 3, Nos. 24 to 27). Differences between the taxa comprising the benthic invertebrate community were very highly significant throughout (Table 3, Nos. 28 to 31).

Changes in individual trophic levels over time

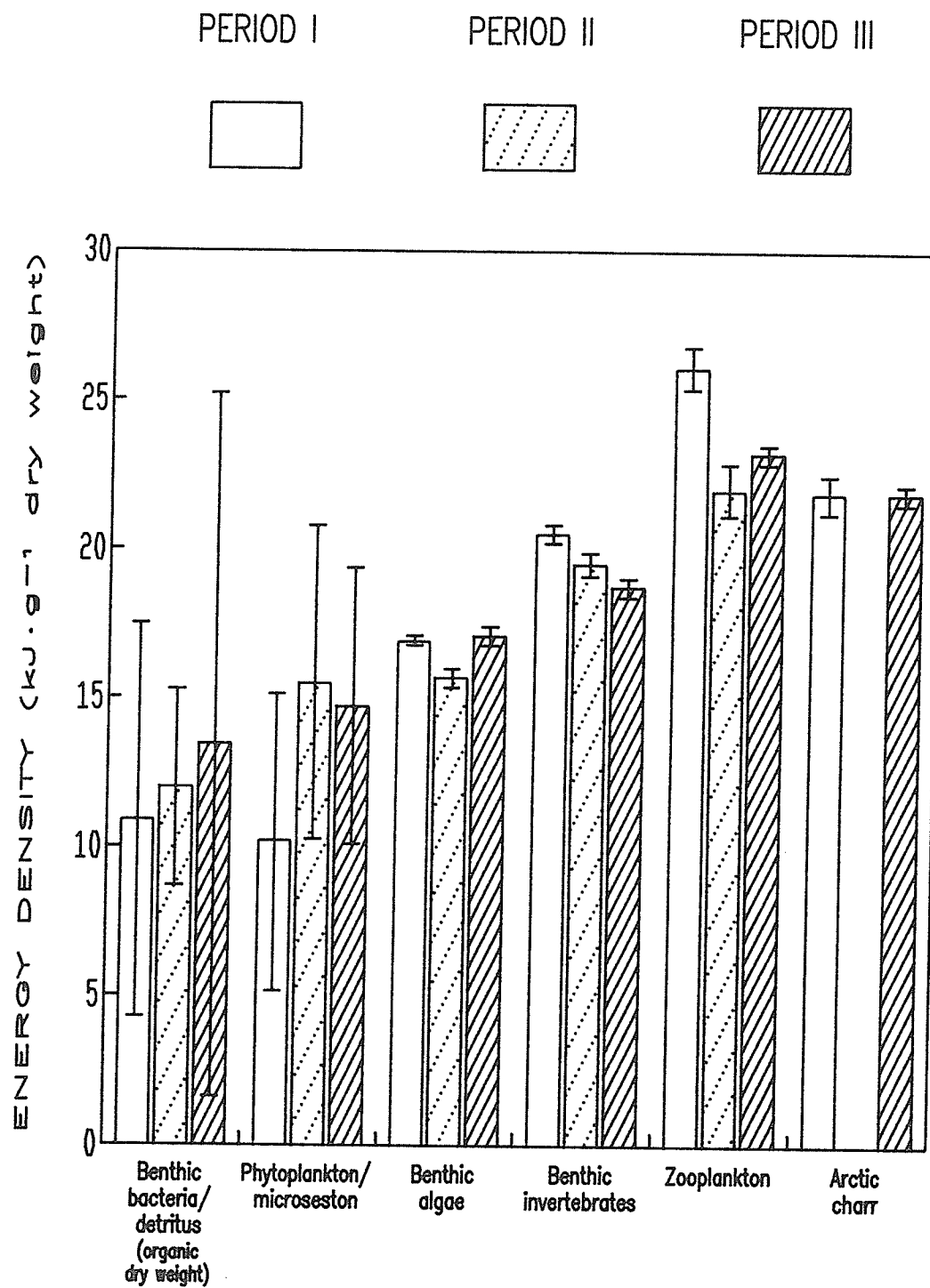
Benthic bacteria and detritus energy density increased over time while phytoplankton and other microseston values peaked during Period II. Benthic algae energy density decreased in Period II but rose slightly above Period I values during Period III. Benthic invertebrate values showed a steady decline while zooplankton energy density slightly increased after reaching minimum values during Period II. Arctic charr energy density remained indential in Periods I and III (Figure 14).

Energy density values were very highly significantly different between periods for zooplankton (Table 3, No. 45) but not significantly different for benthic bacteria and detritus, phytoplankton and other microseston, and Arctic charr (Table 3, Nos. 35, 36, and 46).

Changes in individual taxa over time

The energy densities of both globose blue-green algae and filamentous algae declined in Period II but increased, in Period III, to slightly exceed Period I

Figure 14. Energy density changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston in 1986) (95% confidence intervals).



values. Energy densities of benthic invertebrates generally decreased after the first sampling period. Exceptions were clams (soft tissue only) and caddisfly larvae; both showed an increase after the penultimate sampling period but remained below Period I values. Fluctuations in the energy density of caddisfly larvae were very large (Figure 15).

Differences in dry weight energy density values between periods were significant ($P < 0.025$) to very highly significant for the taxa comprising the benthic algae and benthic invertebrate communities, except for clams (soft tissue only) (Table 3, Nos. 37 to 41 and 43 to 44).

Miscellaneous energy density comparisons

Dry weight energy density differences between the soft tissue of clams and clams complete with shells were pronounced; the latter being much lower (Figure 16). These differences were very highly significant (Table 3, No. 33); however, differences between sampling periods were not significant (Table 3, Nos. 41 and 42).

Dry weight energy density changes between different life stages of chironomids and caddisflies were apparent; energy per unit biomass increased markedly in pupal stages of both taxa (Figure 17). The energy density estimate for chironomid larvae in the preceding figure was not corrected for formalin preservation to ensure consistency in comparing with the formalin preserved pupal stage. Energy density

Figure 15. Energy density changes of taxa within trophic levels during the three sampling periods in 1985 (95% confidence intervals).

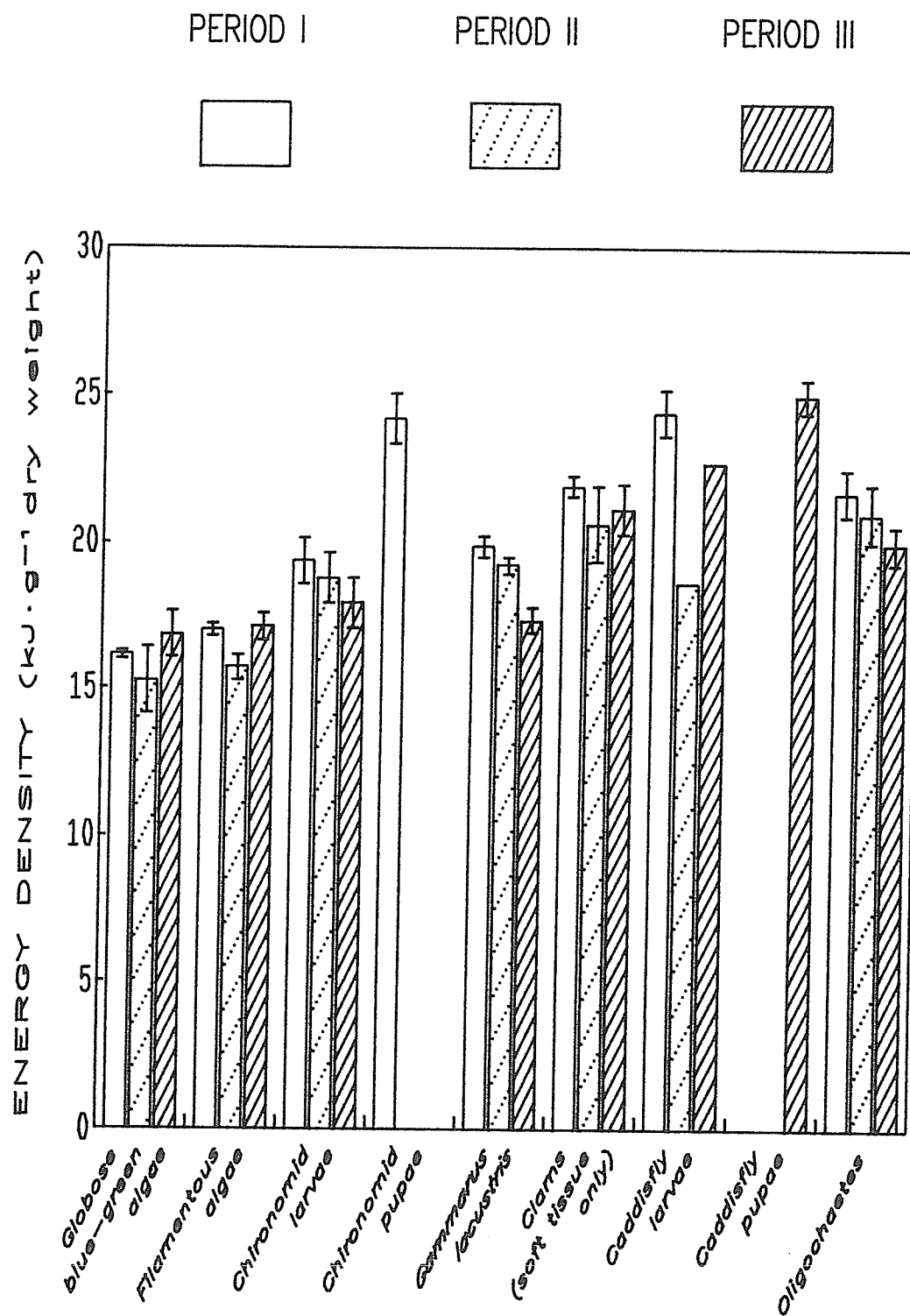


Figure 16. Energy density comparisons between soft tissue of clams and clams with shells in 1985 (95% confidence intervals).

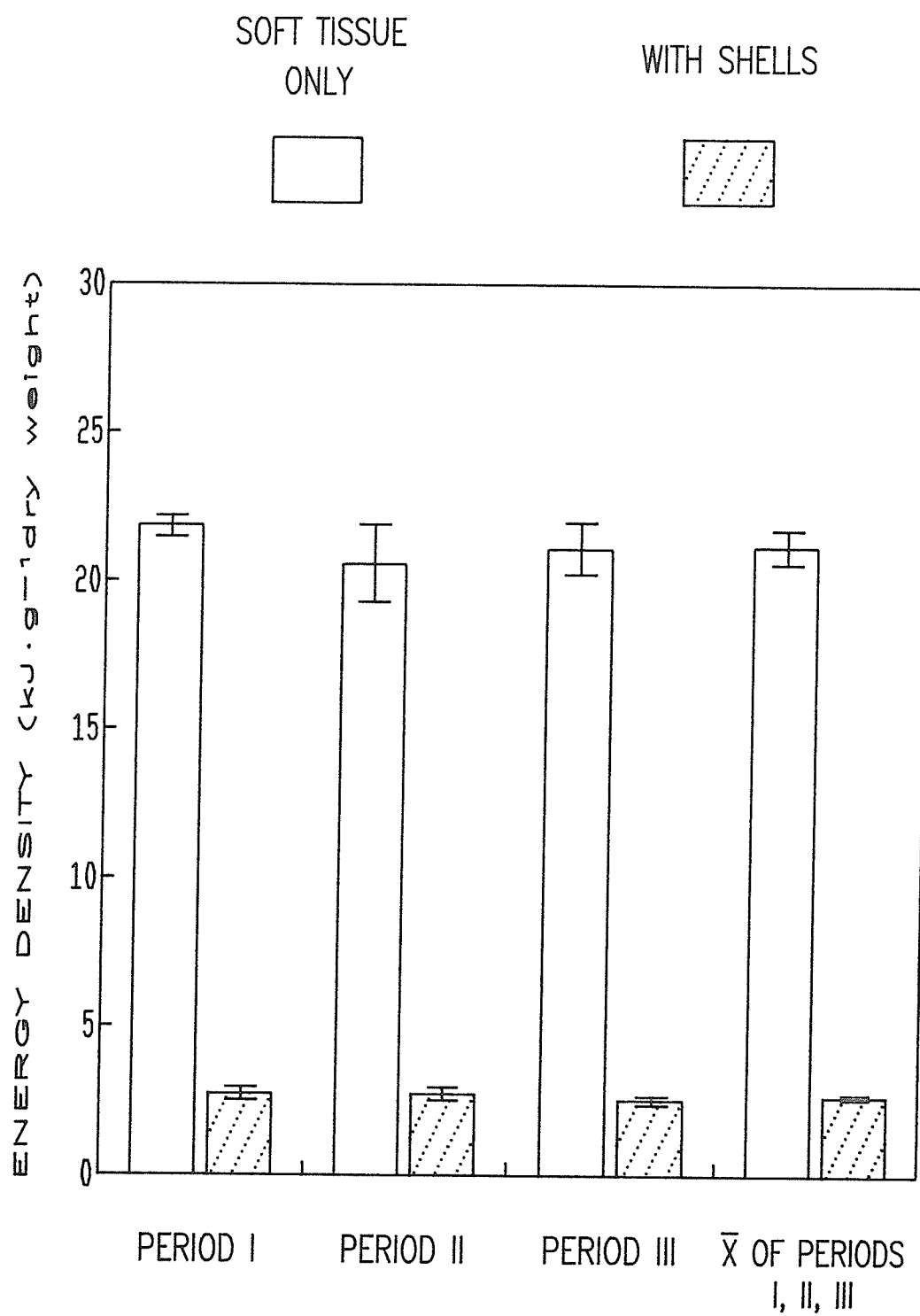
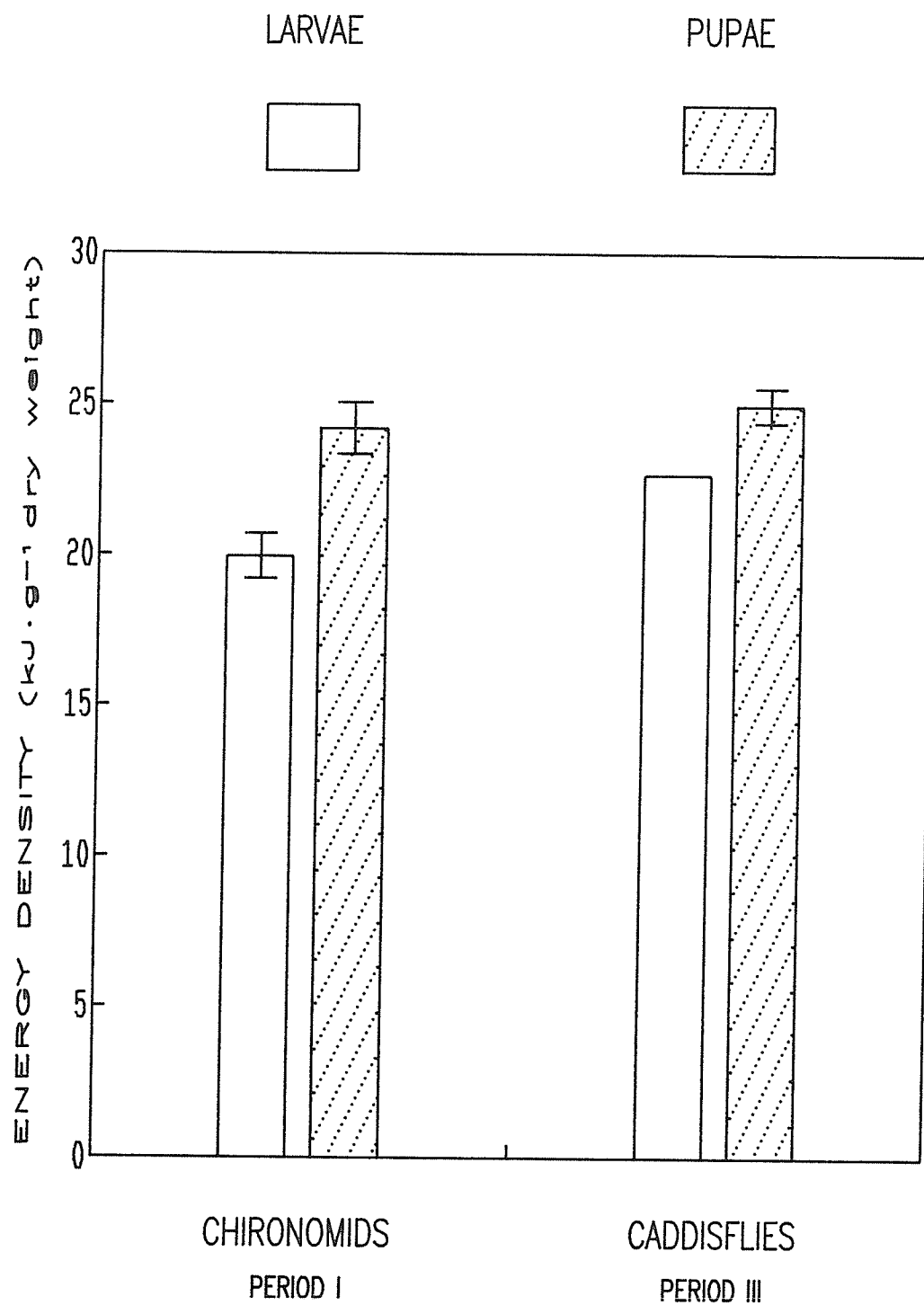


Figure 17. Energy density comparisons between the larval and pupal stages of chironomids and caddisflies in 1985 (95% confidence intervals except for caddisfly larvae since $n = 1$).



differences were very highly significant for chironomids and significant for caddisflies ($P < 0.0025$) (Table 3, Nos. 32 and 34, respectively).

Statistical significances between energy densities of formalin preserved and frozen samples, and energy density differences between individual Arctic charr are listed in Table 3 (Nos. 47 to 53 and No. 54, respectively) (also see Appendix G, Figure G1).

ARCTIC CHARR

Population structure

Data from Hunter (1970) (Figure 18A, B, C) and Johnson (1976, 1983) (Figures 18D and 19A, respectively) are included to permit identification of changes in length-frequency distribution in Keyhole Lake from the inception of Arctic charr population perturbation in 1962.

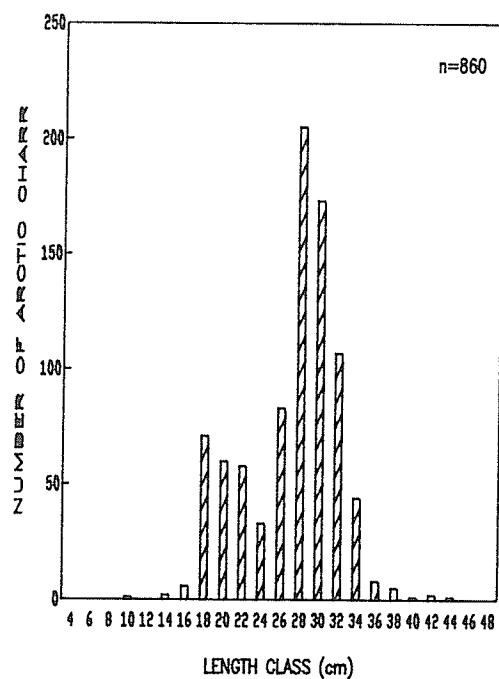
The vast majority of Arctic charr captured in 1985 ($n = 4,144$) were netted with pairs of 10-25 and 10-60 sinking gillnets ($n = 3,962$); electrofishing ($n = 53$), angling ($n = 82$), and a 10-25 floating gillnet ($n = 47$) caught the remainder. The modal length occurred at 360 mm. During the progression of the fishery three smaller modes emerged at 120, 180, and 240 mm (Figure 19B).

In 1986 a further 3,166 Arctic charr were removed exclusively with 10-25 and 10-60 sinking gillnets. The

Figure 18. Length-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1962; (B) 1963; (C) 1965; (D) 1975 (A, B, C after Johnson (1983) compiled from data collected by Hunter (1970); D after Johnson 1976).

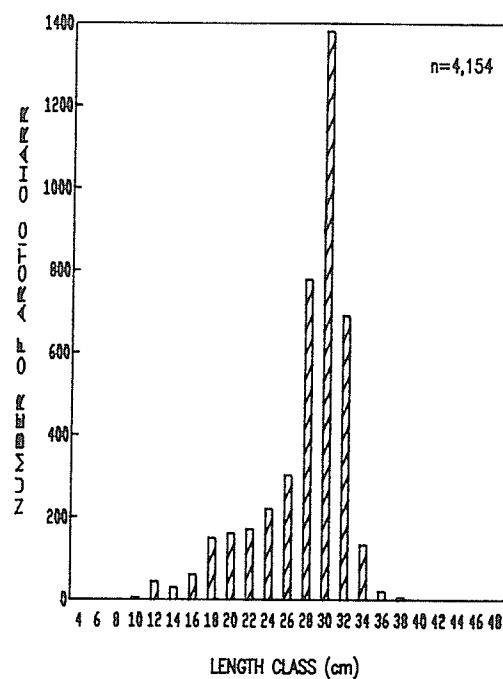
1962

A



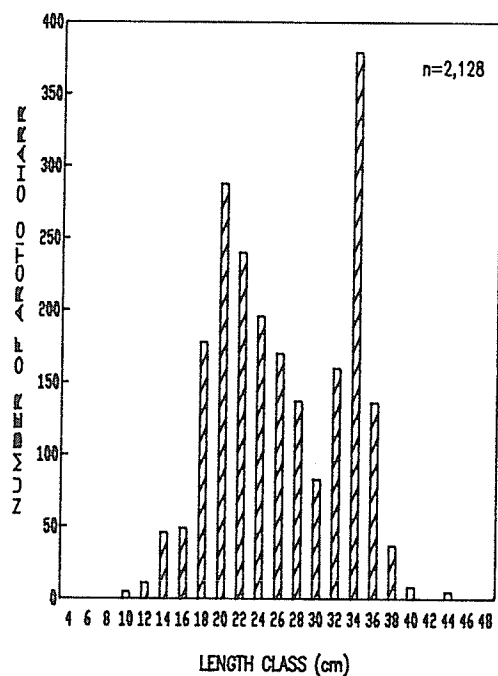
1963

B



1965

C



1975

D

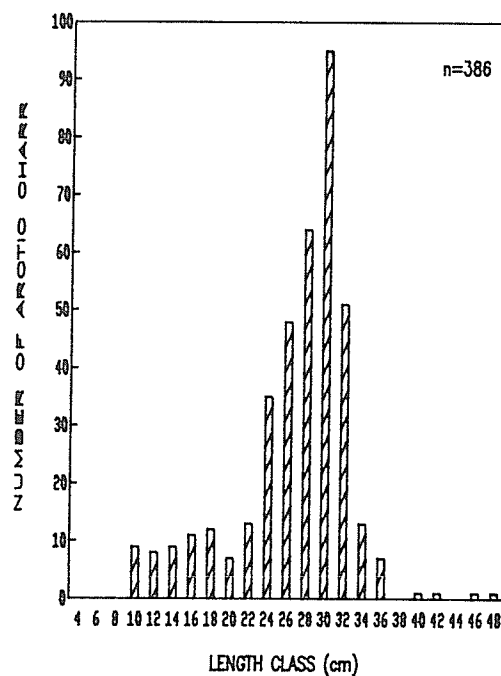
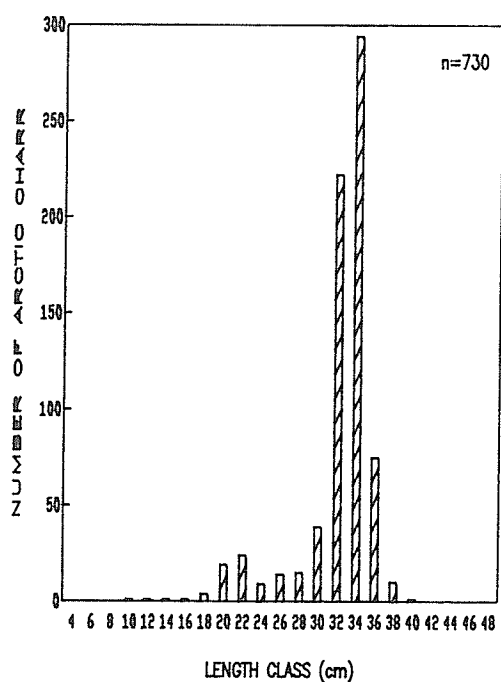


Figure 19. Length-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1980 (after Johnson 1983); (B) 1985; (C) 1986; (D) 1985 and 1986 combined.

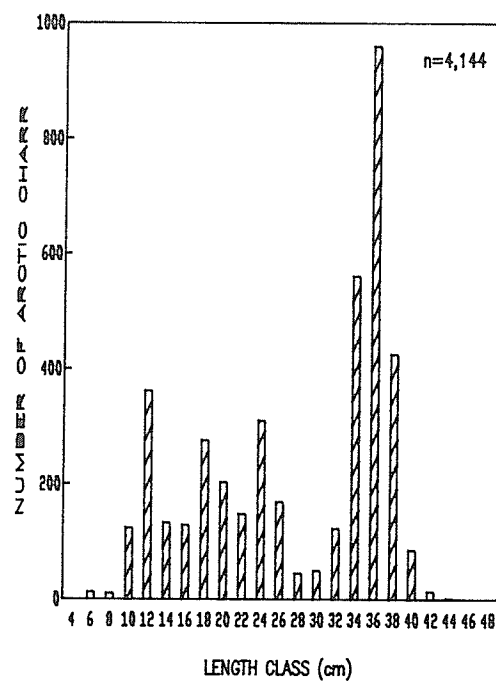
1980

A



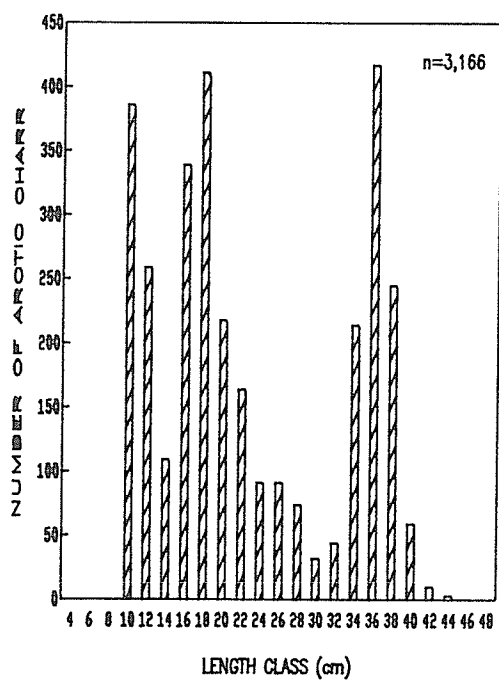
1985

B



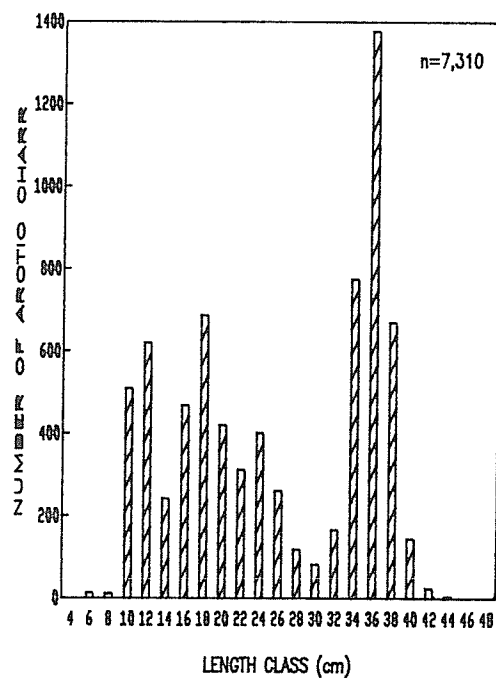
1986

C



1985-86

D



smallest mode shifted downward to 100 mm and the 240 mm mode disappeared. In 1986 the frequency of the 360 mm mode, dominant in 1985, declined and was approximately numerically equivalent to the 180 mm mode (Figure 19C).

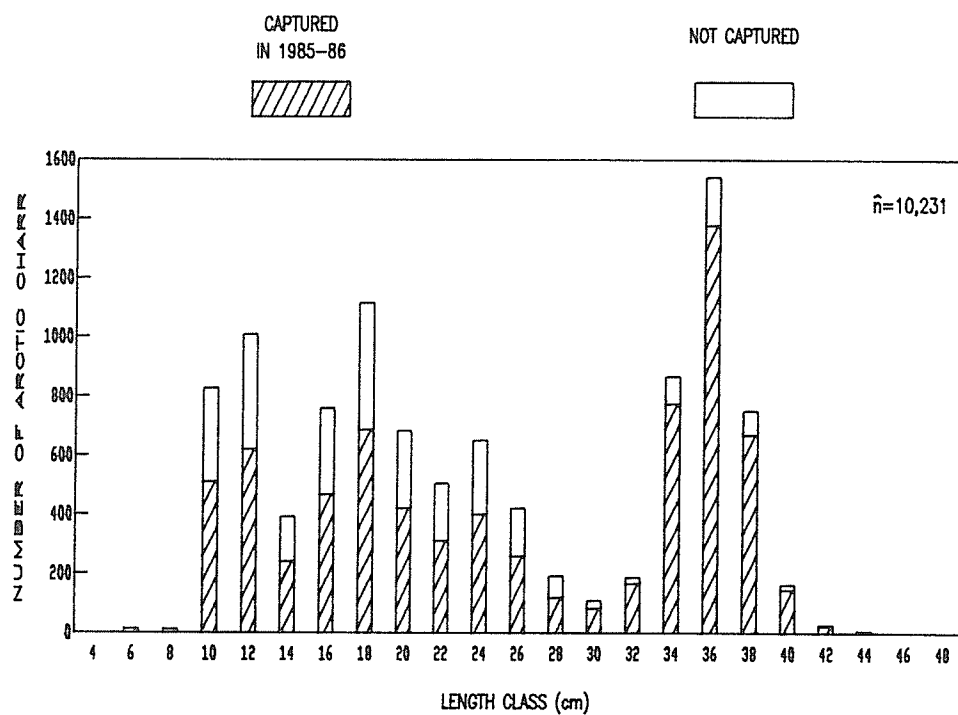
The length-frequency distribution of all Arctic charr captured during the 1985 and 1986 fisheries ($n = 7,310$) indicate that the three smaller modes are still evident at 120, 180, and 240 mm but are less pronounced than in 1985. The larger mode (360 mm) maintains its dominance and is quite distinct from the smaller modes (Figure 19D). Some growth must have taken place between the 1985 and 1986 fisheries. However, this appeared slow, at least in fish 30 cm or larger. The only Arctic charr tagged in 1985 and recovered in 1986 had increased in length by 1 mm, from 338 to 339 mm.

An approximation of the length-frequency distribution of the total estimated population just prior to its decimation in 1985 ($\hat{n} = 10,231$) shows a dominant mode at 360 mm with the smaller modes being well pronounced (Figure 20). This figure assumes that the combined 1985 and 1986 catch length-frequency distribution is a true representation of the population greater than 9 to 10 cm. Therefore, the estimated number of individuals in the juvenile (< 30 cm) and adult (≥ 30 cm) length classes were proportionally allocated to each length class in their respective length class range.

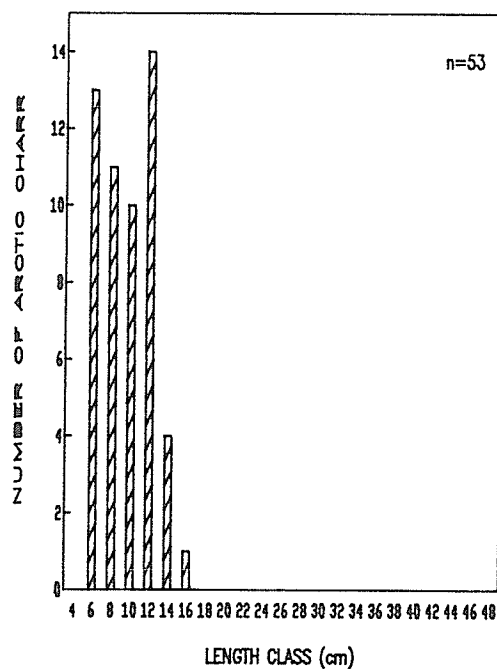
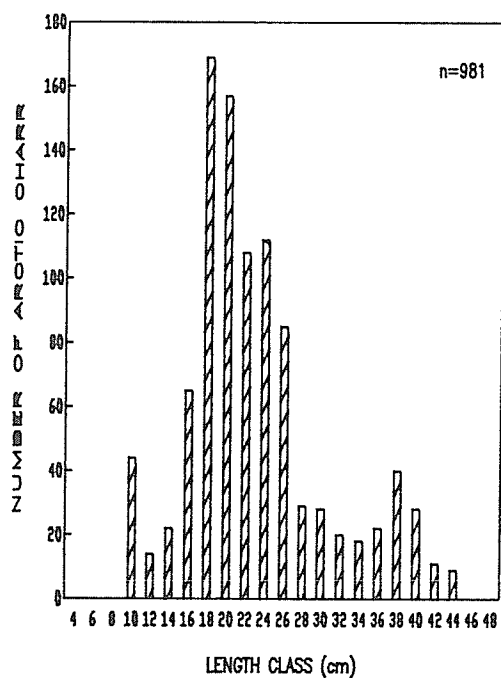
Figure 20. Estimated length-frequency distribution of the total estimated Arctic charr population in Keyhole Lake prior to the 1985 fishery (top).

Figure 21. Length-frequency distribution of all Arctic charr captured in 1988 from Keyhole Lake (bottom, left).

Figure 22. Length-frequency distribution of Arctic charr captured by electrofishing in 1985 from Keyhole Lake (bottom, right).



1988

ELECTROFISHING
1985

A recovery stage of the Arctic charr population is depicted in the length-frequency distribution of 1988 ($n = 981$). The dominant mode is at 180 mm and a small mode is apparent at 100 mm. The severe depletion of the adult population during the 1985-86 fishery is reflected by their low numerical representation in the 1988 catch data. The adult modal length increased to 380 mm (Figure 21).

Electrofishing data on length-frequency distribution, collected in 1985, indicates modes at 60 and 120 mm (Figure 22). The total number of Arctic charr captured by this method was small ($n = 53$) and the modes maybe an artifact of the small sample size. However, 120 mm was a distinct modal length in 1985 and consisted predominantly of net caught Arctic charr.

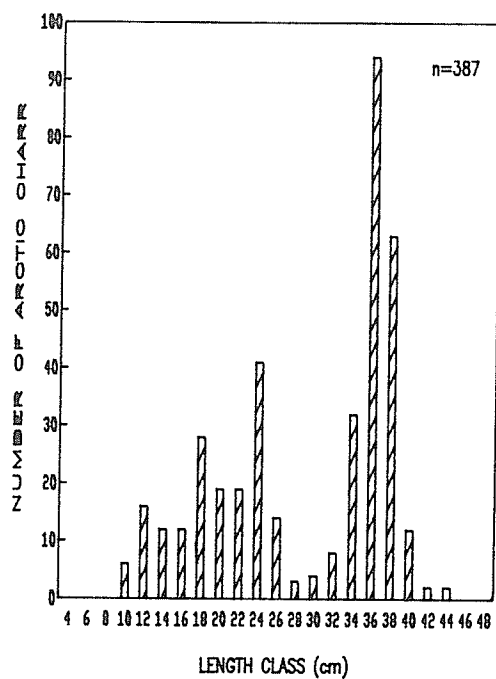
A total of 1,420 Arctic charr were sexed during the first two field seasons; 669 in 1985 and 751 the following year. The length-frequency distributions for each sex, juxtaposed in Figure 23, approximate total distributions for the respective years (cf. Figure 19B, C). However, in 1986 a fourth mode vaguely appeared at 280 mm and 260 mm in males and females, respectively. The number of females in the 360 mm mode was distinctly higher than that of males in the same length class in 1986 (Figure 23C, D). In both years the frequency of males surpassed that of females in the upper part of their length range; the large male mode shifted upward to 380 mm in 1986 (Figure 23).

Figure 23. Length-frequency distribution by sex of Arctic charr captured in Keyhole Lake; (A) 1985, males; (B) 1985, females; (C) 1986, males; (D) 1986, females.

1985

A

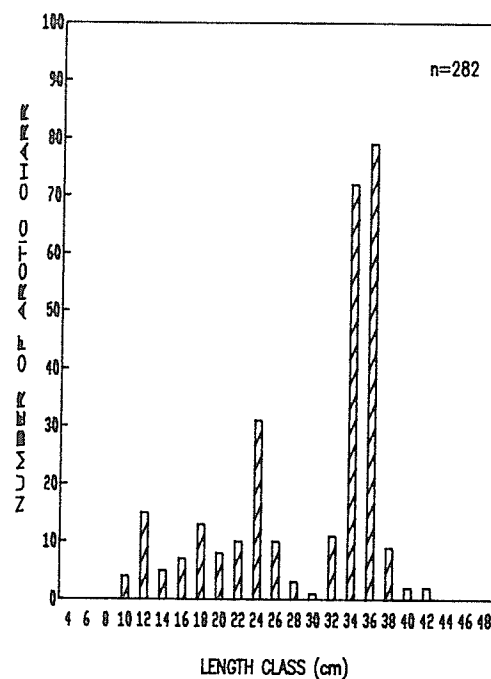
MALES



1985

B

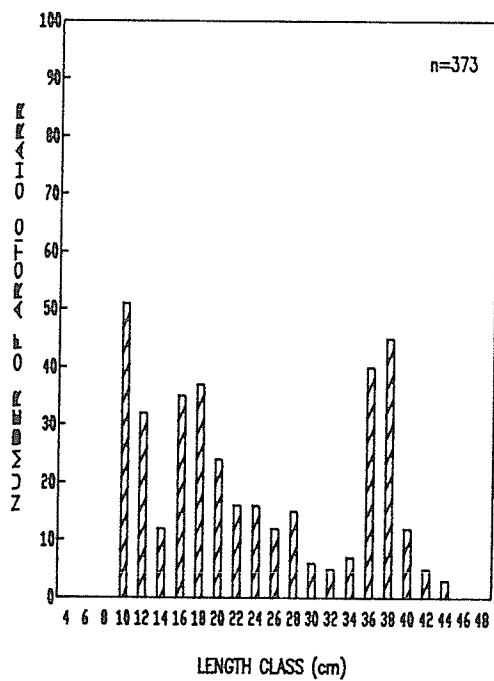
FEMALES



1986

C

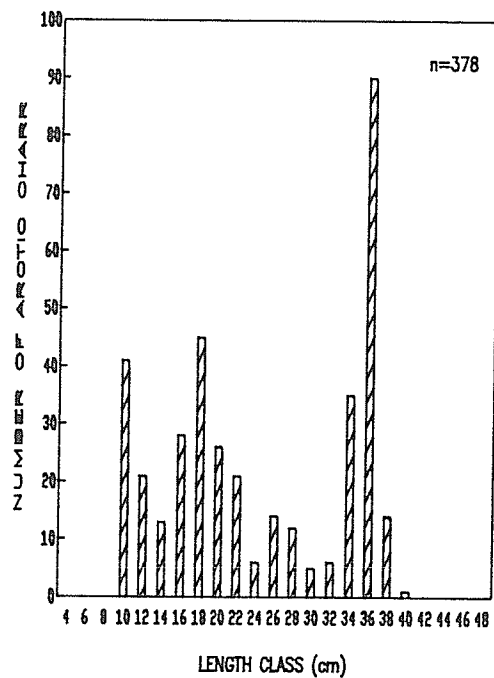
MALES



1986

D

FEMALES



Sex ratios were generally unequal; in 1985 more males occurred in both the smaller length classes (< 30 cm) and the larger length classes (≥ 30 cm). In 1986 the sex ratio for Arctic charr less than 30 cm also favoured males; however, this trend was reversed in the larger length classes (≥ 30 cm). The overall sex ratio for 1986 was almost equal. Under the hypothesis of an equal sex ratio the differences for 1985 were significant ($P < 0.05$) to highly significant ($P < 0.005$), however, for 1986 the differences were not significant ($P > 0.05$). The sex ratio for both years combined was 33:38 for females and males, respectively. The difference between this ratio and a 1:1 ratio is highly significant ($P < 0.01$) (Table 4). Hunter (1970) found the sex ratio of Arctic charr in Keyhole Lake not significantly different from a 1:1 ratio when the 1962, 1963, and 1965 catches were combined; however, significant differences were found in some net hauls and some years.

It is estimated that 71.4% of the total population number was captured during the 1985-86 fishery; 89.3% of the larger length classes (≥ 30 cm) and 61.8% of net catchable fish less than 30 cm were removed. The 1985-86 fishery reduced the estimated total biomass by 82.9%. The largest fraction of the biomass (76.6%) of the estimated total biomass was contained in Arctic charr 30 cm or larger (Table 5).

Table 4. Sex frequency distribution of Arctic charr from Keyhole Lake captured in 1985 and 1986. Percent of male Arctic charr are indicated. Chi-square (X^2) values under the hypothesis of an equal sex ratio.

Year	Length range (cm)	Number males	Number females	Percent males	χ^2	Prob> χ^2
1985	<30	171	107	61.51	14.734	<0.005
	≥30	216	175	55.24	4.299	<0.05
	All	387	282	57.85	16.480	<0.005
1986	<30	253	231	52.27	1.000	>0.05
	≥30	120	147	44.94	2.730	>0.05
	All	373	378	49.67	0.033	>0.05
1985-86	<30	424	338	55.64	9.706	<0.005
	≥30	336	322	51.06	0.298	>0.05
	All	760	660	53.52	7.042	<0.01

Table 5. Numbers and weights of Arctic charr removed from Keyhole Lake during the 1985-86 fishery, and estimates of numbers and weights of the total population prior to the 1985 fishery. Upper and lower 95% confidence intervals are represented by $\bar{N}_T$, $\bar{W}_T$ and $\underline{N}_T$, $\underline{W}_T$, respectively.

	Removed during the 1985-86 fishery			Estimation of population prior to the 1985 fishery			95% confidence intervals
	<30 cm	≥30 cm	Total	<30 cm	≥30 cm	Total	
Numbers	4,100	3,210	7,310	6,638	3,593	10,231	$\bar{N}_T$ 11,832 $\underline{N}_T$ 9,163
Wet weight (kg)	276.8	1,314.2	1,591.0	449.1	1,471.1	1,920.2	$\bar{W}_T$ 2,220.6 $\underline{W}_T$ 1,719.8

The standing stock of net catchable Arctic charr prior to the 1985 exploitation was estimated at 211 individuals·ha⁻¹, or 39.48 kg·ha⁻¹ wet weight. Hunter's (1970) estimate prior to the 1962 fishery was 169 individuals·ha⁻¹ or 43.5 kg·ha⁻¹ of fish 7 years of age or older (i.e. with a mean length over 228 mm). The catch per unit effort for 1985 was 84 individuals with a weight of 21.17 kg. In 1986 this declined to 75 fish weighing 13.24 kg. The means for both years were 80 individuals weighing 17.42 kg. The 1988 fishery produced 70 individuals per unit of effort with a weight of 10.99 kg. Johnson (1976, 1983) netted an average of 81 individuals weighing 27.6 kg per unit of effort in 1975; the 1980 fishery yielded 84 fish at 33.8 kg per unit of effort. The mean weight of all Arctic charr captured in 1985 and 1986 was 217.6 g; in 1988 this declined to 156.9 g. The mean weight of the larger length classes (≥ 30 cm) during the 1985-86 fishery was 409.4 g and increased in 1988 to 496.7 g. As expected, these values exceeded the mean weight at modal length obtained in 1962 (294 g), 1975 (276 g), and 1980 (376 g) (Hunter 1970; Johnson 1976, 1983), concomitant with the increase in modal length over the period of investigation (Figures 18 to 21).

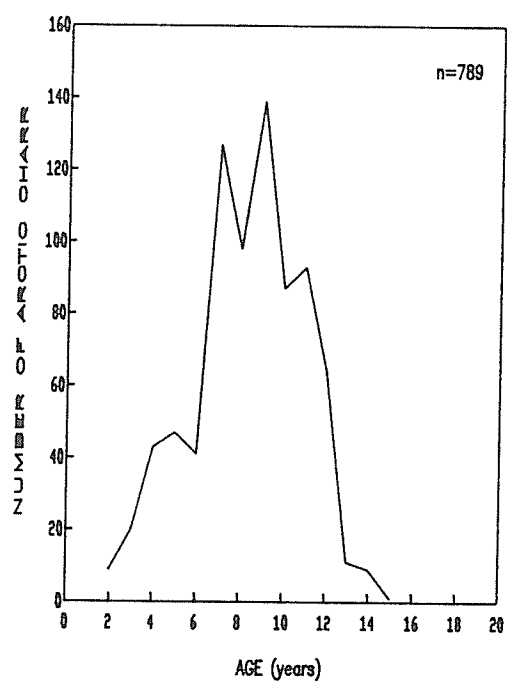
Age structure

Data from Hunter (1970) (Figure 24A, B, C) and Johnson (1976, 1983) (Figures 24D and 25A, respectively) are included to aid in discerning long-term age structure

Figure 24. Age-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1962; (B) 1963; (C) 1965; (D) 1975 (A, B, C after Hunter 1970; D after Johnson 1976).

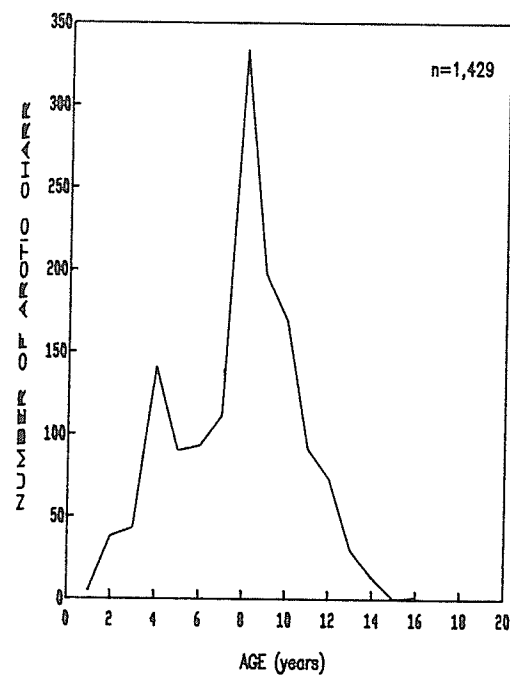
1962

A



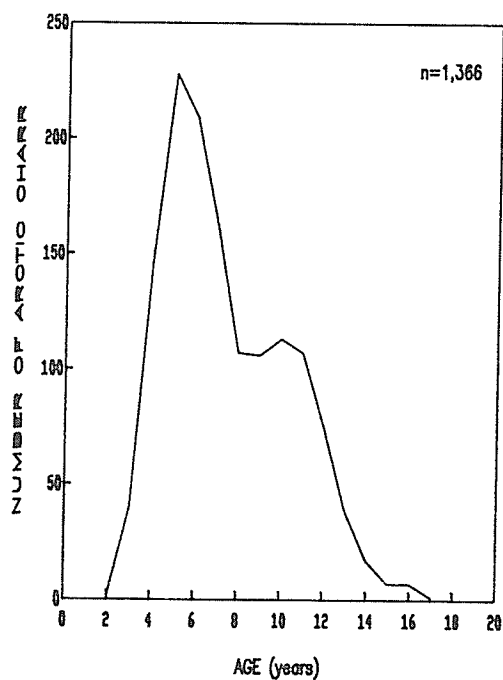
1963

B



1965

C



1975

D

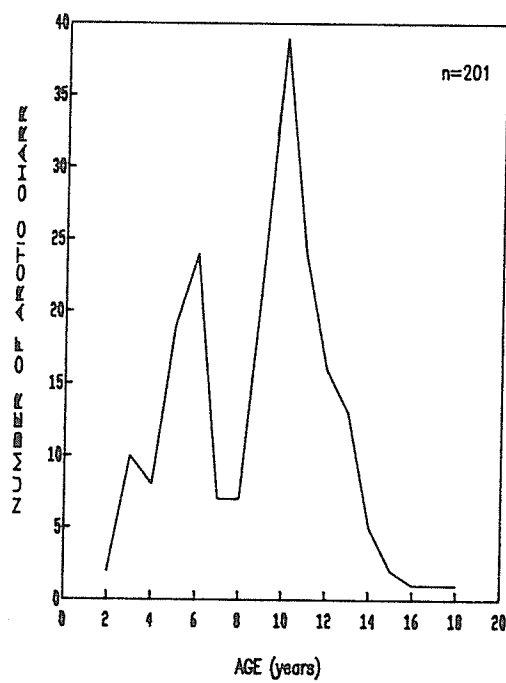
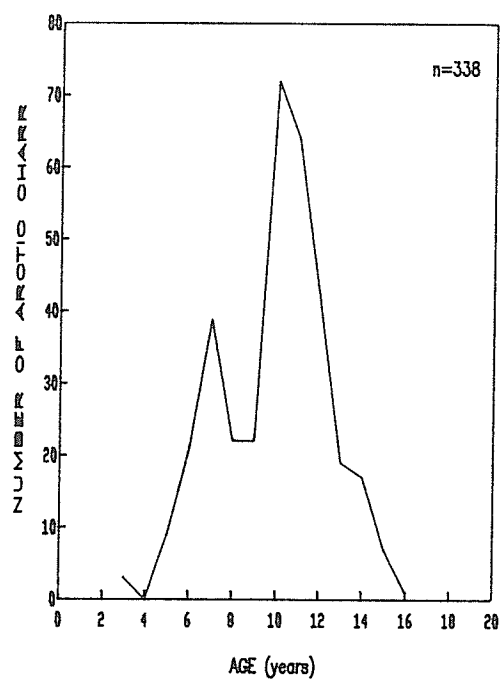


Figure 25. Age-frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1980 (after Johnson 1983); (B) 1985; (C) 1986; (D) 1985 and 1986 combined (ages obtained in the 1986 fishery were reduced by 1 year to approximate 1985 ages).

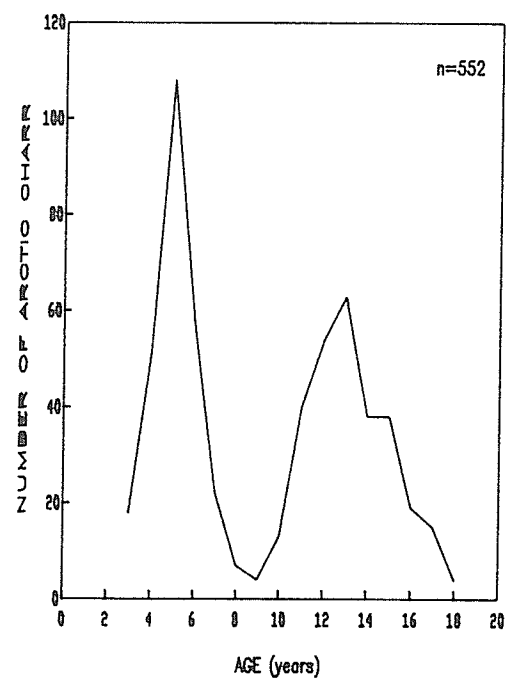
1980

A



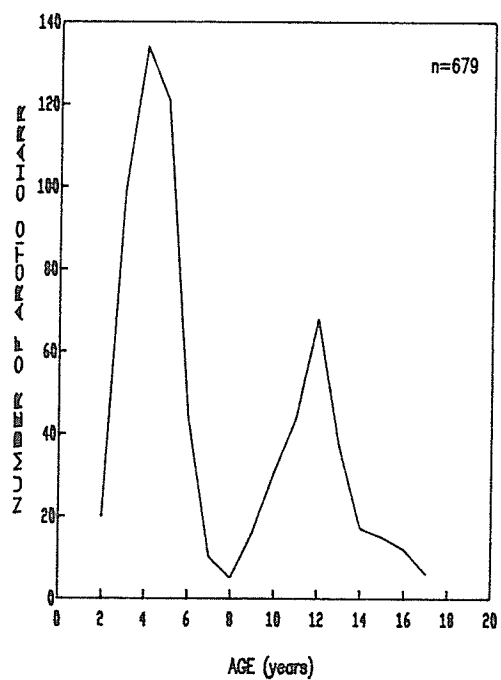
1985

B



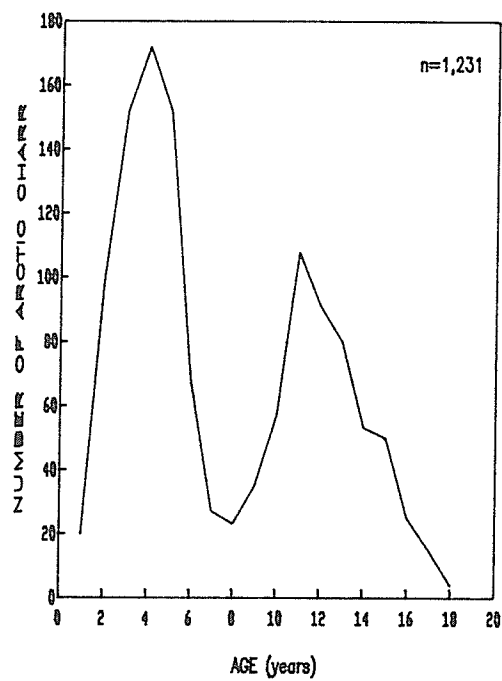
1986

C



1985-86

D



changes in Keyhole Lake. The 1985 age-frequency distribution ($n = 552$) indicates a large juvenile mode at age 5 years with an adult modal age of 13 years (Figure 25B). The 1986 distribution ($n = 679$) displayed a 1 year downward shift in both juvenile and adult age modes (Figure 25C). Interestingly, the multi-modal length-frequency distributions of the juveniles in 1985 (Figure 19B) and 1986 (Figure 19C) were not evident in the age-frequency distributions of those years. Since the inception of the Keyhole Lake fishery until 1985 the adult age mode generally became gradually older (Figures 24A to 25C). The excepting years were 1975 and 1980 when the adult age mode remained stationary at 10 years (Figures 24D and 25A). Figure 25D indicates the estimated age-frequency distribution in 1985 of all Arctic charr aged ($n = 1,231$); 1986 ages were reduced by 1 year to approximate 1985 ages. The influence of the large juvenile portion netted in 1986 resulted in a juvenile age mode identical to 1986 (4 years). The adult age mode was reduced to 11 years; below 1985 and 1986 values (Figure 25B, C).

The 1985 and 1986 age-frequency distributions for each sex, juxtaposed in Figure 26, indicate no obvious differences. Age-frequency modes were very similar for males and females during the same year.

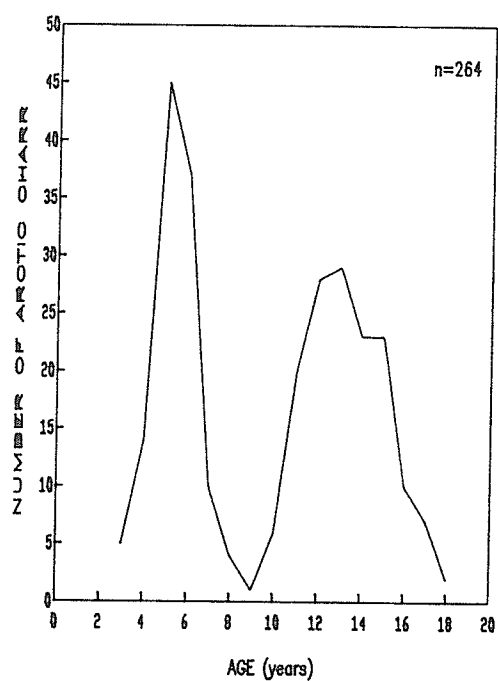
Age-length frequency distributions for both 1985 and 1986 display clustering near the juvenile and adult modes.

Figure 26. Age-frequency distribution by sex of Arctic charr captured in Keyhole Lake; (A) 1985, males; (B) 1985, females; (C) 1986, males; (D) 1986, females.

1985

A

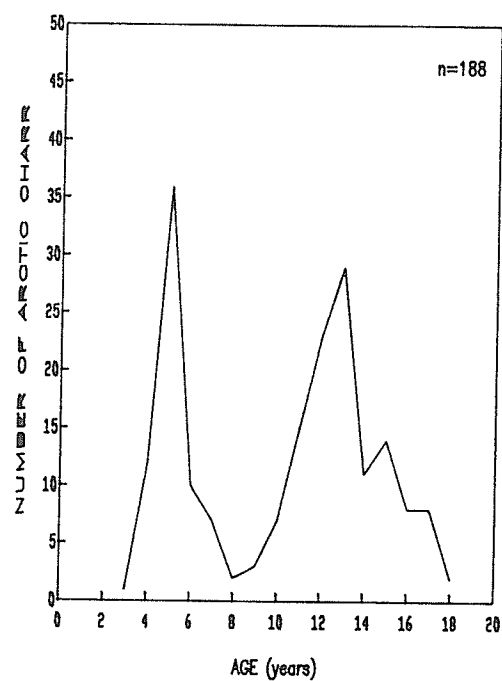
MALES



1985

B

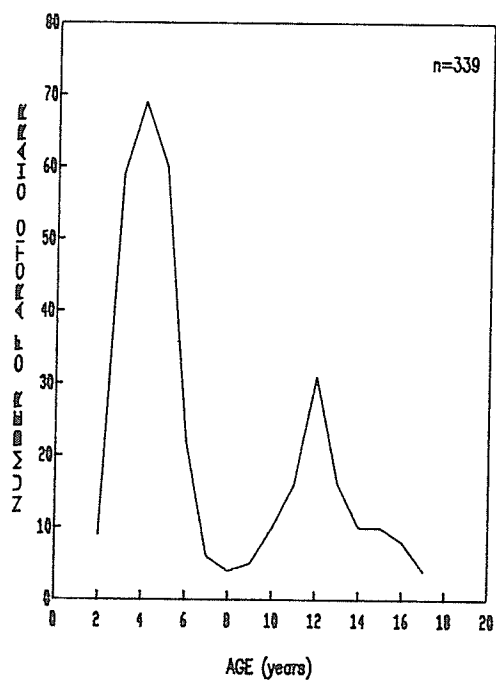
FEMALES



1986

C

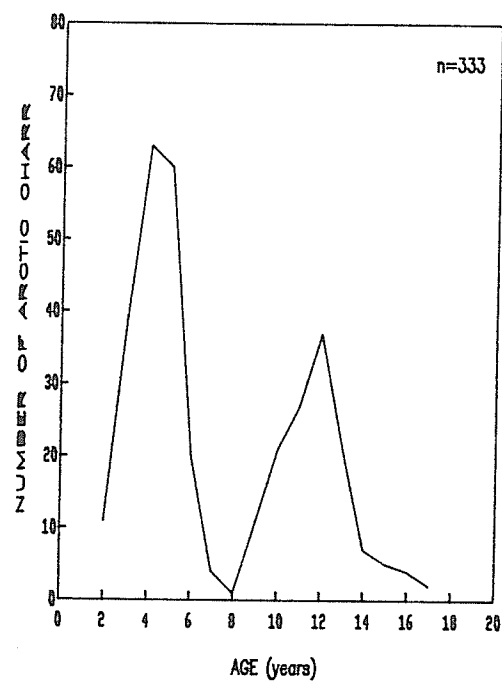
MALES



1986

D

FEMALES



The modal length-classes show a wide range of ages; conversely, length-at-age is highly variable (Figure 27).

Food class frequency

Of the 503 Arctic charr stomachs examined during the 1985-86 fishery 118 (or 23.5%) were empty. Chironomid larvae were the most frequently encountered food source (52.1%), followed by chironomid pupae (10.9%), caddisfly larvae (10.7%), and Gammarus lacustris (9.7%). Only one instance of cannibalism was recorded (Figure 28).

The frequency of chironomid larvae incidence in Arctic charr stomachs declined slightly as length increased. Incidence of chironomid pupae also declined from small (< 15 cm) to medium size (≥ 15 cm to < 30 cm) Arctic charr but increased markedly in the larger size (≥ 30 cm). Gammarus lacustris was not utilized by small Arctic charr; however, incidence rose rapidly from the medium size Arctic charr to the larger size. Zooplankton was found only in the stomach of one specimen in the larger length range (≥ 30 cm). The frequency of empty stomachs increased from the small to medium size ranges but declined noticeably in the larger Arctic charr (Figure 29).

BIOMASS

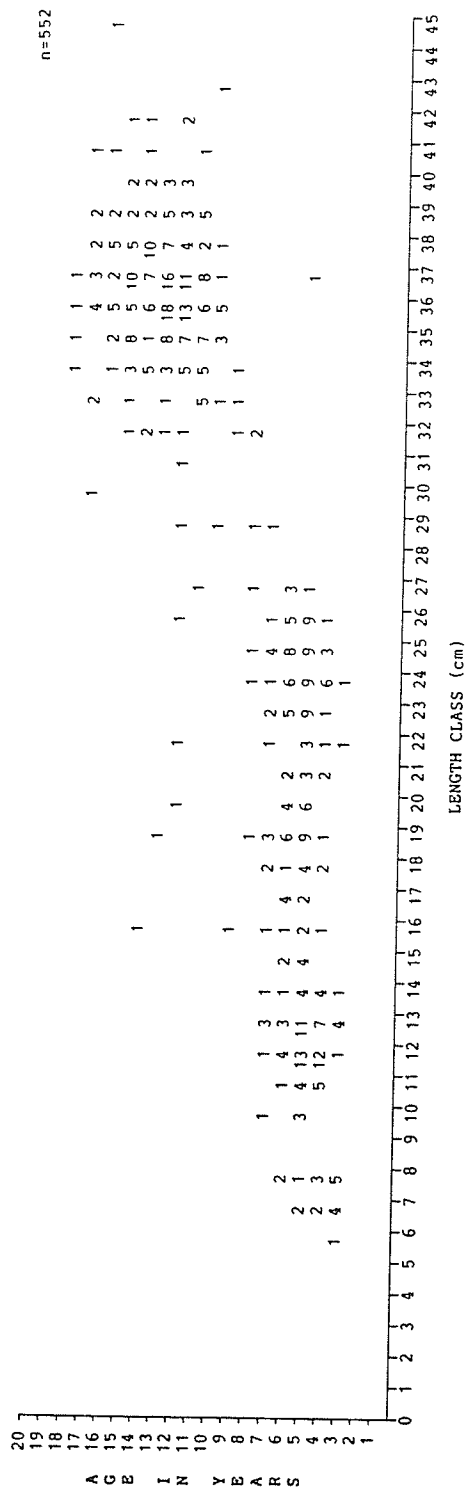
Estimates of trophic levels and taxa

Biomass comparisons between trophic levels along the main food chain, which terminates with Arctic charr, can be

Figure 27. Age-length frequency distribution of Arctic charr captured in Keyhole Lake; (A) 1985; (B) 1986. Frequency is given at age-length intersections.

1985

A



1986

B

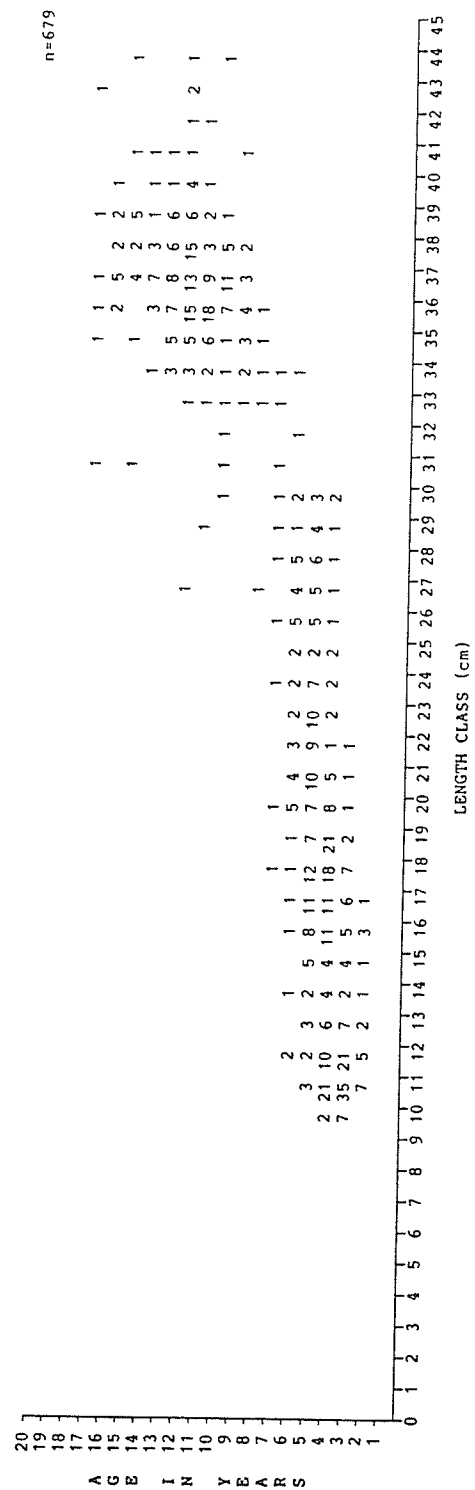


Figure 28. Frequency of food item incidence in Arctic charr stomachs examined (n = 503) during the 1985-86 Keyhole Lake fishery.

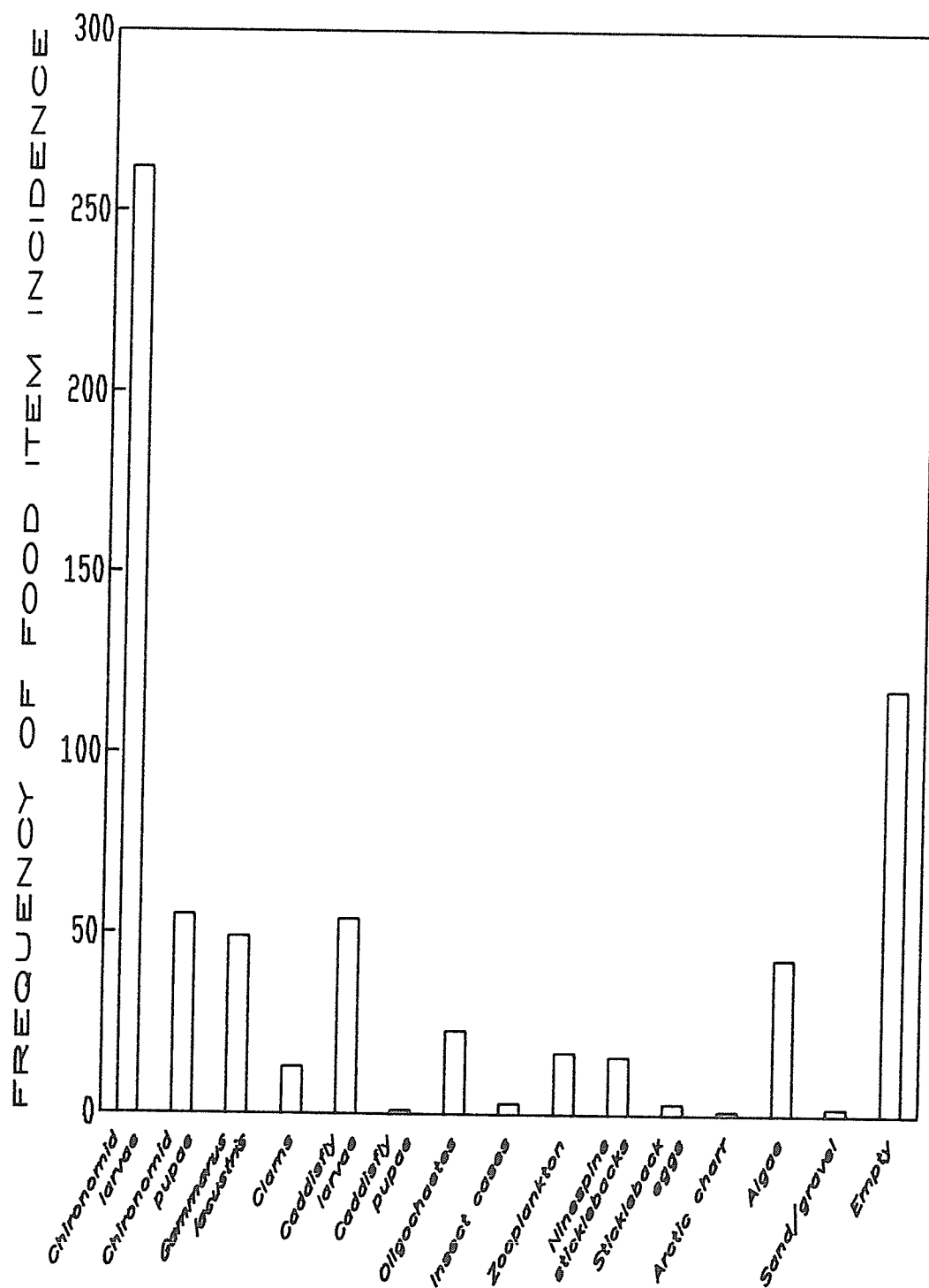
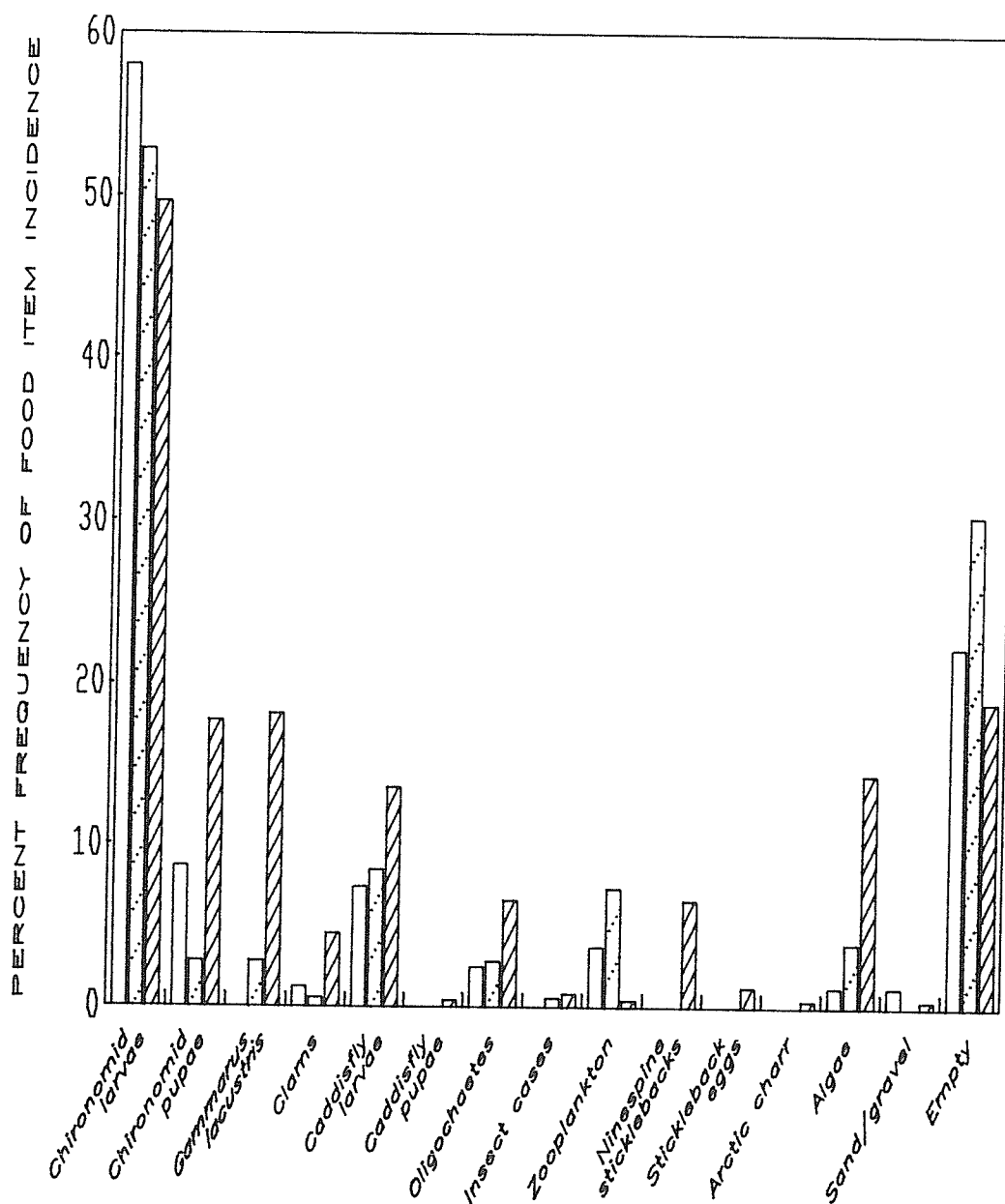
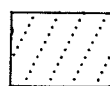
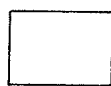


Figure 29. Percentage frequency of food item incidence in stomachs examined ($n = 503$) in three length ranges of Arctic charr during the 1985-86 Keyhole Lake fishery.

LENGTH RANGE OF ARCTIC CHARR

< 15 cm

 ≥ 15 < 30 cm ≥ 30 cm

approximated by the ratio 2,960:84:2:1 representing benthic bacteria and detritus (organic dry weight only), benthic algae, benthic invertebrates (excluding clamshell weight), and Arctic charr, respectively. The ratio between phytoplankton and other microseston, and zooplankton was approximately 9.4:1, respectively (Table 6, Figure 30).

Filamentous algae comprised about 92.1% of the total benthic algae biomass; the remainder consisted of globose blue-green algae (Table 6, Figure 31).

Clamshells contributed markedly to the total benthic invertebrate biomass (Figure 32) and are excluded in Figure 33 to show rarer taxa and life stages more clearly; i.e. the scale on the Y axis of Figure 33 is enlarged. Any further reference to benthic invertebrate biomass excludes clamshell weight. The largest fraction of benthic invertebrate biomass consisted of chironomid larvae (47.8%) followed by Gammarus lacustris (16.9%), clams (soft tissue only) (16.3%), and oligochaetes (15.3%). The remaining taxa and life stages contributed only 3.7% to the benthic invertebrate biomass (Table 6).

Wet weight biomass estimates for selected trophic levels and taxa are compiled in Appendix H, Table H1. Appendix H, Table H2 lists (1) estimated number of organisms in Keyhole Lake and (2) mean organism weight of the various taxa that comprise the benthic invertebrate community. Dry

Table 6. Biomass estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $\text{kg} \cdot \text{lake}^{-1}$ dry weight unless noted otherwise (95% confidence intervals).

Trophic Level	Taxon	Period I		Period II	
Benthic bacteria/detritus (organic dry weight)		1,346,874	± 247,246	1,092,149	± 268,185
Phytoplankton/microseston (organic dry weight)		1,346.66 ± 953.54 ±	395.61 280.12	1,286.71 ± 911.10 ±	952.51 674.46
Benthic algae	Globose blue-green algae Filamentous algae	3,085.76 ± 30,829.44 ±	2,237.07 13,716.51	3,697.59 ± 32,172.59 ±	1,184.58 9,248.04
Benthic algae total		33,915.20 ±	14,070.05	35,870.18 ±	9,303.44
Benthic invertebrates	Chironomid larvae Chironomid pupae Gammarus lacustris Clams (soft tissue only) (with shells) Caddisfly larvae Caddisfly pupae Oligochaetes Nematodes (free-living)	405.55 ± 22.69 ± 90.79 ± 147.30 ± 1,310.86 ± 28.30 ± 0 ± 120.53 ± 1.04 ±	239.31 12.35 98.68 44.40 395.13 33.21 — 45.19 1.00	385.73 ± 0.47 ± 98.30 ± 136.63 ± 1,215.98 ± 5.23 ± 0 ± 118.25 ± 0 ±	163.72 0.47 76.45 36.95 328.84 9.44 — 46.68 —
Benthic invertebrates total (with clams—soft tissue only) (with clams—shells included)		816.19 ± 1,979.75 ±	298.36 527.34	744.62 ± 1,823.96 ±	219.89 407.99
Zooplankton		110.92 ±	13.90	124.49 ±	15.42
Arctic charr		423.60 + —	66.27 44.20	423.60 + —	66.27 44.20

Continued

Trophic Level	Taxon	Period III	Periods $\bar{x}$
Benthic bacteria/detritus (organic dry weight)		1,325,584 $\pm$ 191,411	1,254,869 $\pm$ 141,954
Phytoplankton/microseston (organic dry weight)		866.20 $\pm$ 209.28 613.34 $\pm$ 148.19	1,161.30 $\pm$ 283.45 822.29 $\pm$ 200.71
Benthic algae	Globose blue-green algae Filamentous algae	1,667.27 $\pm$ 465.39 35,559.22 $\pm$ 13,526.29	2,816.87 $\pm$ 867.13 32,853.75 $\pm$ 6,721.46
Benthic algae total		37,226.50 $\pm$ 13,445.52	35,670.63 $\pm$ 6,751.58
Benthic invertebrates	Chironomid larvae Chironomid pupae Gammarus lacustris Clams (soft tissue only) (with shells) Caddisfly larvae Caddisfly pupae Oligochaetes Nematodes (free-living)	411.51 $\pm$ 176.91 0 $\pm$ — 237.32 $\pm$ 228.68 127.00 $\pm$ 46.56 1,130.24 $\pm$ 414.38 4.46 $\pm$ 6.68 30.23 $\pm$ 36.57 146.80 $\pm$ 86.76 0.16 $\pm$ 0.23	400.93 $\pm$ 101.41 7.72 $\pm$ 4.55 142.13 $\pm$ 82.55 136.98 $\pm$ 23.64 1,219.02 $\pm$ 210.43 12.66 $\pm$ 10.99 10.08 $\pm$ 12.67 128.53 $\pm$ 34.32 0.40 $\pm$ 0.34
Benthic invertebrates total (with clams—soft tissue only) (with clams—shells included)		957.48 $\pm$ 374.87 1,960.72 $\pm$ 658.02	839.43 $\pm$ 163.55 1,921.48 $\pm$ 292.55
Zooplankton		135.47 $\pm$ 22.42	123.18 $\pm$ 10.21
Arctic charr		423.60 $\pm$ 66.27 — 44.20	423.60 $\pm$ 66.27 — 44.20

Figure 30. Biomass estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).

ORGANIC
DRY WEIGHT

DRY WEIGHT

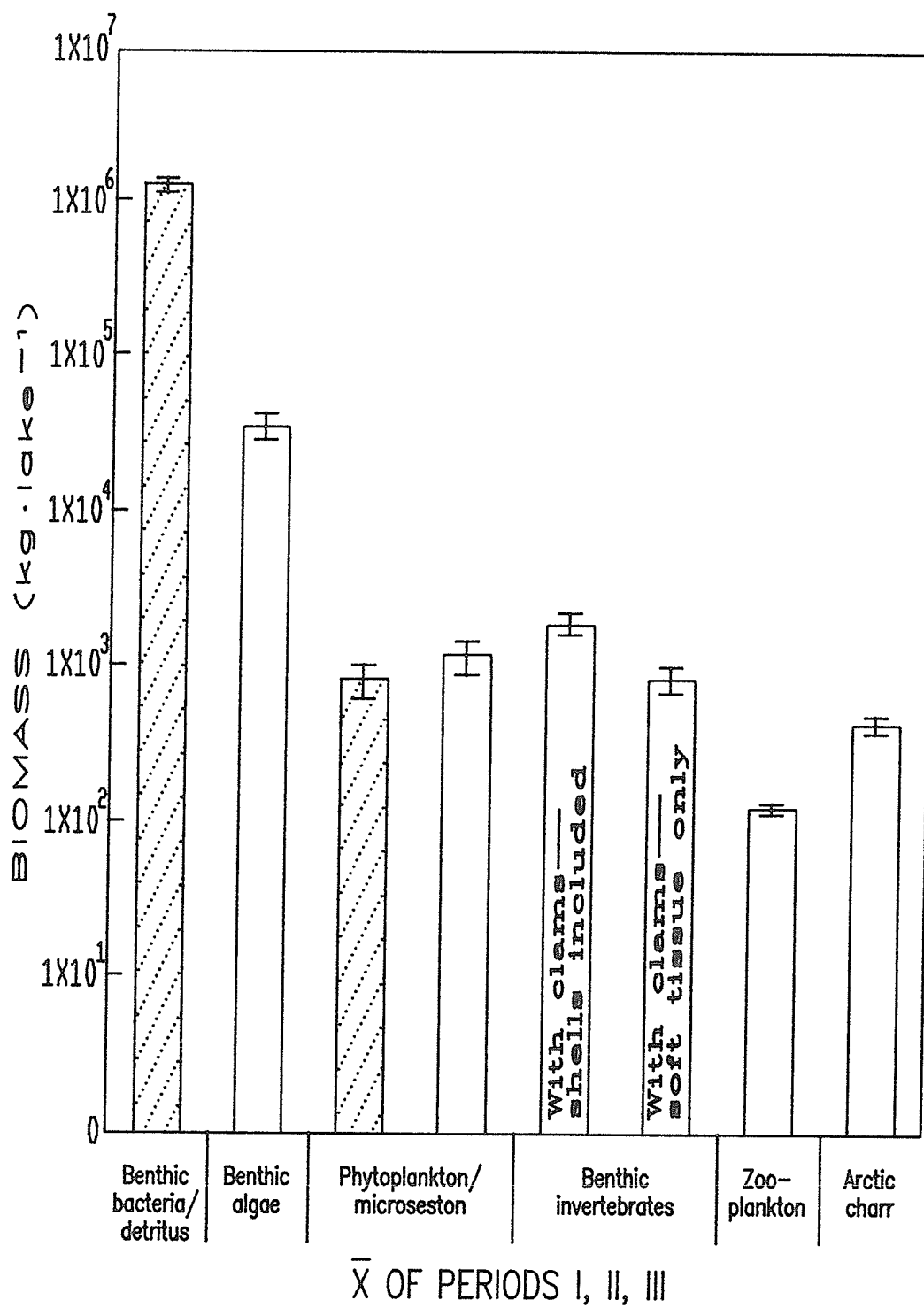
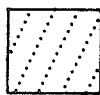


Figure 31. Biomass estimates of taxa comprising benthic algae representing the means of Periods I, II, and III, 1985 (95% confidence intervals).

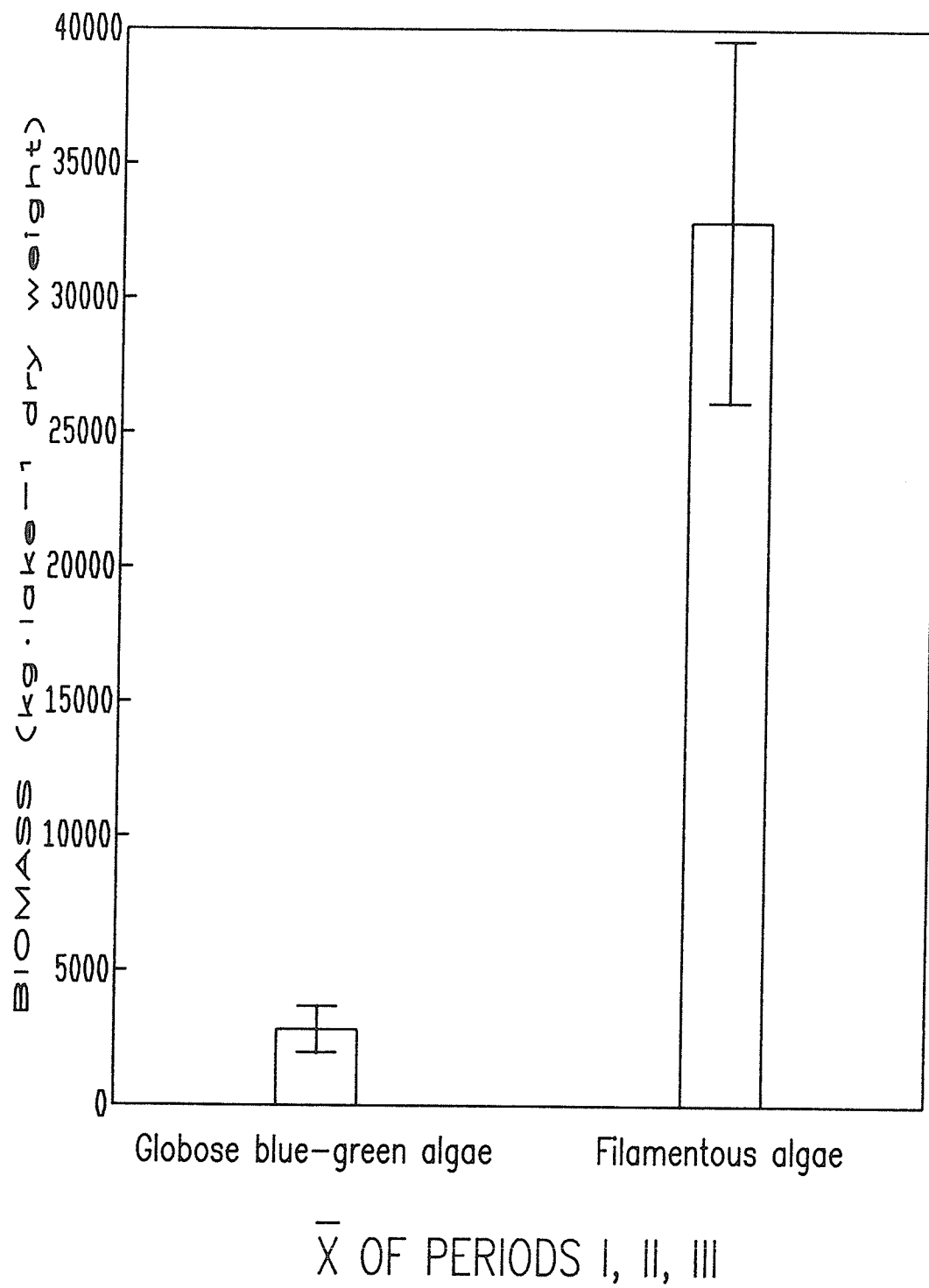


Figure 32. Biomass estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals). Broken bar represents soft tissue of clams.

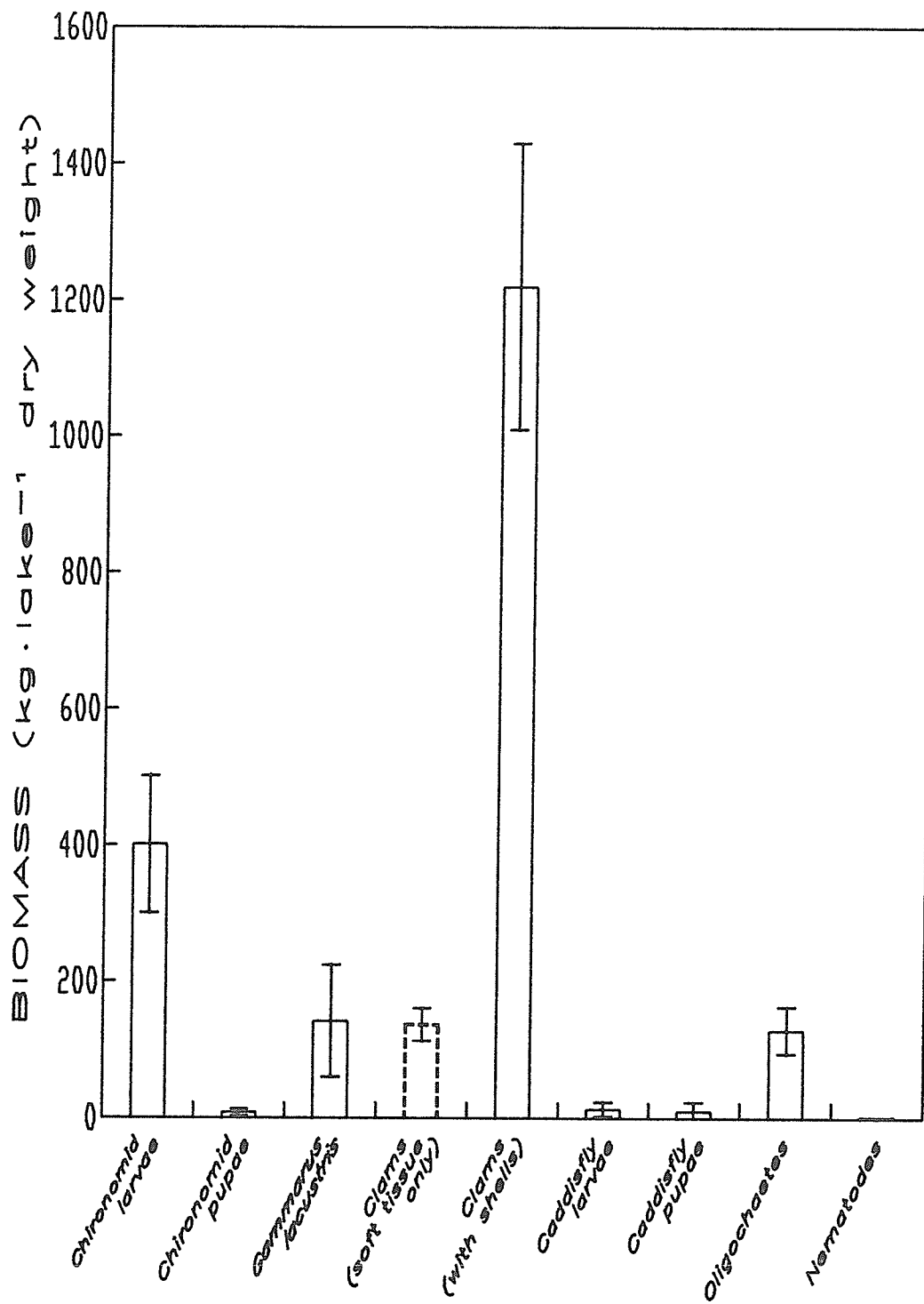
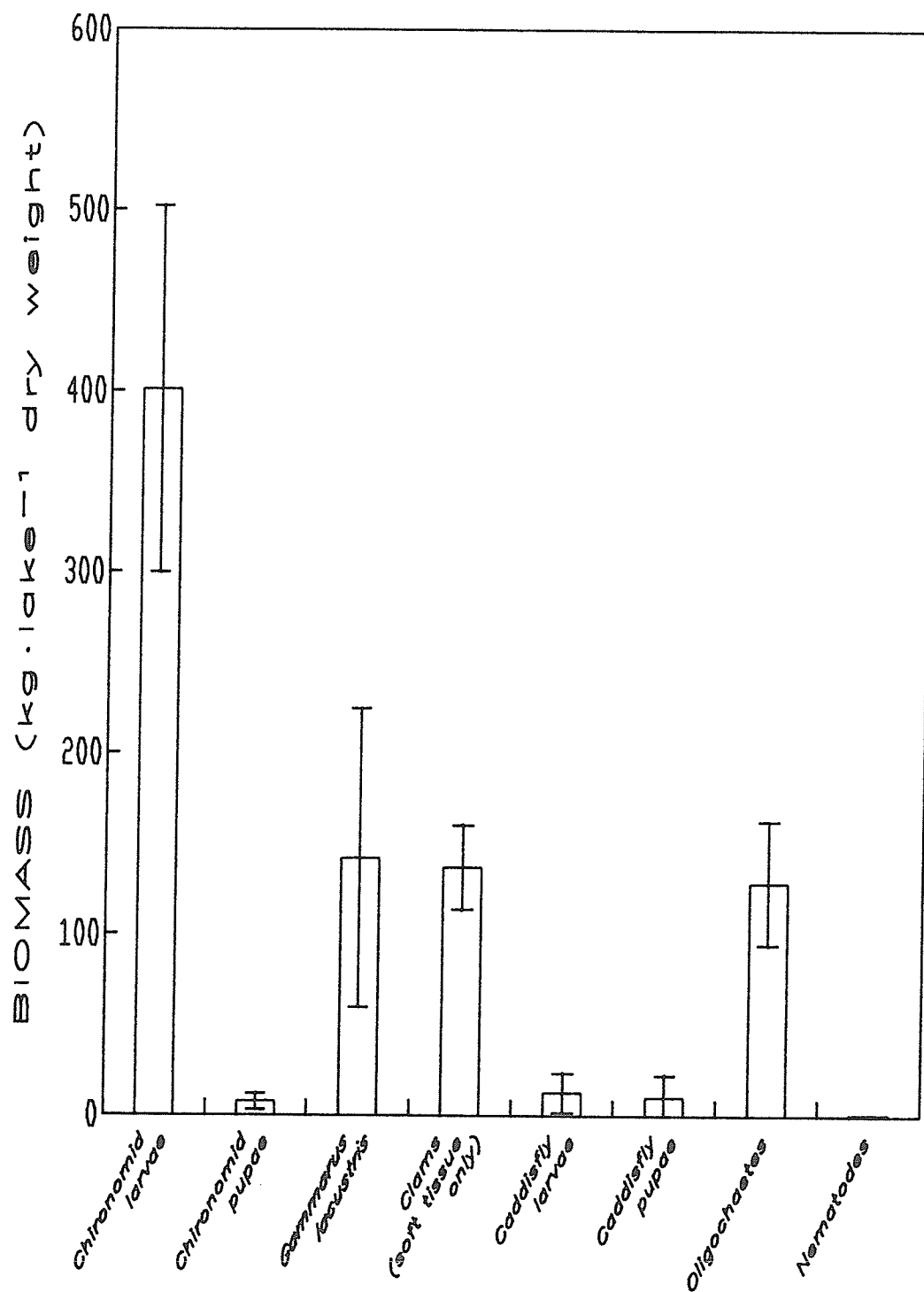
$\bar{X}$ OF PERIODS I, II, III

Figure 33. Biomass estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals). Clams with shells are excluded.

$\bar{X}$ OF PERIODS I, II, III

weights and wet weights of different taxonomic groups are compared in Appendix H, Table H3.

Changes over time

Benthic bacteria and detritus biomass noticeably declined during Period II but regained a level similar to Period I in the last sampling period. Benthic algae biomass showed a slight but constant rise during the sampling periods. Phytoplankton and the other microseston declined during the collecting periods in 1986. Initially benthic invertebrate biomass declined slightly but climbed above period I levels after the penultimate sampling period. Zooplankton levels gradually increased during the progression of the 1985 field season (Figure 34). The Arctic charr biomass approximation is included in Figure 34 (and Table 6) for comparison only; the data represent the standing crop estimation just prior to the 1985 fishery. If unperturbed, changes would probably have been infinitesimally small over the relatively short sampling period (discussed in the following chapter).

Both filamentous algae and globose blue-green algae biomass increased up to Period II; filamentous algae continued this trend but globose blue-green algae declined after the second sampling period (Figure 35).

Chironomid larvae biomass declined and subsequently increased after the penultimate sampling period.

Figure 34. Biomass changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).

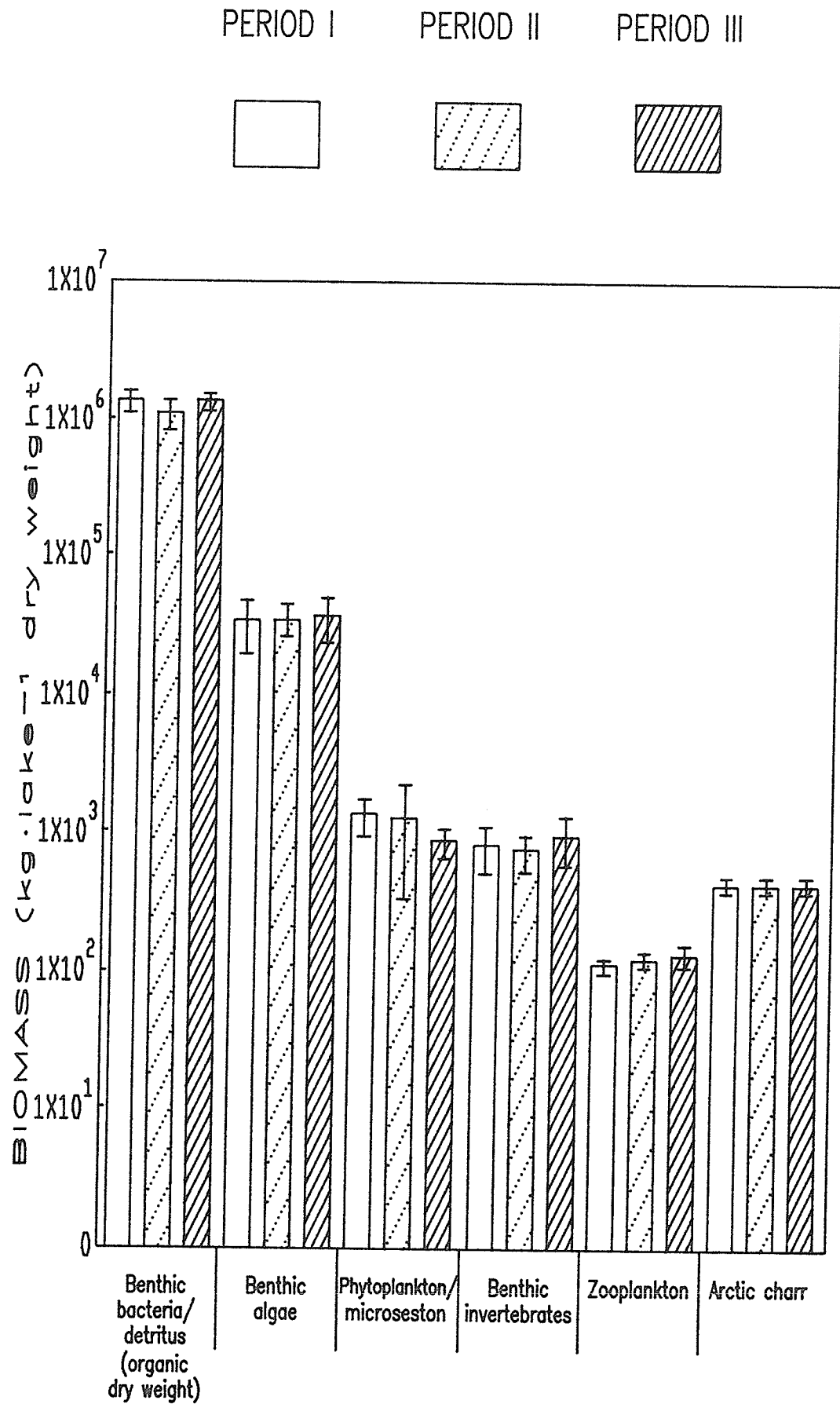
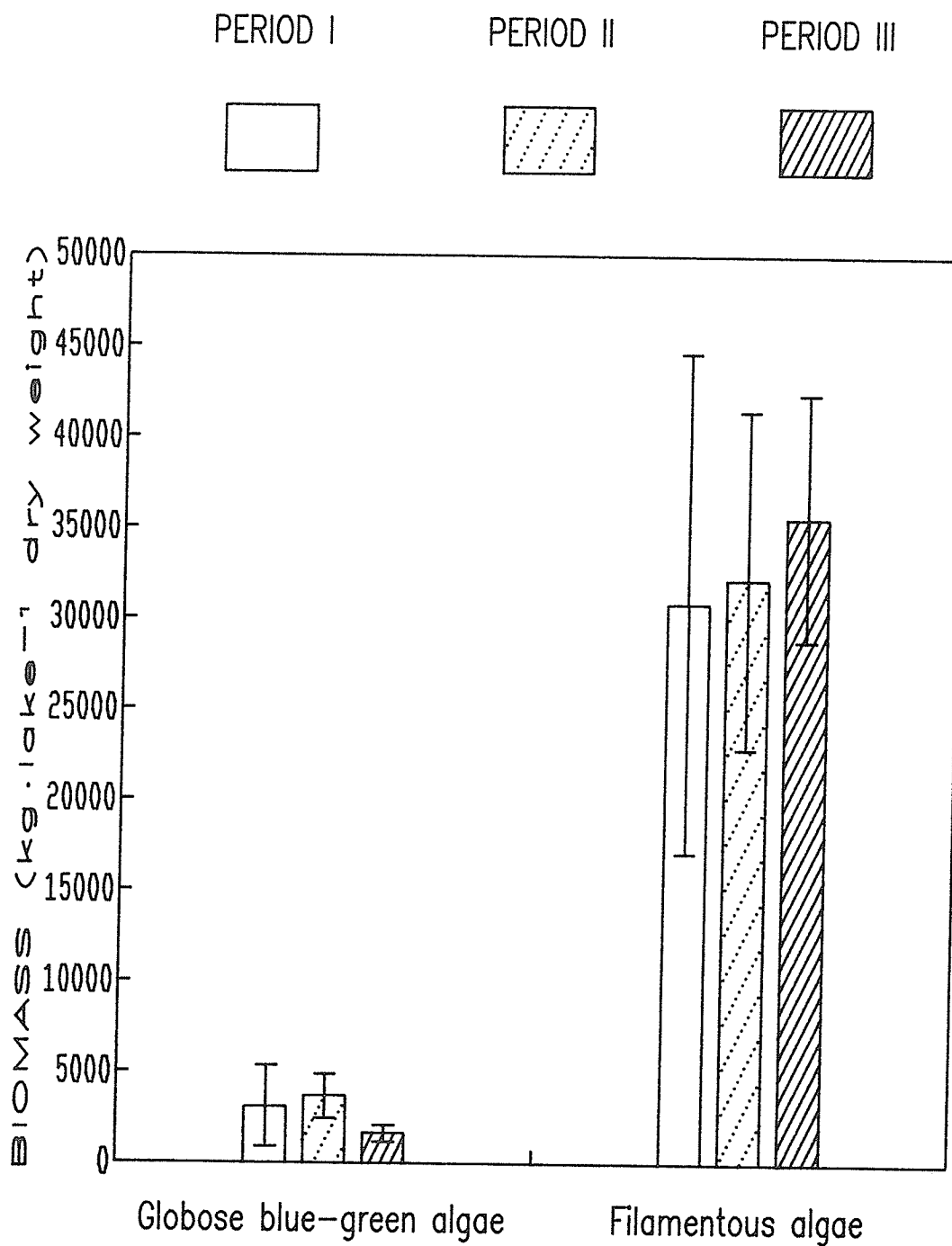


Figure 35. Biomass changes of taxa comprising benthic algae during the three sampling periods in 1985 (95% confidence intervals).



Oligochaetes followed a similar pattern; however, differences between Period I and Period II were minimal. Gammarus lacustris biomass rose slightly in Period II but sharply increased to over 2.5 times its initial level in Period III. Biomass of clams (soft tissue only), caddisfly larvae, and chironomid pupae slightly declined during the 1985 field season (Figure 36).

Depth distribution of benthic organisms

The distribution of benthic algae biomass at various depth ranges was similar during the three sampling periods, except for Period I in the 1-2 m depth range; biomass was markedly higher in this depth range than in the other two periods. During Period II no benthic algae were collected in water shallower than 1 m in depth. The highest biomass occurred in the 4-5 m depth range (Figure 37A). This is readily discernable in Figure 37B which displays the mean values for the three sampling periods.

Biomass peaked at the 2-3 m depth range for globose blue-green algae; the spherical balls were uncommonly encountered in water shallower than 2 m or exceeding 4 m in depth (Figure 38A). The 4-5 m depth range supported the highest biomass of filamentous algae (Figure 38B).

The biomass distribution of benthic invertebrates at different depth ranges approximated each other during Periods I, II, and III (Figure 39A). The modal frequency

Figure 36. Biomass changes of taxa comprising benthic invertebrates during the three sampling periods in 1985 (95% confidence intervals).

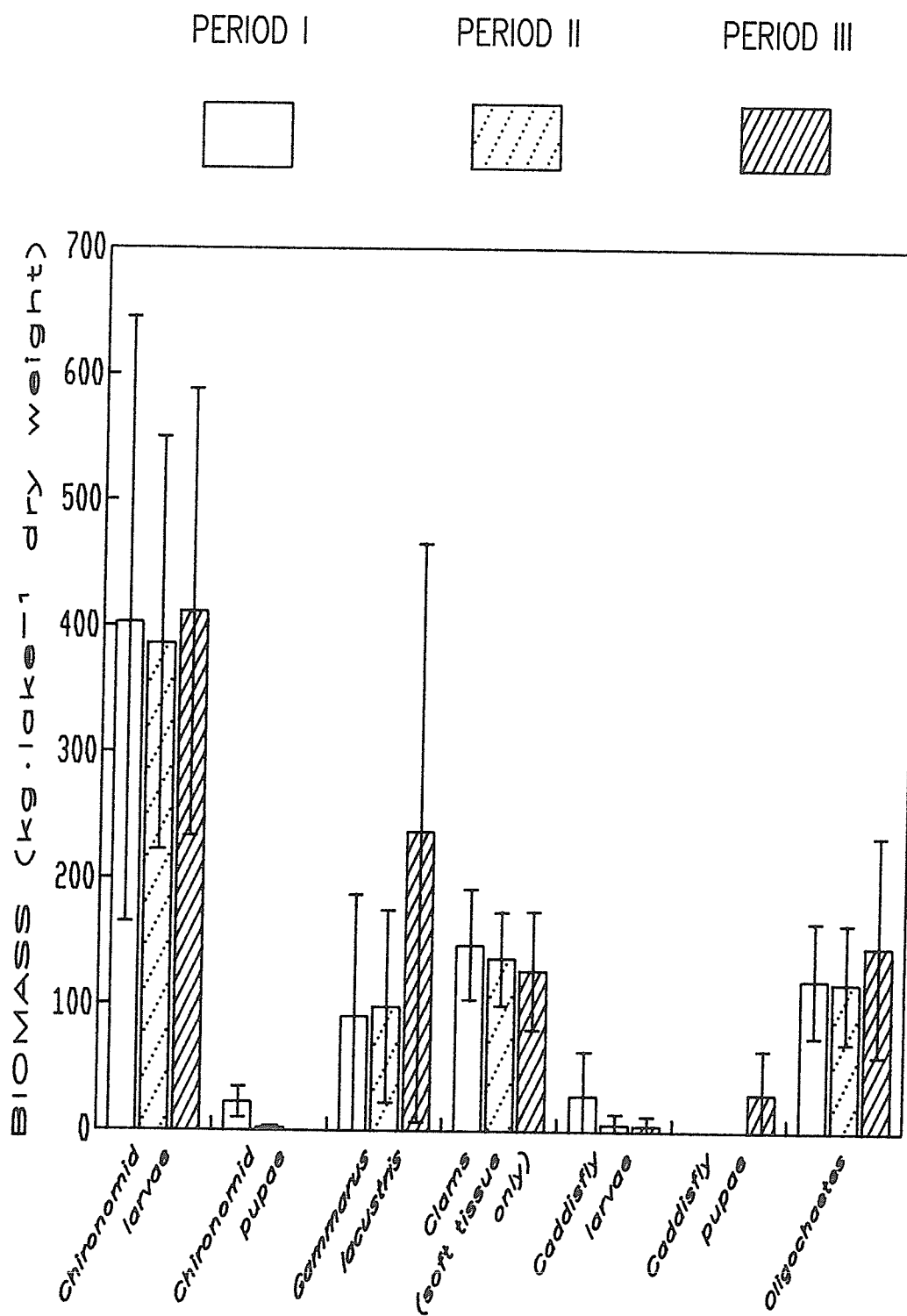


Figure 37. Distribution of benthic algae biomass at various depth ranges in 1985 (95% confidence intervals); (A) distribution during Periods I, II, and III; (B) means of Periods I, II, and III.

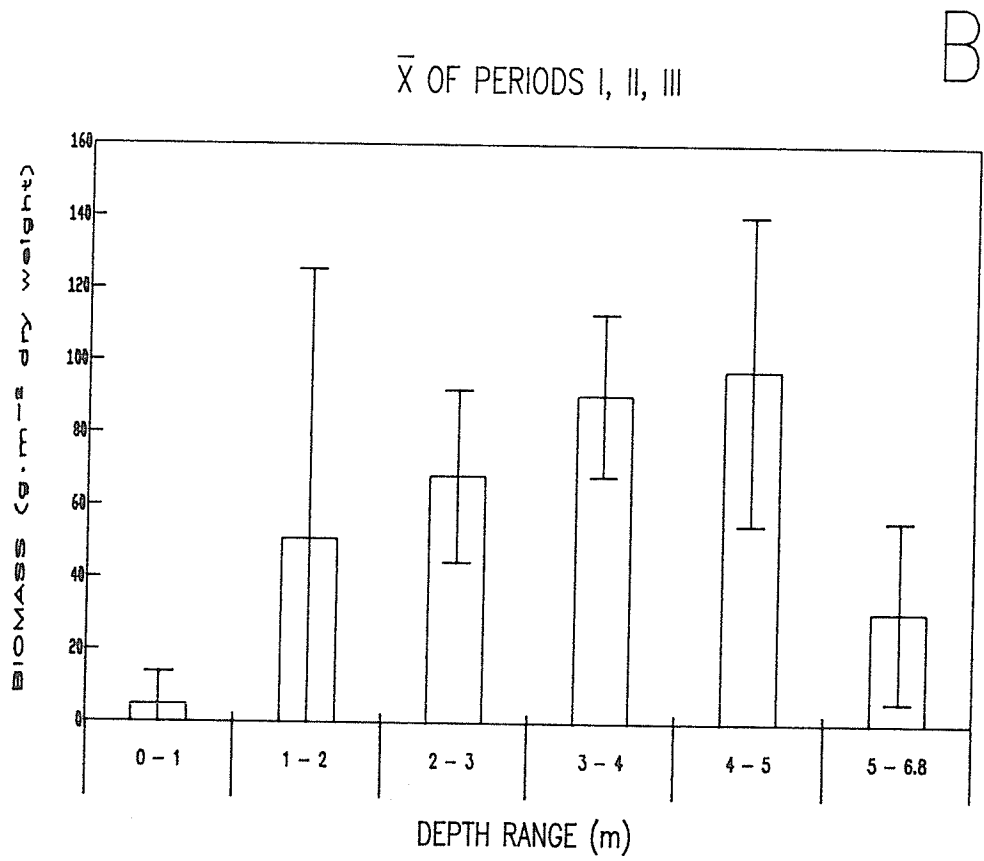
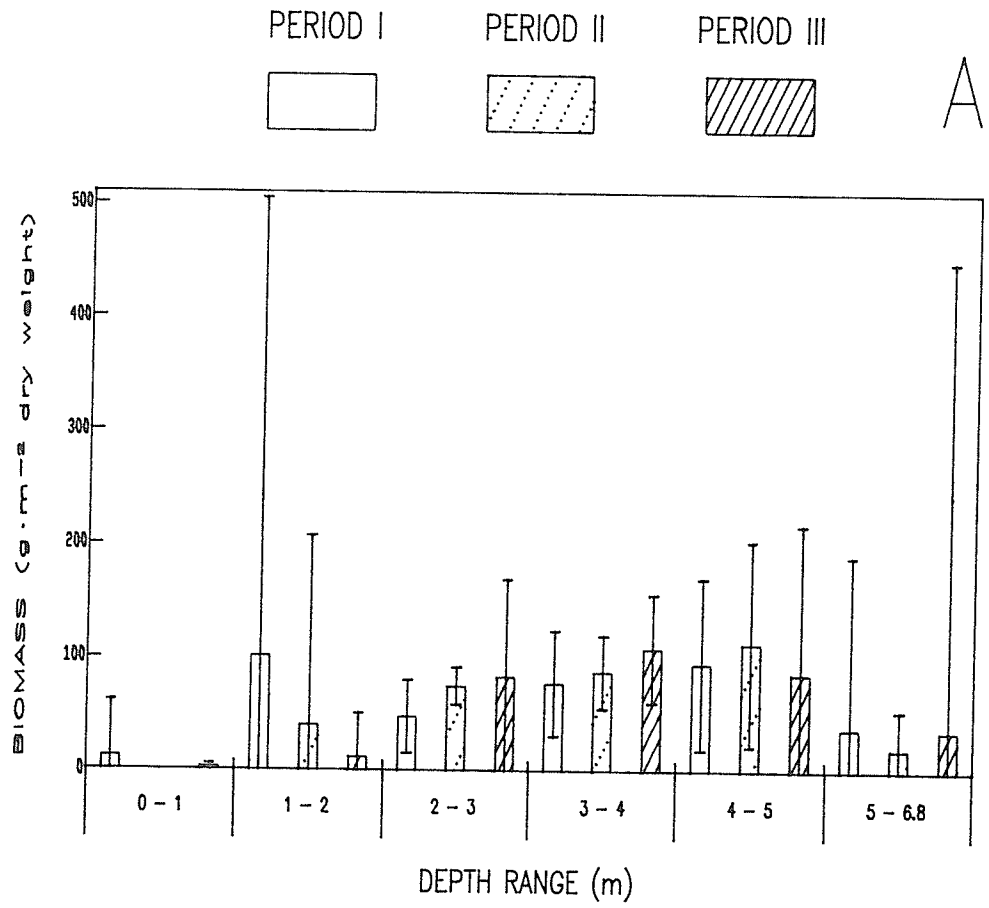
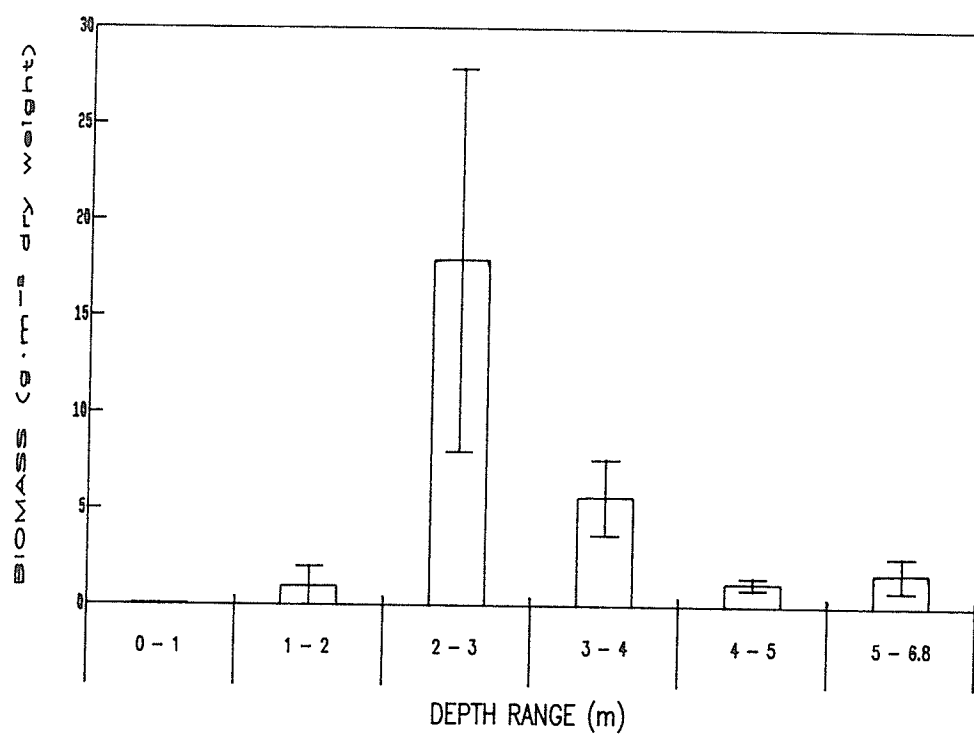


Figure 38. Distribution of biomass of taxa within benthic algae at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) globose blue-green algae; (B) filamentous algae.

$\bar{X}$ OF PERIODS I, II, III

A

 $\bar{X}$ OF PERIODS I, II, III

B

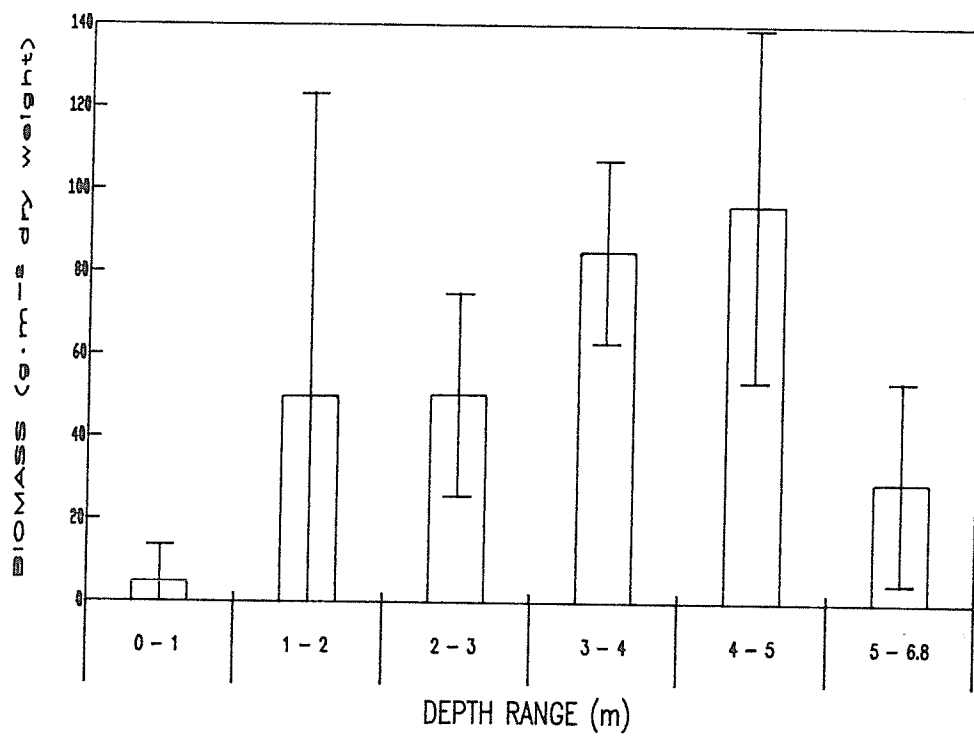
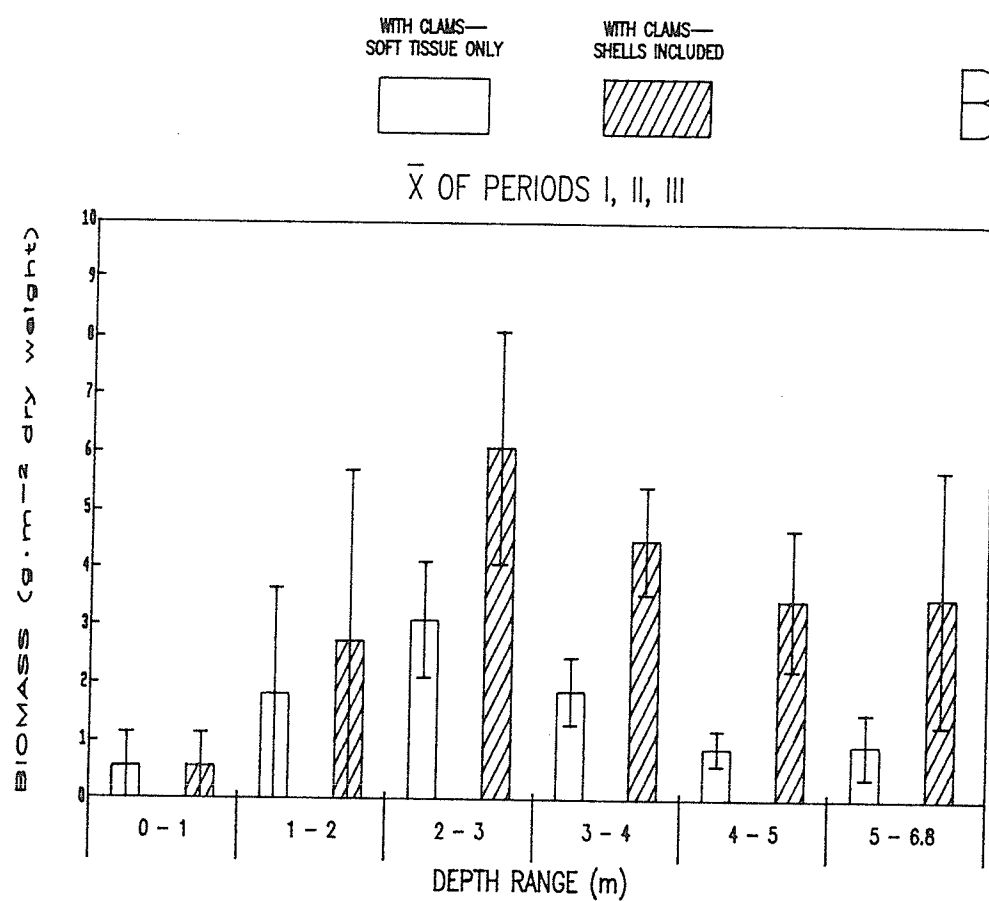
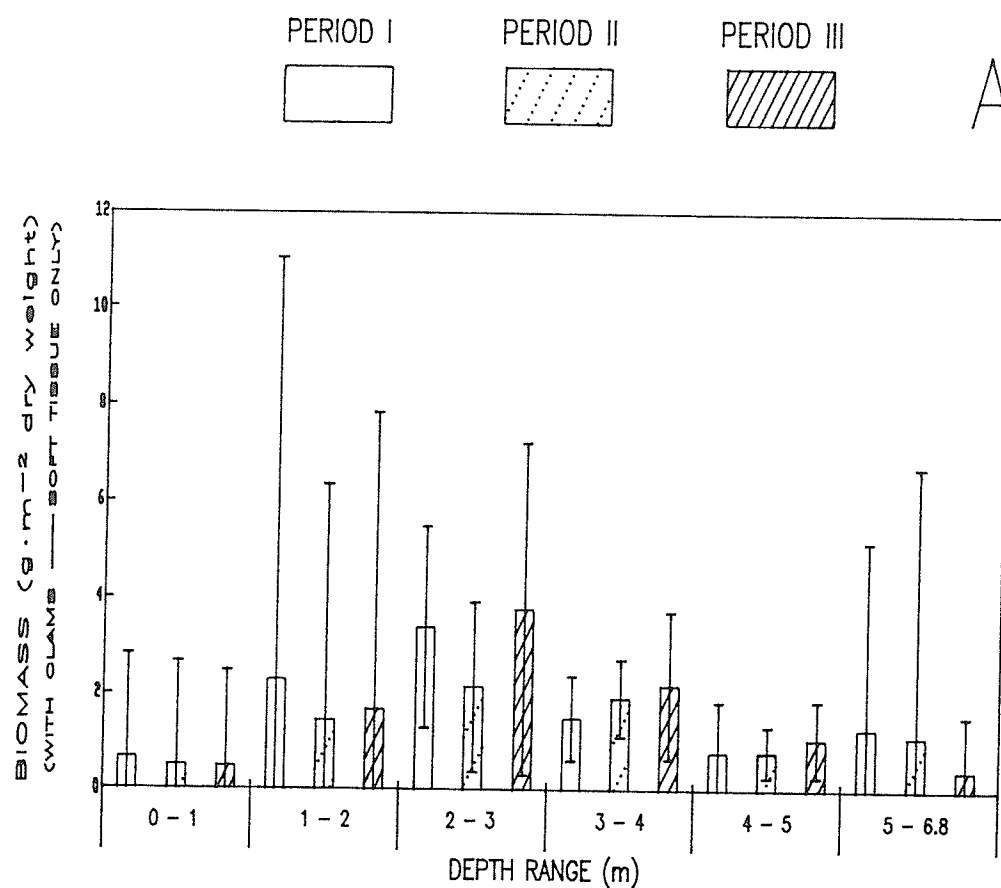


Figure 39. Distribution of benthic invertebrate biomass at various depth ranges in 1985 (95% confidence intervals); (A) distribution during Periods I, II, and III; (B) means of Periods I, II, and III.



was found at a depth of 2-3 m and this is clearly illustrated in Figure 39B (mean values for the three sampling periods).

Chironomid larvae showed an almost equal preference for the 1-2 and 2-3 m depth ranges (Figure 40A). Pupal stages of chironomids were only rarely encountered in water shallower than 2 m; their greatest abundance was found in water 2 to 4 m deep (Figure 40B). Gammarus lacustris were not encountered in the shallowest (0-1 m) and the deepest (5-6.8 m) regions of Keyhole Lake; the maximum frequency was found at a depth of 2-3 m (Figure 41A). Clams inhabited only regions exceeding 1 m in depth. From 2 to 6.8 m their biomass distribution was almost uniform. An indistinct peak occurred at 2-3 m (Figure 41B). Caddisfly larvae and pupae were absent from water deeper than 4 m. Pupal stages were encountered only in water 2 to 4 m deep. Modes occurred at the 1-2 and 2-3 m depth ranges for caddisfly larvae and pupae, respectively (Figure 42A). Oligochaetes were found at all depths but their greatest biomass was reached at a depth of 2-3 m (Figure 42B). Free-living nematodes appeared to shun deeper regions; their highest biomass was encountered at a depth of 0-2 m (Figure 43).

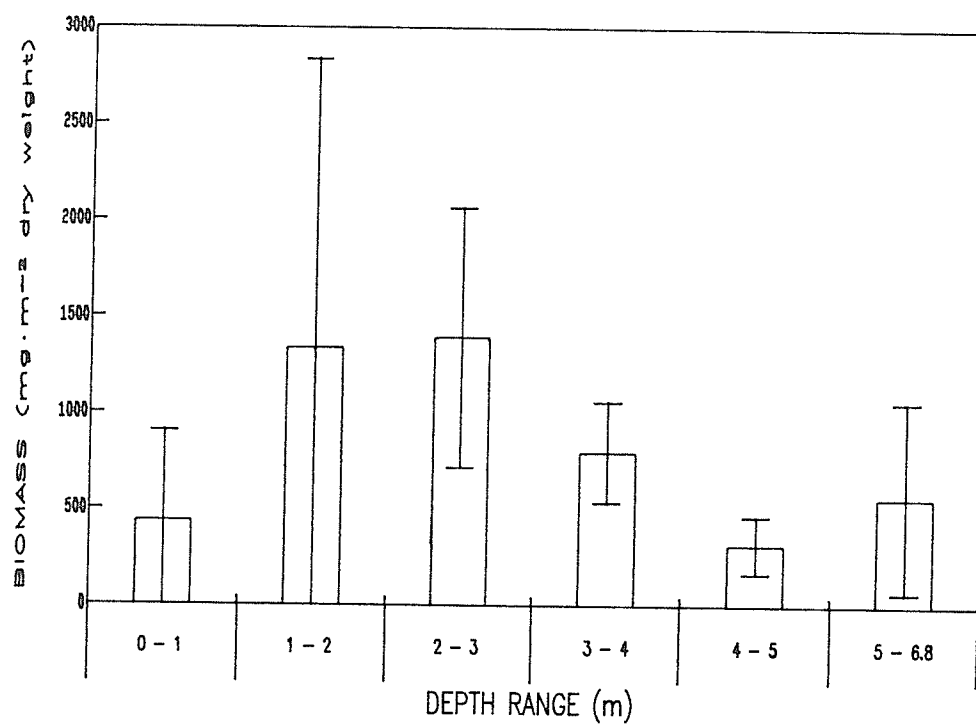
Chlorophyll content

Chlorophyll- α content was quite stable during both field seasons. A small, steady decline occurred during the sampling periods in 1985, concentrations decreasing from

Figure 40. Distribution of chironomid biomass at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) larvae; (B) pupae.

$\bar{X}$ OF PERIODS I, II, III

A

 $\bar{X}$ OF PERIODS I, II, III

B

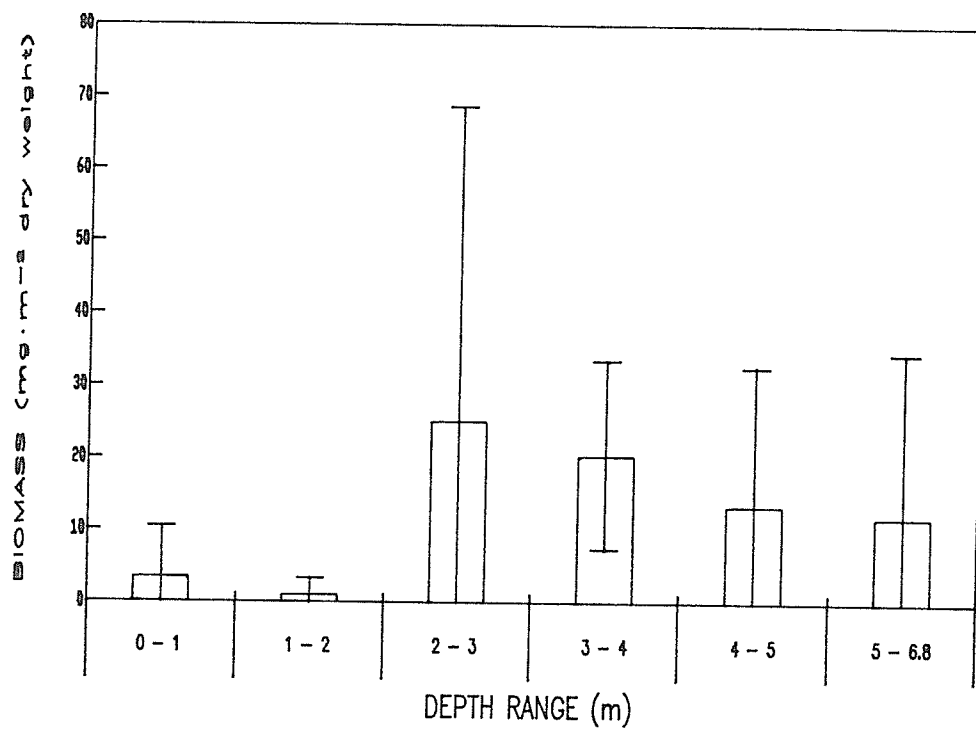
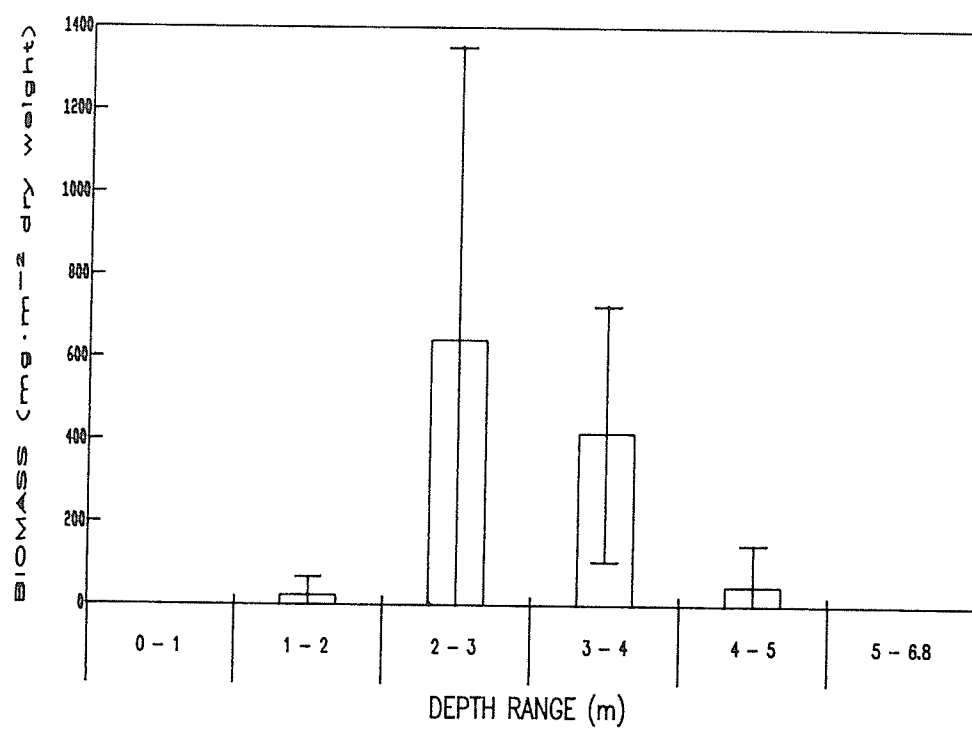


Figure 41. Distribution of biomass of taxa within benthic invertebrates at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) Gammarus lacustris; (B) clams.

$\bar{X}$ OF PERIODS I, II, III

A



SOFT TISSUE ONLY

WITH SHELLS



B

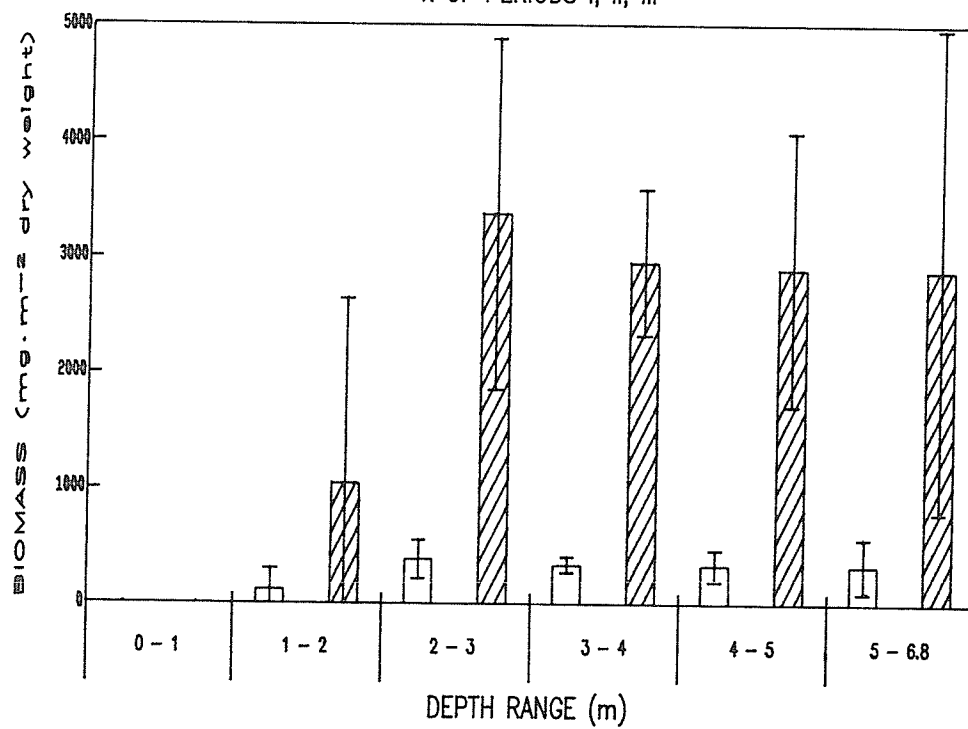
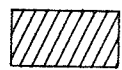
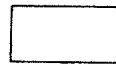
 $\bar{X}$ OF PERIODS I, II, III

Figure 42. Distribution of biomass of taxa within benthic invertebrates at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals); (A) caddisfly larvae and pupae; (B) oligochaetes.

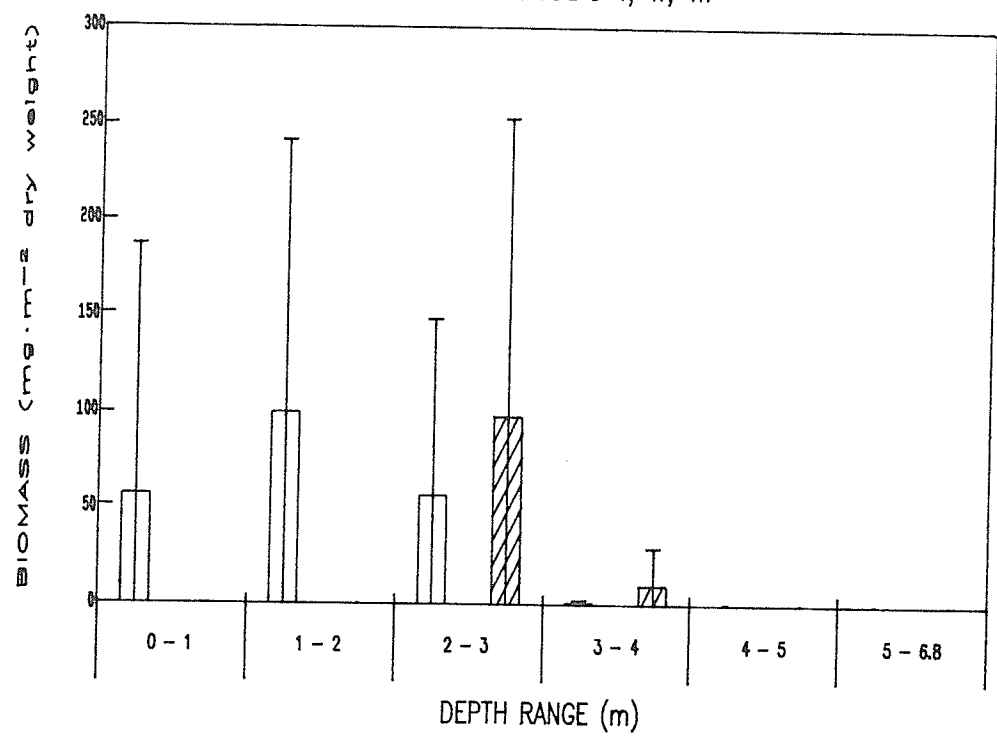
LARVAE

PUPAE



A

$\bar{X}$ OF PERIODS I, II, III



$\bar{X}$ OF PERIODS I, II, III

B

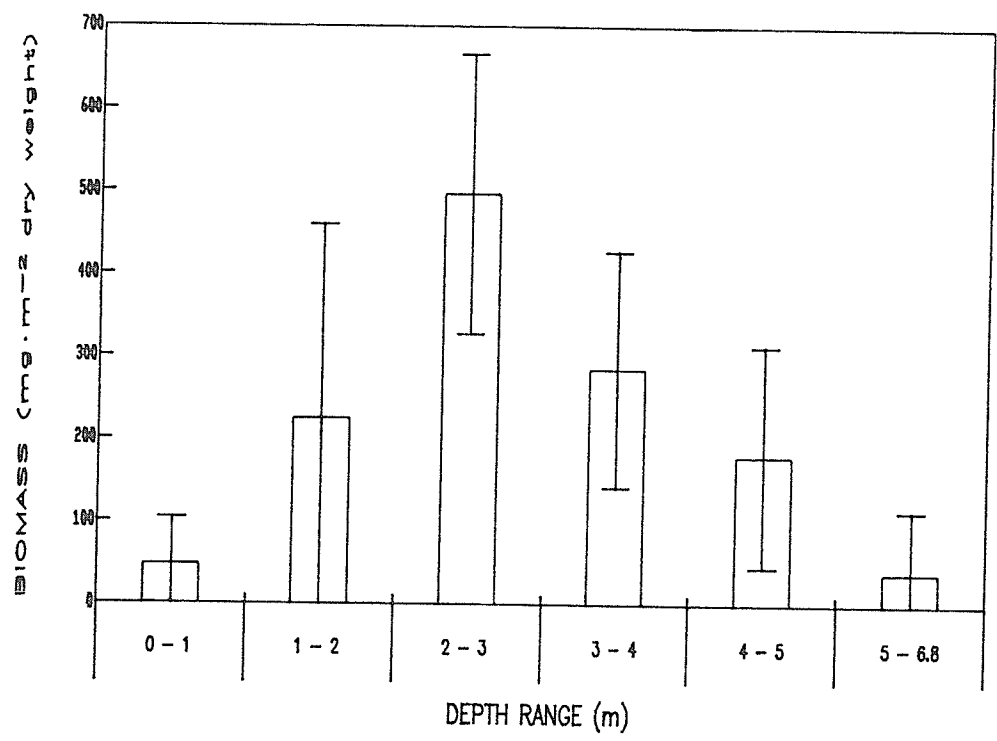
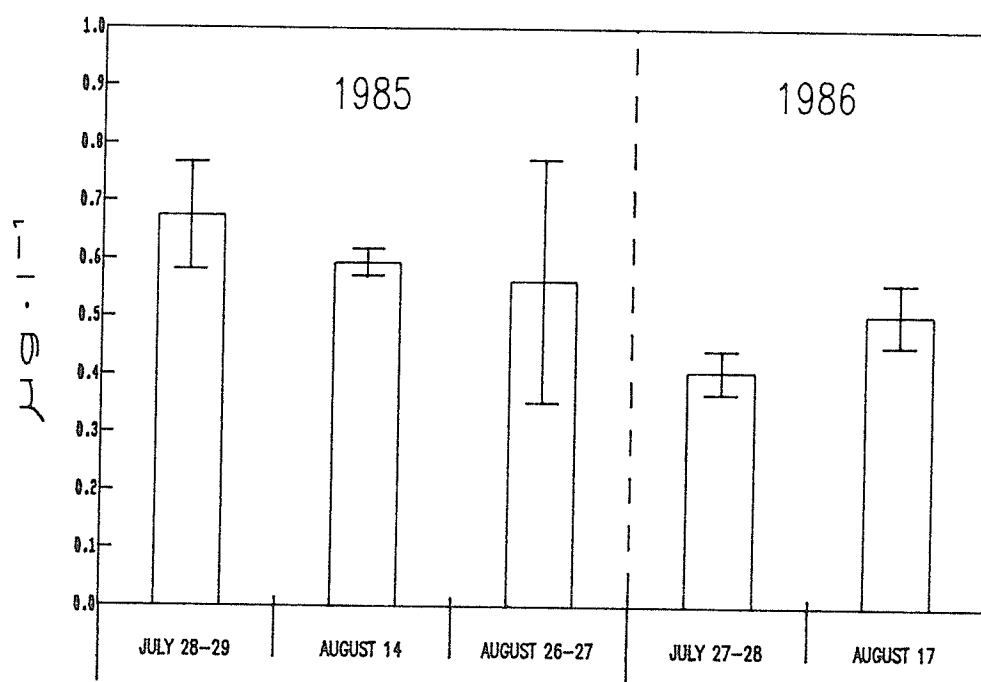
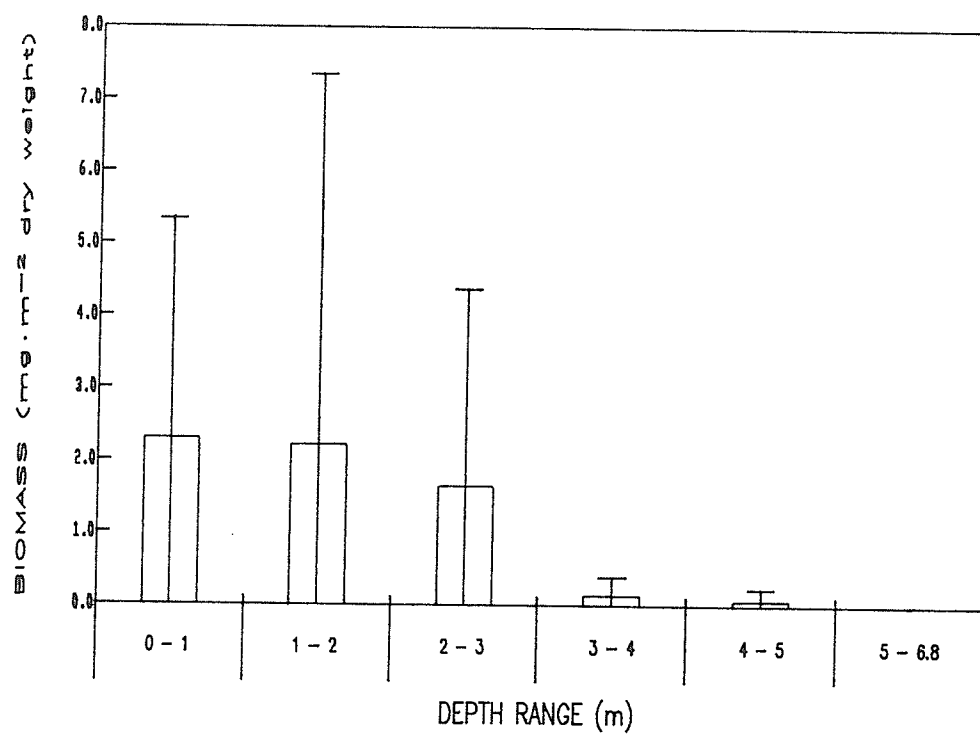


Figure 43. Distribution of free-living nematode biomass at various depth ranges representing the means of Periods I, II, and III, 1985 (95% confidence intervals) (top).

Figure 44. Chlorophyll- α content of Keyhole Lake water per sampling period (95% confidence intervals) (bottom).

$\bar{X}$ OF PERIODS I, II, III

0.675 to 0.563 $\mu\text{g}\cdot\text{l}^{-1}$. The mean for the 1985 season was 0.610 $\mu\text{g}\cdot\text{l}^{-1} \pm 0.072 \mu\text{g}\cdot\text{l}^{-1}$ (95% confidence intervals). In the following year levels ranged from 0.406 to 0.506 $\mu\text{g}\cdot\text{l}^{-1}$ and increased with the progression of the field season. The seasonal mean decreased to 0.456 $\mu\text{g}\cdot\text{l}^{-1} \pm 0.030 \mu\text{g}\cdot\text{l}^{-1}$ (95% confidence intervals) (Figure 44).

Chlorophyll- α content did not appear to be a reliable estimator for phytoplankton biomass. Comparisons between chlorophyll- α content and organic dry weight of phytoplankton and other microseston indicated virtually no correlation ($r^2 = 0.002$, $P > 0.05$, $n = 16$ pairs).

BIOMASS ENERGY

Estimates of trophic levels and taxa

The ratio 1,640:64:1.8:1 indicates the biomass energy relationships between trophic levels along the main food chain consisting of benthic bacteria and detritus, benthic algae, benthic invertebrates, and Arctic charr, respectively. A ratio of 5.3:1 was estimated for phytoplankton and other microseston, and zooplankton, respectively (Table 7, Figure 45).

Approximately 92.3% of the energy in benthic algae was contained in filamentous algae; globose blue-green algae contributed only 7.7% (Table 7, Figure 46).

Table 7. Biomass energy estimates for trophic levels and taxa within trophic levels in Keyhole Lake for 1985 (phytoplankton and other microseston for 1986). All values in $\text{kJ} \cdot \text{lake}^{-1}$ (95% confidence intervals).

Trophic Level	Taxon	Period I	Period II
Benthic bacteria/detritus		$1.468 \times 10^{10} \pm 6.347 \times 10^9$	$1.309 \times 10^{10} \pm 1.960 \times 10^9$
Phytoplankton/microseston		$1.376 \times 10^7 \pm 6.351 \times 10^6$	$1.993 \times 10^7 \pm 1.379 \times 10^7$
Benthic algae	Globose blue-green algae	$4.982 \times 10^7 \pm 3.249 \times 10^7$	$5.636 \times 10^7 \pm 1.662 \times 10^7$
	Filamentous algae	$5.235 \times 10^8 \pm 2.039 \times 10^8$	$5.059 \times 10^8 \pm 1.263 \times 10^8$
Benthic algae total		$5.733 \times 10^8 \pm 2.021 \times 10^8$	$5.623 \times 10^8 \pm 1.252 \times 10^8$
Benthic invertebrates	Chironomid larvae	$7.844 \times 10^6 \pm 3.948 \times 10^6$	$7.227 \times 10^6 \pm 2.641 \times 10^6$
	Chironomid pupae	$5.486 \times 10^5 \pm 2.693 \times 10^5$	$1.141 \times 10^4 \pm 1.036 \times 10^4$
	Gammarus lacustris	$1.802 \times 10^6 \pm 1.851 \times 10^6$	$1.889 \times 10^6 \pm 1.389 \times 10^6$
	Clams (with shells)	$3.594 \times 10^6 \pm 9.851 \times 10^5$	$3.323 \times 10^6 \pm 8.523 \times 10^5$
	Caddisfly larvae	$6.897 \times 10^5 \pm 6.803 \times 10^5$	$9.710 \times 10^4 \pm 1.429 \times 10^5$
	Caddisfly pupae	0 ± 0	0 ± 0
	Oligochaetes	$2.611 \times 10^6 \pm 8.809 \times 10^5$	$2.476 \times 10^6 \pm 9.235 \times 10^5$
Benthic invertebrates total		$1.709 \times 10^7 \pm 4.499 \times 10^6$	$1.502 \times 10^7 \pm 3.203 \times 10^6$
Zooplankton		$2.893 \times 10^6 \pm 3.306 \times 10^5$	$2.736 \times 10^6 \pm 3.094 \times 10^5$
Arctic charr		$9.269 \times 10^6 \pm 2.675 \times 10^5$	9.269×10^6
Total biomatter		$1.530 \times 10^{10} \pm 4.850 \times 10^9$	$1.370 \times 10^{10} \pm 1.383 \times 10^9$

Continued

Trophic Level	Taxon	Period III	Periods $\bar{x}$
Benthic bacteria/detritus		$1.782 \times 10^{10} \pm 1.127 \times 10^{10}$	$1.520 \times 10^{10} \pm 7.517 \times 10^9$
Phytoplankton/microseston		$1.274 \times 10^7 \pm 3.934 \times 10^6$	$1.564 \times 10^7 \pm 1.067 \times 10^7$
Benthic algae	Globose blue-green algae Filamentous algae	$2.801 \times 10^7 \pm 7.391 \times 10^6$ $6.078 \times 10^8 \pm 2.061 \times 10^8$	$4.524 \times 10^7 \pm 3.214 \times 10^7$ $5.453 \times 10^8 \pm 1.977 \times 10^8$
Benthic algae total		$6.358 \times 10^8 \pm 2.022 \times 10^8$	$5.905 \times 10^8 \pm 1.877 \times 10^8$
Benthic invertebrates	Chironomid larvae Chironomid pupae Gammarus lacustris Clams (with shells) Caddisfly larvae Caddisfly pupae Oligochaetes	$7.370 \times 10^6 \pm 2.882 \times 10^6$ $4.104 \times 10^6 \pm 3.664 \times 10^6$ $2.865 \times 10^6 \pm 9.064 \times 10^5$ $1.010 \times 10^5 \pm 1.279 \times 10^5$ $7.547 \times 10^5 \pm 8.125 \times 10^5$ $2.926 \times 10^6 \pm 1.531 \times 10^6$	$7.482 \times 10^6 \pm 3.173 \times 10^6$ $1.867 \times 10^5 \pm 5.337 \times 10^5$ $2.670 \times 10^6 \pm 3.208 \times 10^6$ $3.254 \times 10^6 \pm 1.056 \times 10^6$ $2.769 \times 10^5 \pm 6.721 \times 10^5$ $2.516 \times 10^5 \pm 8.264 \times 10^5$ $2.679 \times 10^6 \pm 1.173 \times 10^6$
Benthic invertebrates total		$1.812 \times 10^7 \pm 4.764 \times 10^6$	$1.680 \times 10^7 \pm 4.885 \times 10^6$
Zooplankton		$3.145 \times 10^6 \pm 4.675 \times 10^5$	$2.927 \times 10^6 \pm 5.008 \times 10^5$
Arctic charr		$9.269 \times 10^6 \pm 1.488 \times 10^5$	$9.269 \times 10^6 \pm 1.257 \times 10^5$
Total biomass		$1.850 \times 10^{10} \pm 8.610 \times 10^9$	$1.584 \times 10^{10} \pm 5.702 \times 10^9$

Figure 45. Biomass energy estimates of trophic levels representing the means of Periods I, II, and III, 1985 (phytoplankton and other microseston during 1986) (95% confidence intervals).

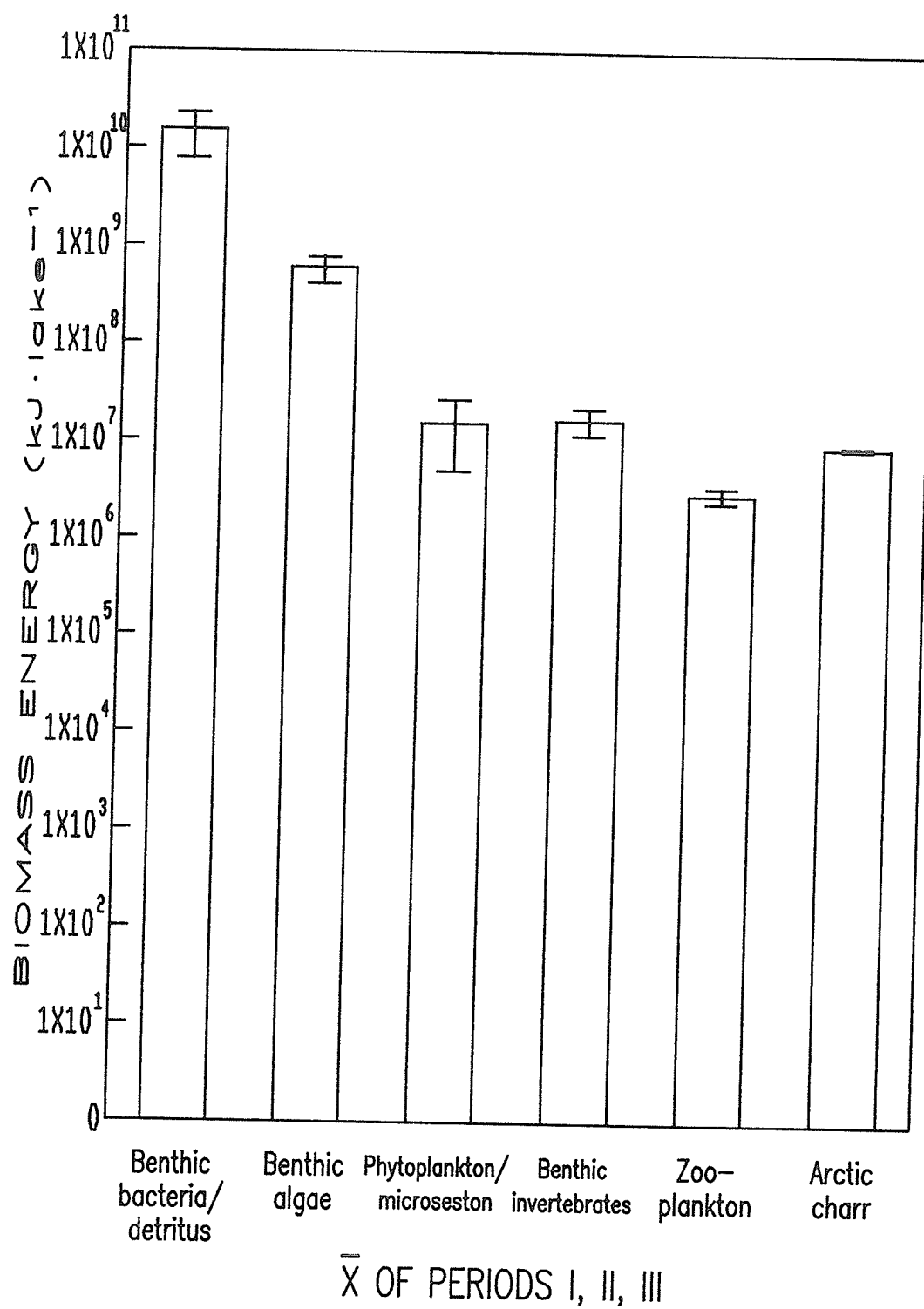
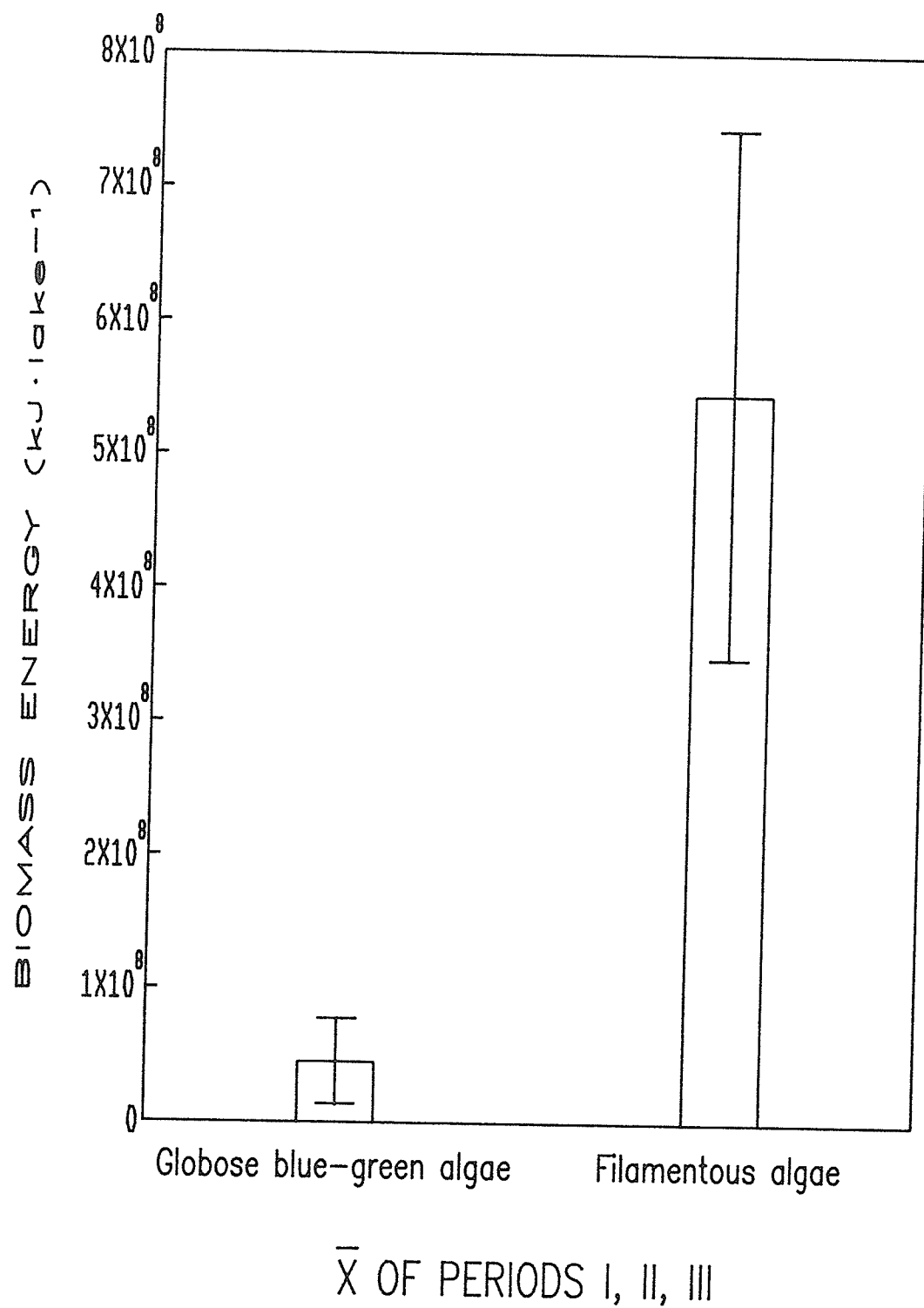


Figure 46. Biomass energy estimates of taxa comprising benthic algae representing the means of Periods I, II, and III, 1985 (95% confidence intervals).



Chironomid larvae contained 44.5% of the biomass energy in benthic invertebrates. Other important contributors were clams (including shells) (19.4%), oligochaetes (15.9%), and Gammarus lacustris (15.9%). Chironomid pupae, and caddisfly larvae and pupae contained a mere 4.3% of the total benthic invertebrate biomass energy (Table 7, Figure 47).

The total biomass energy (mean of the three sampling periods) contained in Keyhole Lake was estimated at 1.584×10^{10} kJ $\pm 5.702 \times 10^9$ kJ (95% confidence intervals) (Table 7).

Changes over time

A general pattern is apparent in the distribution of biomass energy for most trophic levels during the three sampling periods: total biomass energy declines in Period II, but subsequently increases to levels exceeding Period I. The exception is phytoplankton and other microseston; the pattern is inverted (Figure 48). However, the results for this trophic level represents data collected in 1986, not 1985, as were the others. The Arctic charr's biomass energy approximations in Figure 48 were calculated from the estimated biomass just prior to the 1985 fishery and energy densities determined from samples collected in Periods I and III. Short-term biomass changes in the Arctic charr population, if unexploited, would probably be minimal. Furthermore, energy densities of the fish were identical

Figure 47. Biomass energy estimates of taxa comprising benthic invertebrates representing the means of Periods I, II, and III, 1985 (95% confidence intervals).

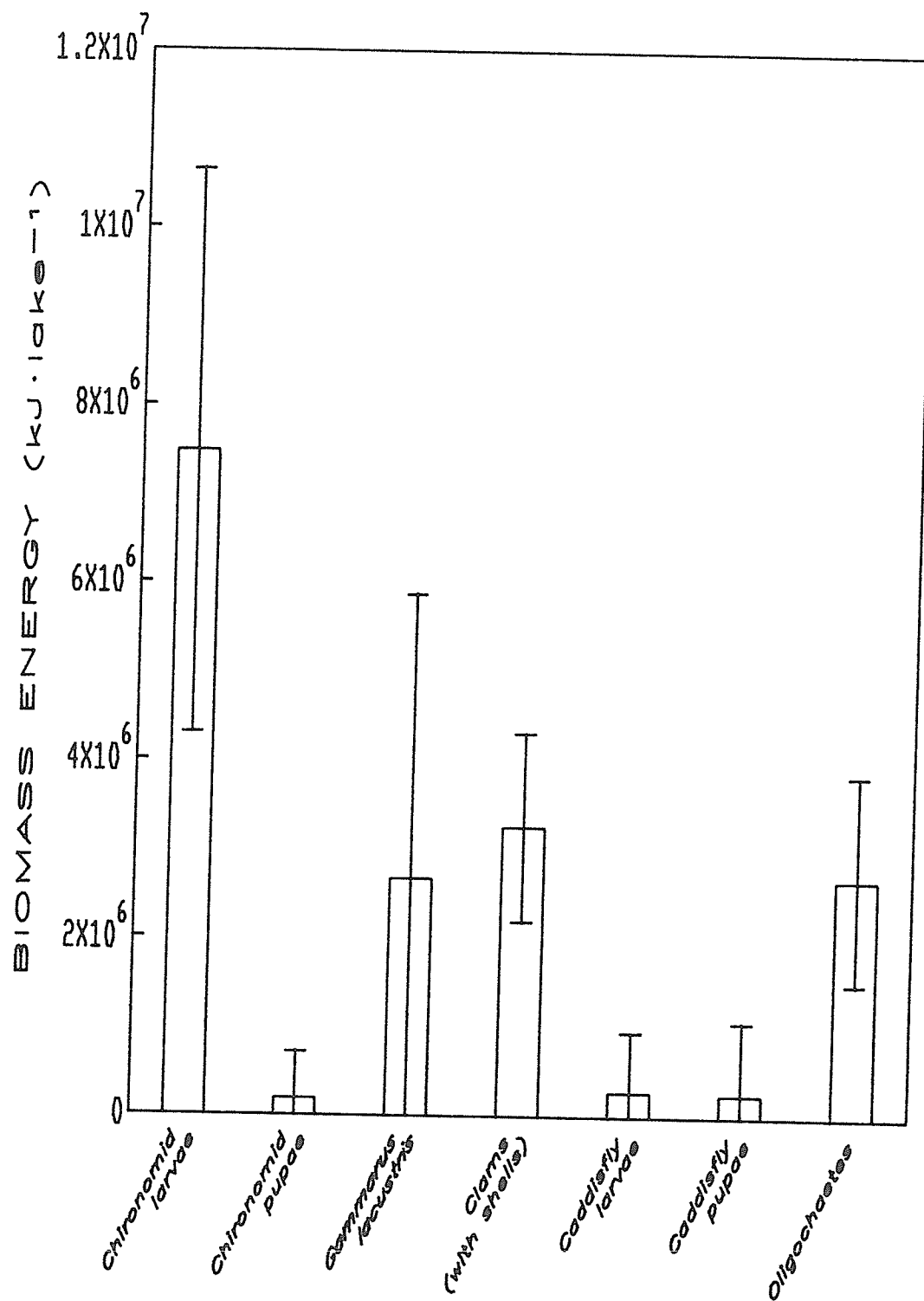
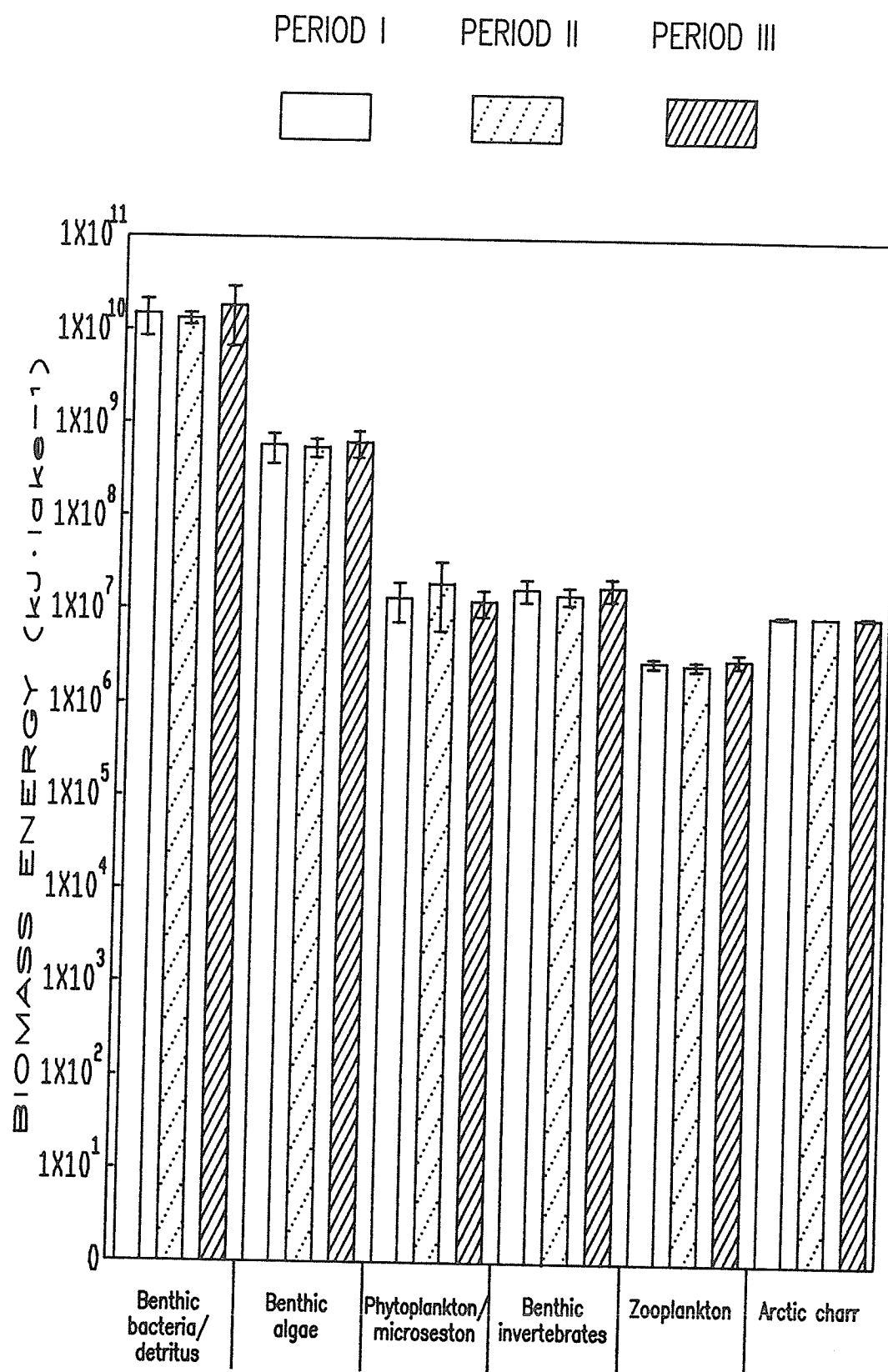
$\bar{X}$ OF PERIODS I, II, III

Figure 48. Biomass energy changes of trophic levels during the three sampling periods in 1985 (phytoplankton and other microseston in 1986) (95% confidence intervals).



during both sampling periods. The constant level of the biomass energy of Arctic charr in Figure 48 (and Table 7) appears a reasonable short-term approximation if the population was left unperturbed.

Filamentous algae exhibited a decline in biomass energy followed by an increase in excess of Period I levels after the second sampling period. Globose blue-green algae displayed the reverse; values increased in Period II and subsequently decreased below Period I levels (Figure 49).

Biomass energy fluctuations of the taxa within the benthic invertebrate community generally followed independent patterns. Chironomid larvae biomass energy levels declined in Period II followed by a slight increase; pupal stages, found only in the first two sampling periods, displayed a similar decrease in Period II. Gammarus lacustris showed a minimal increase in Period II but the biomass energy more than doubled during the last sampling period. Biomass energy of clams (including shells), caddisfly larvae, and oligochaetes declined during the penultimate sampling period; clams continued this trend, however, the latter two taxa increased in Period III (Figure 50).

Figure 49. Biomass energy changes of taxa comprising benthic algae during the three sampling periods in 1985 (95% confidence intervals).

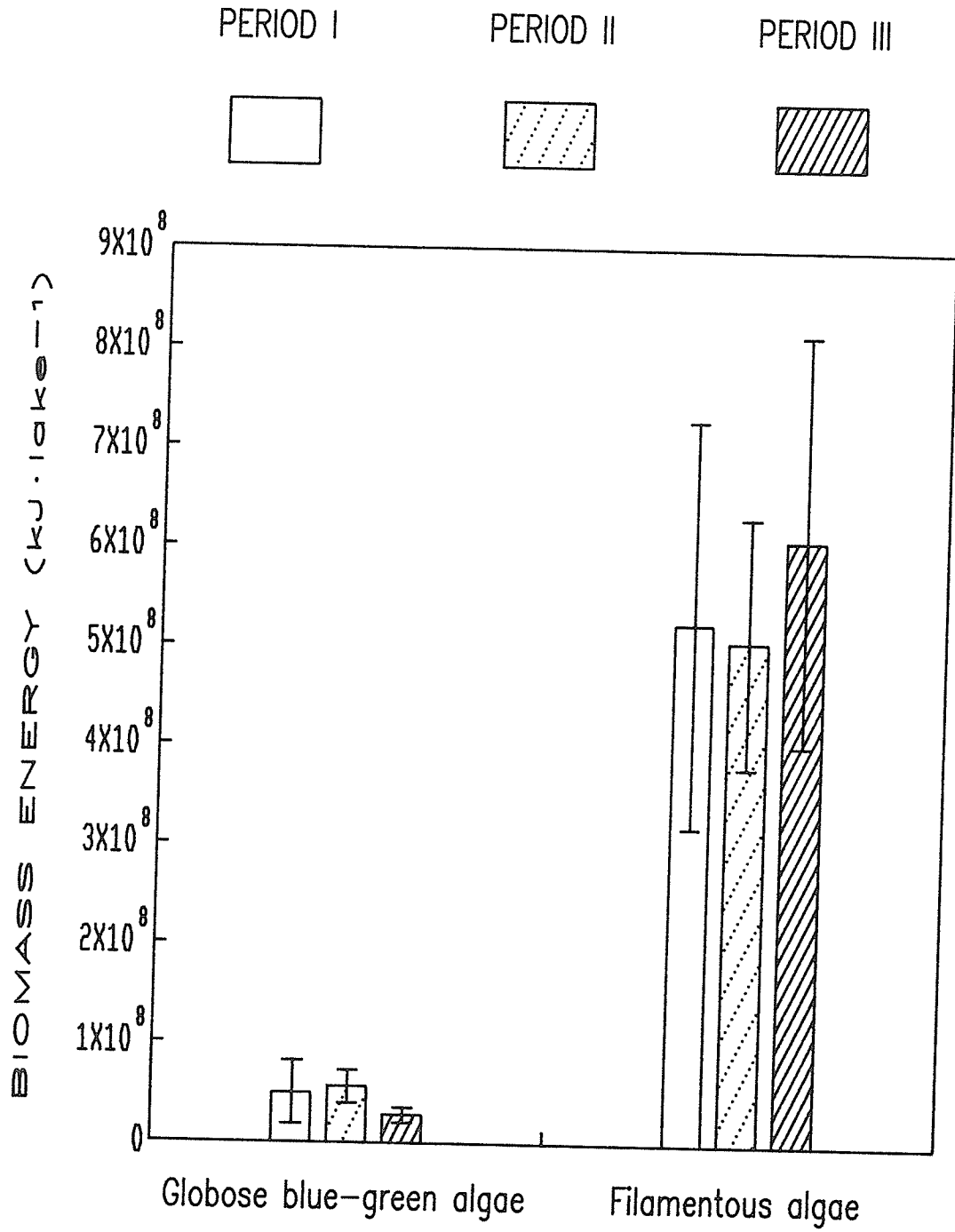
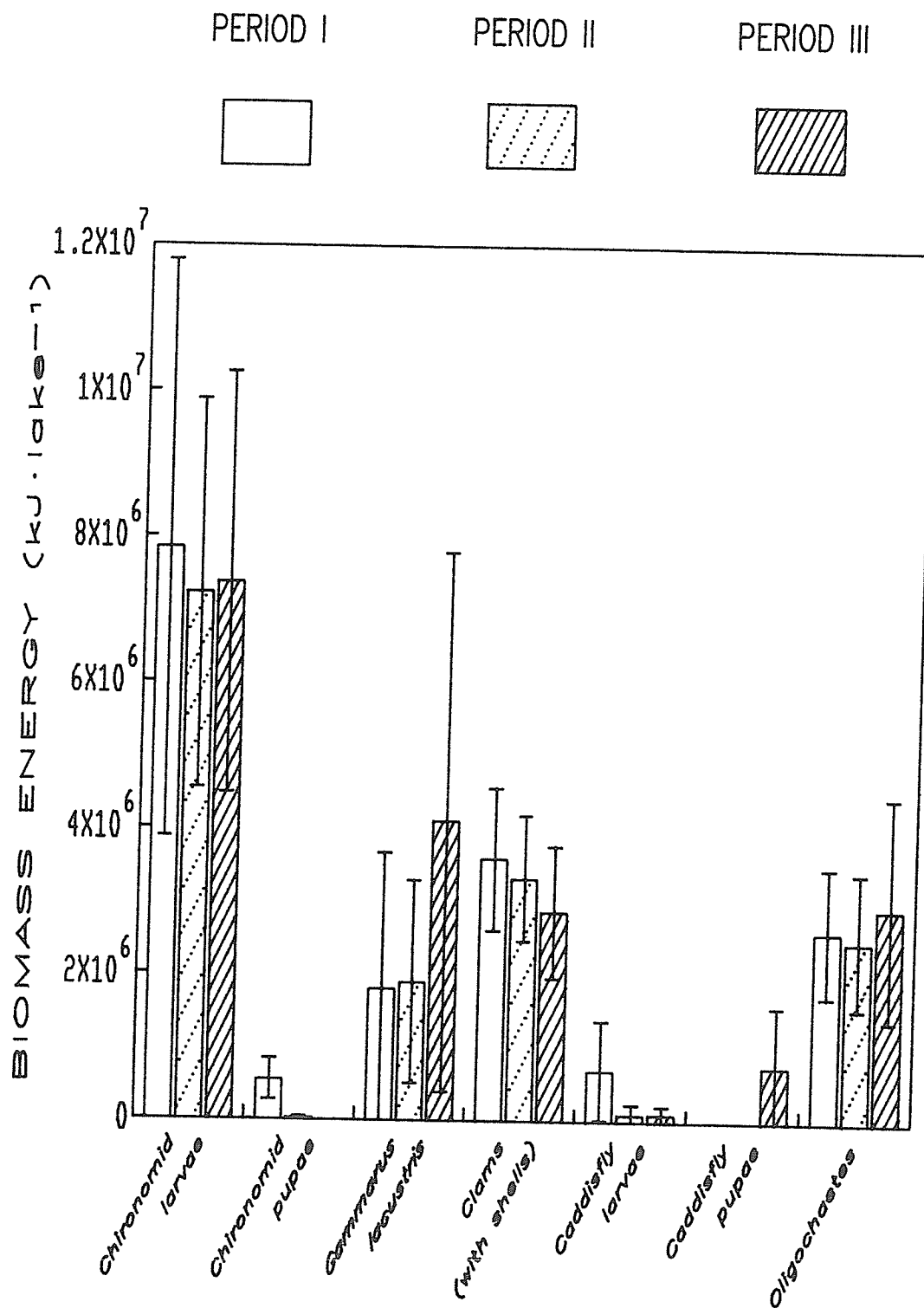


Figure 50. Biomass energy changes of taxa comprising benthic invertebrates during the three sampling periods in 1985 (95% confidence intervals).



MISCELLANEOUS COMPARISONS

Inverse logarithmic relationships

An interesting relationship between energy density and the logarithm of biomass of trophic levels along the main food chain of Keyhole Lake appears to exist. Energy density and the logarithm of biomass are inversely related. The trophic levels display a high degree of (negative) correlation ($r^2 = 0.997$, $P < 0.005$, $n = 4$) (Figure 51). The linear regression equation (using the common logarithm) is as follows:

$$Y = 10.48511 - 0.00036 X. \quad (22)$$

A similar inverse relationship is obtained when energy density is compared to the logarithm of biomass energy contained in each trophic level along the main food chain in Keyhole Lake. As in the preceding relationship the (negative) correlation was high ($r^2 = 0.974$, $P < 0.01$, $n = 4$) (Figure 52). The regression line can be located with the following linear regression equation (using the common logarithm):

$$Y = 14.04980 - 0.00035 X. \quad (23)$$

Figure 51. Relationship between energy density and the common logarithm of biomass of the main food chain in Keyhole Lake.

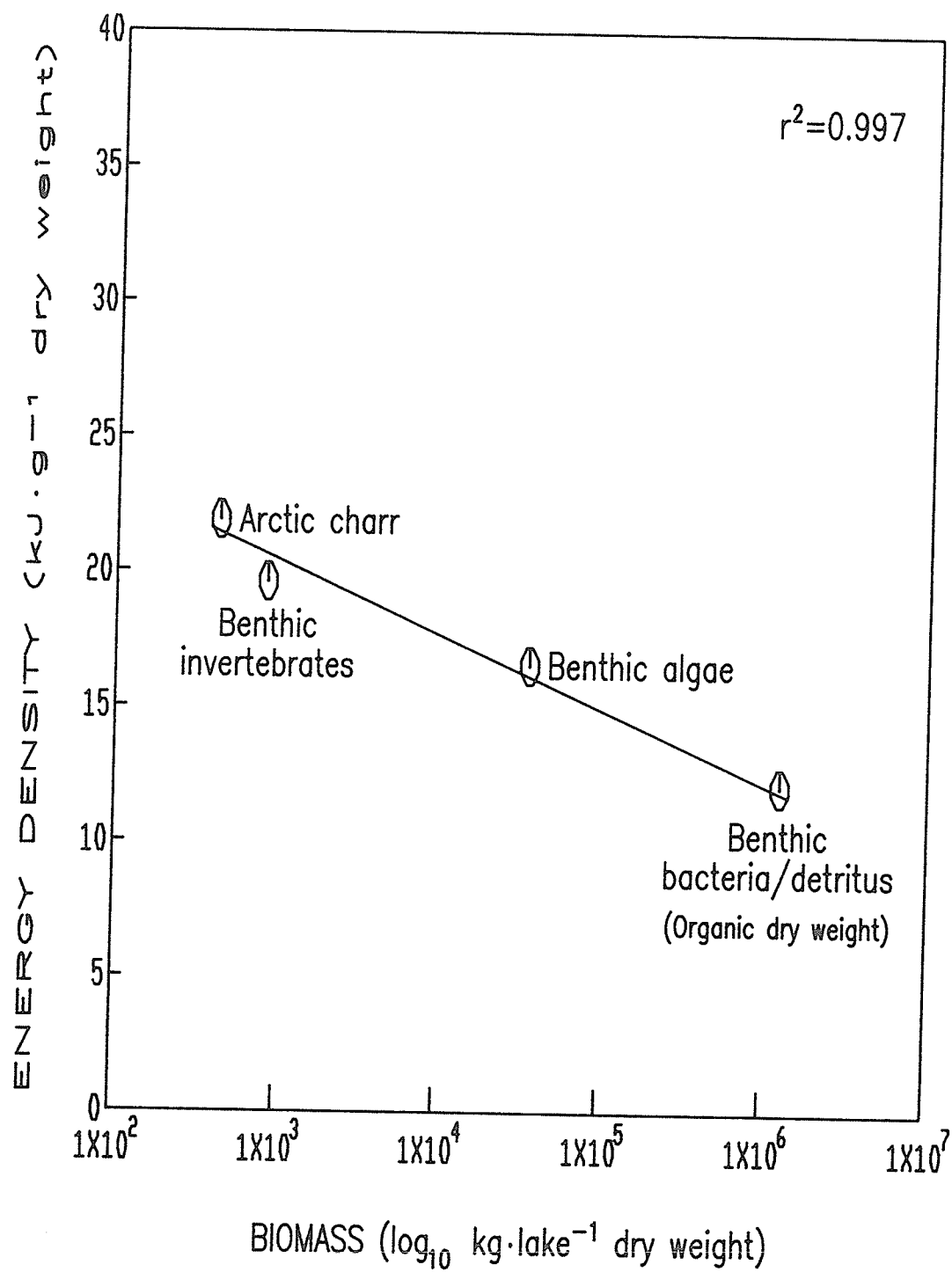
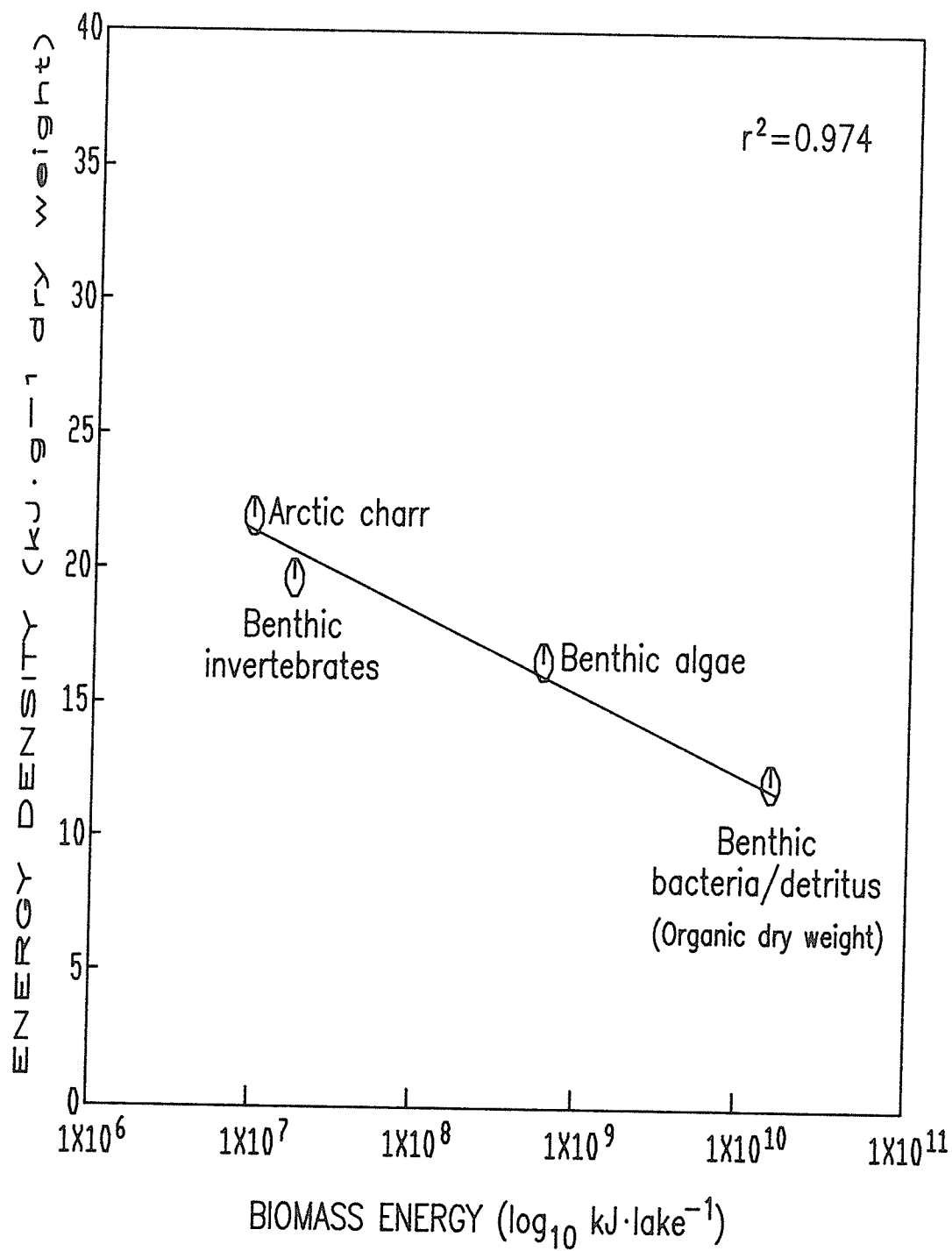


Figure 52. Relationship between energy density and the common logarithm of biomass energy of the main food chain in Keyhole Lake.



It may be noted that in Figures 51 and 52 benthic bacteria and detritus are expressed in organic weight while other trophic levels are expressed in dry weight. This was necessary due to difficulties with separating bacteria from their substrate (see previous chapter under "Biomass analysis—Benthic bacteria and detritus"). This anomaly is eliminated on the X axis of Figure 52; biomass energy is equivalent in the biomass of a taxon or trophic level whether expressed in organic or whole (organic plus inorganic) weight; only organic compounds are combustible and measureable with calorimetry.

Comprehensive trophic level comparisons

Comparisons between energy density, biomass, and biomass energy for individual trophic levels are presented in Appendix I. Changes between periods were previously discussed in this chapter. Energy density estimates of benthic bacteria and detritus not adjusted for inorganic contaminants are included in Figure I1. Figures I3 to I6 additionally contain energy density and biomass energy estimates not corrected for formalin preservation.

DISCUSSION

. . . the most profitable method of analysis lay in reduction of all the interrelated biological events to energetic terms.

(Addendum by Hutchinson in Lindeman 1942)

CHARACTERISTICS OF TROPHIC LEVELS AND ASSOCIATED TAXA

Decomposers

At the bottom of the energy density hierarchy of the Keyhole Lake ecosystem are benthic bacteria and detrital matter. Decomposers comprise a major component of an aquatic ecosystem (Odum and de la Cruz 1963; Efford 1969; Melchiorri-Santolini and Hopton 1972; Hall and Hyatt 1974).

The proportionally vast quantity of benthic bacteria and detritus in Keyhole Lake functions as an energy reservoir for detritivorous benthic invertebrates. This probably stabilizes the energy flow at the lower consumer levels. Most of the respiration in a tundra pond ecosystem at Barrow, Alaska, occurred in the sediments (Hobbie et al. 1972). Congruently, Welch and Kalff (1974) found nearly all of the respiration in Char Lake, Cornwallis Island,

Northwest Territories, to be benthic. They noted that the cycling of benthic production through the detrital pool stabilized gross energy flow. A similar situation occurs in grasslands; organic matter in and on the surface of the mineral soil functions as an energy reservoir (Dyksterhuis and Schmutz 1947; Dix 1960).

Hirata and Fukao (1977), and Hirata's (1980) models of mass and energy flow require, in addition to a hierarchical energy density along the food chain, feedback loops from each trophic level to the decomposers to maintain stability. This appears a reasonable assumption which was proposed earlier by Lindeman (1941, 1942).

Primary producers

Energy densities of the primary producers in Keyhole Lake were below those of consumer levels. Cummins and Wuycheck (1971) noted that the theoretical variation of organismic energy density is approximately $22,610 \text{ J}\cdot\text{g}^{-1}$ organic dry weight; pure carbohydrate contains an average of $17,165 \text{ J}\cdot\text{g}^{-1}$ and fats $39,775 \text{ J}\cdot\text{g}^{-1}$. In Keyhole Lake values ranged from $10,902 \text{ J}\cdot\text{g}^{-1} \pm 6,651 \text{ J}\cdot\text{g}^{-1}$ organic dry weight (benthic bacteria/detritus Period I) to $26,079 \text{ J}\cdot\text{g}^{-1} \pm 720 \text{ J}\cdot\text{g}^{-1}$ dry weight (zooplankton Period I) (95% confidence intervals). Plant carbohydrates and proteins generally have a lower energy density than animal proteins and fats (White et al. in Ulanowicz 1972). It follows that energy densities of plants are generally lower than animals and this is

further supported by literature on organismic energy density values (e.g. Golley 1961; Cummins and Wuycheck 1971; Atkinson and Wacasey 1983).

Benthic algae

Over 96% of the primary producer's biomass in Keyhole Lake was benthic. The relative shallowness (mean depth = 3.01 m) and low turbidity of the lake are probably major reasons for largely benthic primary production. All depths of Keyhole Lake are in the euphotic zone. In deeper Char Lake (mean depth = 10.2 m (Schindler et al. 1974a)) gross benthic photosynthesis represented 80% of the total lake photosynthesis (Welch and Kalff 1974; Rigler 1975).

The benthic algae biomass was over forty-two times the benthic invertebrate biomass. This suggests that little benthic alga was directly utilized by the consumers and its turnover rate was slow. A slow turn-over rate is equivalent to a "low value" of the Production/Biomass (P/B) ratio (Margalef 1968; Odum 1969). Benthic algae are indirectly used by benthic invertebrates through complex detrital pathways. Bray (1961) found that in a mature forest the consumption of living material, such as leaves, averaged only 8.3% of net annual production; most was utilized through detrital pathways.

Johnson's (1987) observations in 1980 and 1985-86 suggested an increase in benthic algae over that time

period. This is consonant with Hunter's (1970) 1965 biomass estimate of benthic algae (106,356 kg wet weight) and the 1985 mean estimate (290,611 kg wet weight); indicating a 2.7 fold increase over the 20 year period.

Phytoplankton and other microseston

The planktonic algae of Keyhole Lake contributed less than 4% to the total biomass of primary producers. The biomass estimate of phytoplankton and other microseston was 9.4 times that of zooplankton. This refutes Sprules (1988) theory that in pelagic communities, under steady-state conditions, each trophic level should contain approximately the same amount of biomass, or slightly less than the previous one. Some aquatic ecosystems exhibit extremely rapid turnover rates ("high value" of the P/B ratio) of phytoplankton; this may result in the herbivore biomass exceeding that of phytoplankton (Winberg 1972; Smith 1980). The preceding may indicate that phytoplankton and other microseston in Keyhole Lake are not intensively grazed by zooplankton and exhibit a fairly slow turnover rate.

The chlorophyll- α content of phytoplankton in Keyhole Lake was found to be an extremely poor estimator of phytoplankton biomass. White et al. (1988) noted variations in chlorophyll- α content to phytoplankton biomass ratios between different species, light regimes, and physiological conditions of the algae. Studies showed that chlorophyll- α to cell volume ratios display seasonal changes; the pigment

to cell volume ratios declined significantly in the winter (Desortova 1981; Pridmore and Hewitt 1984). Tucker (1949) found the standard error of estimation in single samples high (up to 85%) in predicting the number of phytoplankton cells from the quantity of photosynthetic pigment extracted. Graham (1943), and Berman and Pollinger (1974) stated that chlorophyll content varied markedly between different phytoplankton taxa. The pigment concentrations were also influenced by nitrate-nitrogen availability (Berman and Pollinger 1974). Furthermore, Yentsch and Ryther (1957), and Shimada (1958) reported appreciable changes in chlorophyll concentrations during daylight hours.

Consumers

Benthic invertebrates

Benthic invertebrates of Keyhole Lake generally exhibited energy densities below that of Arctic charr; however, the few exceptions are notable. Hirata and Ulanowicz (1986) indicated that inversions in the energy density hierarchy of foodwebs may occasionally occur. The high energy densities of caddisfly larvae during Periods I and III are in accord with these authors' view. Chironomid pupae and caddisfly pupae also exceeded the energy density of the terminal predator. These aberrations, according to Hirata and Ulanowicz (1986), disappear during subsequent periods.

The mean energy density of caddisfly larvae, when taken over the three sampling periods, was distinctly lower than either Periods I or III, and even slightly below that of Arctic charr. High energy densities during pupal stages appear to be a necessity for energetically demanding metamorphosis. Furthermore, adult chironomids do not feed (Coffman 1978) and only a few caddisfly species are known to feed as adults (Wiggins 1978). The pupal stage represents a short period during the insects life cycle. Larval stages of Arctic chironomids usually last from 1 year to over 3 years while the pupal stages frequently exist for only a few weeks (Oliver 1968, 1971). Caddisfly larval stages last from less than 1 year to 2 years; the duration of the pupal stages varies from 2 to 3 weeks (Wiggins 1978). Adult chironomids usually live for only a few days (Coffman 1978) and the life span of adult caddisflies is normally less than 1 month (Wiggins 1978). These data indicate that the energy density means over the whole life cycle of these holometabolous insects approaches that of their lengthy larval stages. The foregoing supports Hirata and Ulanowicz's (1986) conclusion that energy density anomalies disappear when measurements are averaged over long time periods.

The benthic invertebrate biomass was approximately twice that of the Arctic charr biomass. This indicates either that: (1) the turnover rate of benthic invertebrates

is extremely rapid, or (2) a relatively small quantity of energy is required to maintain the Arctic charr population. The lengthy larval stages of Arctic chironomids (Oliver 1968, 1971) (the main food source of Arctic charr in Keyhole Lake) and the climax state characteristics of the Arctic charr population tend to support the second proposition. The turnover rate, at least in chironomids, is very slow. The life cycle of Arctic chironomids usually lasts at least 1 year but may exceed 3 years (Oliver 1968, 1971). Approximately one half of the total benthic invertebrate biomass consisted of chironomid larval and pupal stages. Additionally, the dominant Arctic charr population is highly efficient in energy utilization and thus requires relatively little energy for maintenance (Dutil 1982).

Interestingly, the chironomid larvae biomass in Keyhole Lake was not vastly different from a eutrophic temperate lake. Lake Zbechy, Poland, located in an area of intensive farming, is comparable in depth (mean depth = 4.2 m, maximum depth = 7.5 m) to Keyhole Lake and is approximately twice the surface area (108.9 ha). The littoral zone (0.2-2 m) and profundal zone (2-5 m) contained 2,000 and 500 $\text{mg}\cdot\text{m}^{-2}$ dry weight of chironomid larvae, respectively (Banaszak 1984). The average chironomid larvae biomass of Keyhole Lake was estimated at $824 \text{ mg}\cdot\text{m}^{-2} \pm 209 \text{ mg}\cdot\text{m}^{-2}$ dry weight (95% confidence interval). Congruently, Maciolek (1988) reported little difference between the

standing crops of invertebrates in eutrophic tundra ponds and productive temperate ponds.

A recent introduction to the benthic invertebrate community of Keyhole Lake was apparent: the amphipod Gammarus lacustris was recorded from Keyhole Lake for the first time in 1980 when a single specimen was found on a gillnet (Johnson 1987, and unpublished). This species is extremely abundant in a few of the neighbouring lakes that do not contain fish. Gammarus lacustris was an important component of the Arctic charr diet during the 1985-86 fishery, indicating a proliferation of the species between 1980 and 1985-86. In 1985 nearly 17% of the benthic invertebrate biomass consisted of Gammarus lacustris.

Zooplankton

The planktonic fauna consistently exhibited the highest energy density of any trophic level in Keyhole Lake. However, this appears to be a superficial anomaly in the energy density hierarchy along the food chain of the lake. Zooplankton seems to form the terminus of a separate food chain. Low utilization of this trophic level is apparent; only 3.4% of the Arctic charr stomachs examined contained zooplankton. A distinct energy density hierarchy existed between phytoplankton and other microseston, and zooplankton. Thus, the deviation from theory may be accounted for by the existence of two parallel food chains. The energy densities of the two terminal trophic levels in

these food chains were probably not intrinsically related as they are along the succeeding links of an independent food chain (discussed in this chapter under "Energy density and ecosystem stability").

The planktonic rotifer Keratella cochlearis and the copepod Limnocalanus macrurus were studied in Char Lake over a 4 year period by Rigler et al. (1974). These species represented the most abundant zooplankters in this Arctic lake. The behaviour of these populations were consistent with those characterizing a climax state. Rigler and his co-workers stated that (to their surprise):

. . . there is no sign of gross instability—as indicated by violent fluctuations of population size from year to year—that might be expected in simplified ecosystems. Even the juxtaposition of an unusually warm summer in 1971 and one in which the ice never melted in 1972, did not appreciably affect the production of L. macrurus. Even K. cochlearis (which is not a cold stenotherm like L. macrurus) was no more variable . . . than Keratella spp. observed . . . in biologically diverse temperate waters.

Furthermore, these zooplankton populations exhibited low reproductive and mortality rates. Rigler et al. (1974) attributed these low rates to a lack of adaptation of the zooplankton species to low water temperatures. Such an explanation can, by no means, be ruled out, however, these features are also found in climax state populations (Johnson 1981, 1988, in press a, b). Interestingly, Rigler (1975) did not include zooplankton in his description of food items consumed by Arctic charr in Char Lake. The stable behaviour

of the zooplankton is probably due, at least in part, to low predation rates and suggests that the planktonic fauna in Char Lake, similarly to Keyhole Lake, is positioned at the end of a separate food chain. It is postulated that the zooplankton community in Keyhole Lake displays a similar stable behaviour.

Arctic charr

The great importance of Arctic charr and its history in Keyhole Lake is that it demonstrates the tendency of a dominant species to assume a state of most action (or least entropy production). Most action is expressed in (1) high biomass relative to energy input, (2) long life or great age, (3) uniformity of size, (4) low level of fluctuation (stability), (5) well-damped return following perturbation, (6) tendency to size increase, and (7) high energy density. These attributes can be most readily seen in the terminal species of an autonomous ecosystem.

The Arctic charr population represents the terminal trophic level of the main food chain in Keyhole Lake. The energy density of Arctic charr generally exceeded that of subordinate trophic levels. Exceptions were noted in this subsection under "Benthic invertebrates." Interestingly, the mean energy density values for the subsamples of Arctic charr captured during the first and last sampling periods (no energy density determinations were made for Period II) in 1985 were identical. This was either an artifact of

sample size or the Arctic charr did not increase their fat content as the summer progressed. A large number (23.5%) of the Arctic charr stomachs examined were empty and this suggests a low level of energy intake.

The estimated biomass of Arctic charr in Keyhole Lake ($39.48 \text{ kg}\cdot\text{ha}^{-1}$ wet weight) was markedly higher than Char Lake ($9.23 \text{ kg}\cdot\text{ha}^{-1}$ wet weight). The modal length of the fish population in Char Lake was also much smaller (145 mm) (McCallum and Regier 1984). Johnson (1983) obtained biomass estimates below those of Keyhole Lake for the Arctic charr populations in Notgordie Lake ($7.1 \text{ kg}\cdot\text{ha}^{-1}$ wet weight) and Little Nauyuk Lake ($24.3 \text{ kg}\cdot\text{ha}^{-1}$ wet weight); these small lakes (7.1 ha and 44.6 ha, respectively) are located near a latitude of $68^{\circ} 21' \text{ N}$ on the Kent Peninsula, Northwest Territories. The fish biomass in Keyhole Lake is quite comparable to many temperate lakes (cf. Carlander 1955). The estimate by Gerking (1962) of bluegill (Lepomis macrochirus) biomass in Wyland Lake, Indiana, was higher at $72 \text{ kg}\cdot\text{ha}^{-1}$ wet weight. Winberg et al. (1972) studied the biological productivity of three lakes in northwestern Byelorussia, U.S.S.R. These lakes were classified as mesotrophic (Lake Naroch), intermediate (Lake Myastro), and eutrophic (Lake Batorin); the fish stocks were estimated at 123, 169, and $235 \text{ kg}\cdot\text{ha}^{-1}$ wet weight, respectively. The biomass of planktivorous fish ranged from 16 to $44 \text{ kg}\cdot\text{ha}^{-1}$, 42 to $172 \text{ kg}\cdot\text{ha}^{-1}$ for benthos feeders, and 22 to $47 \text{ kg}\cdot\text{ha}^{-1}$ for predatory fish species.

A steady state of most action of dominant species in autonomous ecosystems is especially apparent when resources are at a premium. This generally occurs when the carrying capacity of the system is reached. The dominant population decreases energy dissipation by slowing down its turnover rate and frequently large, uniform size is the central feature. These attributes are palpable in the Arctic charr population of Keyhole Lake. It is inferred that dominance ensures "top-down" control of energy flows in subordinate trophic levels (Carpenter et al. 1985; Northcote 1988; Johnson in press b).

Keyhole Lake has been under an experimental regime since the early 1960's. The history of exploitation goes back to 1962 when Hunter (1970) initiated an extensive gillnetting program. The data collected on the Arctic charr population of Keyhole Lake over the 27 year period indicates that it behaved in a well-damped manner following perturbation. There was no evidence of any oscillation after the cessation of a perturbation. This implies self-regulation of the population; both near the climax state and at significantly lower population densities (Johnson in press b). The Arctic charr population functioned as a coherent group; intensive exploitation did not induce any breakdown of organization which would have been evident in random size distribution (Johnson 1987). The principle of homeokinesis appeared to regulate the

Arctic charr population by ensuring equal energy distribution among the members of the population.

In 1962 Hunter (1970) removed 860 Arctic charr from Keyhole Lake. The adult mode occurred at 280 mm while a very small juvenile mode existed at 180 mm. This bimodality, according to Johnson (1987), may have been due to gillnet selectivity; wide intervals existed between the mesh sizes. During the 1963 fishery an additional 4,154 fish were removed by Hunter (1970). Although two small mesh sizes were added, the smaller mode was not evident; the adult mode shifted upward to 300 mm. In 1965 a further 2,128 Arctic charr were netted. Another small mesh size was added that year. A small juvenile mode became evident at 200 mm while the adult mode continued the upward shift to 340 mm (Hunter 1970). It appeared that the remaining adult population had increased in size. Age data indicated that the fish comprising the smaller length classes (< 30 cm) were present during the earlier fisheries; however, these were probably too small to be captured by the sampling gear (Johnson 1987). The final fishery by Hunter (1970) in 1967 produced only 86 fish; the population seemed to have been almost completely depleted.

A re-sampling by Johnson (1976, 1983) in 1975 indicated that the population appeared to have returned to a unimodal configuration similar to that found in 1963; the modal length was 300 mm. The sample size, captured with

10-25 and 10-60 gillnets, was small ($n = 386$). Electrofishing showed the existence of a smaller mode at 120 mm occupying the littoral zone. The 1980 re-sampling, employing identical mesh sizes, captured 730 specimens. The population maintained its unimodality but modal length increased to 340 mm (Johnson 1983).

The 1985-86 fishery was extensively covered in the preceding chapter under "Arctic charr—Population structure." As noted, the length-frequency distribution of the first 750 to 800 Arctic charr netted in 1985 closely resembled the length-frequency distributions of the population samples captured in 1975 and 1980; however, the modal length had increased to 360 mm. Distinct juvenile modes appeared as the fishery progressed. Similar observations were made in the Arctic charr population of Lake Tasersuaq, Greenland (lat. $67^{\circ} 10' N$); juvenile modes appeared during the second year of an intense fishery (Riget et al. 1986).

The 1962-63 fishery indicated that few juveniles were present during the virgin phase of the lake. The smaller mesh sizes employed by Hunter (1970) and large number of fish removed should have indicated the existence of a significant juvenile mode. During the exploitation phase important changes to the population, especially in terms of recruitment, appeared to have occurred. The juveniles, at least during the early phase of exploitation,

displayed rapid growth rates after the depletion of a large portion of the adult population. Furthermore, the latter stages of exploitation (1985-88) indicated that significant numbers of juveniles were present. However, their numerical importance became evident only after a large portion of the adult population had been removed. It appears that a large adult population suppresses the movement of juveniles, confining them to marginal habitats (Johnson 1987). Exploitation experiments by Healey (1980) on lake whitefish (Coregonus clupeaformis) in four Northwest Territorial lakes indicated that the growth and recruitment of juvenile fish is regulated by the adult population. Johnson (1975b) believed that young lake trout (Salvelinus namaycush) in Great Bear Lake were forced into marginal habitats through interactions with adult lake trout. Larger fish are probably dominant in interspecific encounters, thus excluding smaller specimens from the desired resources (Morse 1980; Brown and Maurer 1986).

The population number and biomass estimates just prior to the 1962 and 1985 fisheries indicate a high degree of similarity (discussed in the foregoing chapter under "Arctic charr—Population structure"). The adult population increased in length but declined in number during the latter part of the exploitation phase. The juvenile population was more numerous just prior to the 1985 fishery compared to 1962 (probably sampling in 1975 and 1980 caused a

disturbance) and sufficiently influenced the total population estimate to exceed that of the pre-exploitation phase. However, the relatively small biomass of the juvenile population contributed little to the total biomass, which was slightly lower during the latter part of the exploitation phase. The catch per unit effort remained remarkably constant (range of 81 to 84 individuals) in 1975, 1980, and 1985; as expected, due to severe exploitation, it decreased during subsequent fisheries (75 and 70 individuals in 1986 and 1988, respectively).

The gradual increase in adult modal length from 1962 to 1965, and from 1975 to 1988 may be explained in thermodynamic terms; a larger size reduces entropy production. The reduction of the adult population increased the resources available to the remaining individuals; these, in turn, increased in size to reduce energy dissipation (Johnson 1987). Energy dissipation was further reduced by the equal distribution of energy resources which was reflected by the uniform size distribution of the adult population (Johnson in press b). The length reduction between the 1965 and 1975 fishery may be a function of the turnover time of the population. Adult age modes indicate that this ranges from 8 to 13 years. The larger adults were gradually replaced by more numerous but slightly smaller adults. It appears that the population was "re-setting" itself to a pre-exploitation configuration. The foregoing

suggests that sampling frequencies shorter than the turnover time of the population disrupts normal replacement processes. This consequently prevents the return to a configuration approximating its virgin state.

An early stage of the recovery process appears in the 1988 length-frequency distribution. The configuration indicates predominantly juveniles and few adults. It was estimated that 2,538 Arctic charr less than 30 cm and only 383 specimens 30 cm or larger remained after the 1985-86 fishery. Thus a configuration favouring juveniles might be expected, considering the relatively short time interval after the intense 1985-86 fishery (cf. 1965 length-frequency distribution (Figure 18C)). The adult mode in 1988 is less distinct when compared to previous years. Reasons may include: (1) growth of adults surviving previous fisheries, and (2) a relatively rapid influx of recruits into the adult population. Proposition (1) appears plausible due to an increase of resources available to the decimated adult population. The second proposition is supported by relatively high representations in length-frequencies poorly represented in 1985 and 1986 (i.e. 280 mm, especially 300 mm, and 320 mm); juveniles are increasing in size in order to fill the adult niche. These data indicate that two years is insufficient time for the population to "regroup."

Aging data indicated that the ages of the adult modes also increased during periods of adult modal length

increase. These increases in both turnover time and size promote a decline in energy dissipation.

The weight-specific metabolic rate declines with an increase in body size (Kleiber 1932; Miller 1968; Eckert and Randall 1983; Hoar 1983). Adult Arctic charr optimize low metabolic rates by maintaining a relatively large individual size. The long, indeterminate life span further decreases energy dissipation by reducing the turnover rate; energy residence time is thus increased. The ages of Arctic charr are highly variable at the adult modal length indicating the importance of a uniform size for equal distribution of energy resources. However, length and age must be correlated to some degree since size is a function of time (Medawar in Johnson 1988). Reproductive energy expenditure is reduced by infrequent spawnings (Hunter 1970) and this contributes to a low juvenile population especially in the pre-exploitation state. The preceding characteristics are intrinsically related and produce a state of most action (or "least value" of the P/B ratio).

Exploitation, as expected, increased the energy flux (i.e. the value of the P/B ratio increased). Experimental perturbation reduced the mean age of the population. This was also documented by Healey (1980) in lake whitefish populations. Furthermore, these populations exhibited concomitant growth rate increases.

The bell-shaped length-frequency configuration of the Arctic charr stock of Keyhole Lake in its virgin state is not restricted to that population. It appears that all undisturbed Arctic fish populations maintain this configuration (Johnson 1972, 1973, 1975c, 1976, 1980, 1981, 1983, 1984, in press a). A survey by Johnson (1984, in press a) of dominant populations in generally simple, autonomous ecosystems indicated that bell-shaped size-frequency distributions are found throughout the biosystem. These configurations are evident in organisms of determinate size (e.g. mammals and birds) but are also commonly encountered in populations in which the species have an indeterminate growth pattern. All these populations apparently have a common goal: the reduction of energy dissipation.

THE TROPHIC SYSTEM

The trophic levels comprising the ecosystem of Keyhole Lake appear to exhibit slow turnover rates. This, it is postulated, is due to the low level of annual insolation and low water temperature further augmented by the high degree of autonomy of the ecosystem. This slow turnover locks up nutrients, thereby further delaying turnover processes.

It is evident from the preceding section that trophic levels along a food chain are intrinsically related.

Unfortunately, even in simple ecosystems, trophic levels are often difficult to distinguish. Both herbivorous and carnivorous species of zooplankton inhabit Keyhole Lake (Fryer 1957; Barnes 1980), confounded by the fact that protozoa and bacteria frequently contribute significantly to the plankton community (Boyd and Boyd 1963; Pace and Orcutt 1981; Hunt and Chein 1983; Gates 1984; Gates and Lewg 1984). Water samples from Imikpuk Lake, Barrow, Alaska, were found to contain substantial numbers of heterotrophic bacteria during June and July (Boyd and Boyd 1963). The trophic interactions especially between lower trophic levels are not perfectly linear; multiple pathways exist between benthic algae, benthic bacteria (part of a complex detrital cycle), and the variety of trophic life styles encountered in the benthic invertebrate community. Welch and Kalff (1974) found the benthic invertebrates in Char Lake to be mainly detritivores. Although most benthic invertebrates in Keyhole Lake were probably detritivores, the benthic community may have contained a few herbivores and predatory species (Coffman 1978; Wiggins 1978; Fry 1982). For example, chironomid larval communities frequently contain, not only detritivorous and herbivorous species, but also predatory ones (Coffman 1978). Furthermore, phytoplankton and zooplankton may be more important to the ecosystem of Keyhole Lake than static measurements in this study suggest; turnover rates are perhaps faster.

The foregoing indicates that the foodweb of even a relatively simple ecosystem, such as Keyhole Lake, is still extremely complex. The complexities of foodweb interactions of most ecosystems, which contain a multiplicity of species, are almost beyond comprehension. The combining of various, not readily separable trophic levels within an arbitrarily selected trophic level was necessary owing to the need to maintain a holistic view of the system. Additionally, any further division might have obscured the general trends of the energy paths in this ecosystem. The overall contributions, in terms of energy flow, of the predatory species in the planktonic and benthic invertebrate communities to the lake's ecosystem are probably minimal.

The obscure, nevertheless interesting, inverse relationships between energy density and the logarithms of biomass and biomass energy of the main food chain in Keyhole Lake were disclosed in the preceding chapter. The reasons for their existence are open to speculation. The consumed biomass energy of a lower trophic level is transformed into biomass of the next trophic level with low efficiency (Paloheimo and Dickie 1966). It is frequently estimated that, in a very general way, biomass energy is reduced in magnitude by ten from lower to higher trophic levels (Harvey 1950; Smith 1980; Cole 1983), with 90% of the energy being dissipated as heat during its transformation (Brylinsky and Mann 1973). The relationships suggest that energy

transformation, in terms of both biomass production and subsequent energy utilization, becomes more efficient towards the terminus of the food chain. This is consonant with the decrease in entropy production through the ecosystem. A correspondence between energy density versus the logarithm of biomass energy and a "cooling curve" is apparent, except energy flows in opposite directions. However, this is expected: in ecosystems energy flows (is "pumped") from low biological temperature to high biological temperature, while in physical systems the direction of energy flow is from high temperature to low temperature.

A simplified model of the energy and mass flow in Keyhole Lake is illustrated in Figure 53. The two food chains terminating with Arctic charr and zooplankton are displayed. Energy densities of the trophic levels are indicated. Respiration is included since it is part of the total energy flux. The energy loss in the form of low grade heat at each energy transformation along the food chain is shown.

It is manifest from this study that, in Keyhole Lake, energy density and biomass configurations of trophic levels are inversely related. Eltonian Pyramids in Figure 54 illustrate this relationship for the main food chain. The absolute value of energy density at each trophic level and the value (expressed in absolute values and as a ratio) of the biomass of each trophic level are indicated. The

Figure 53. Energy and mass flow of the trophic system in Keyhole Lake. Trophic level locations on the y axis were determined from energy density values representing the means of Periods I, II, and III, 1985 (phytoplankton/microseston during 1986).

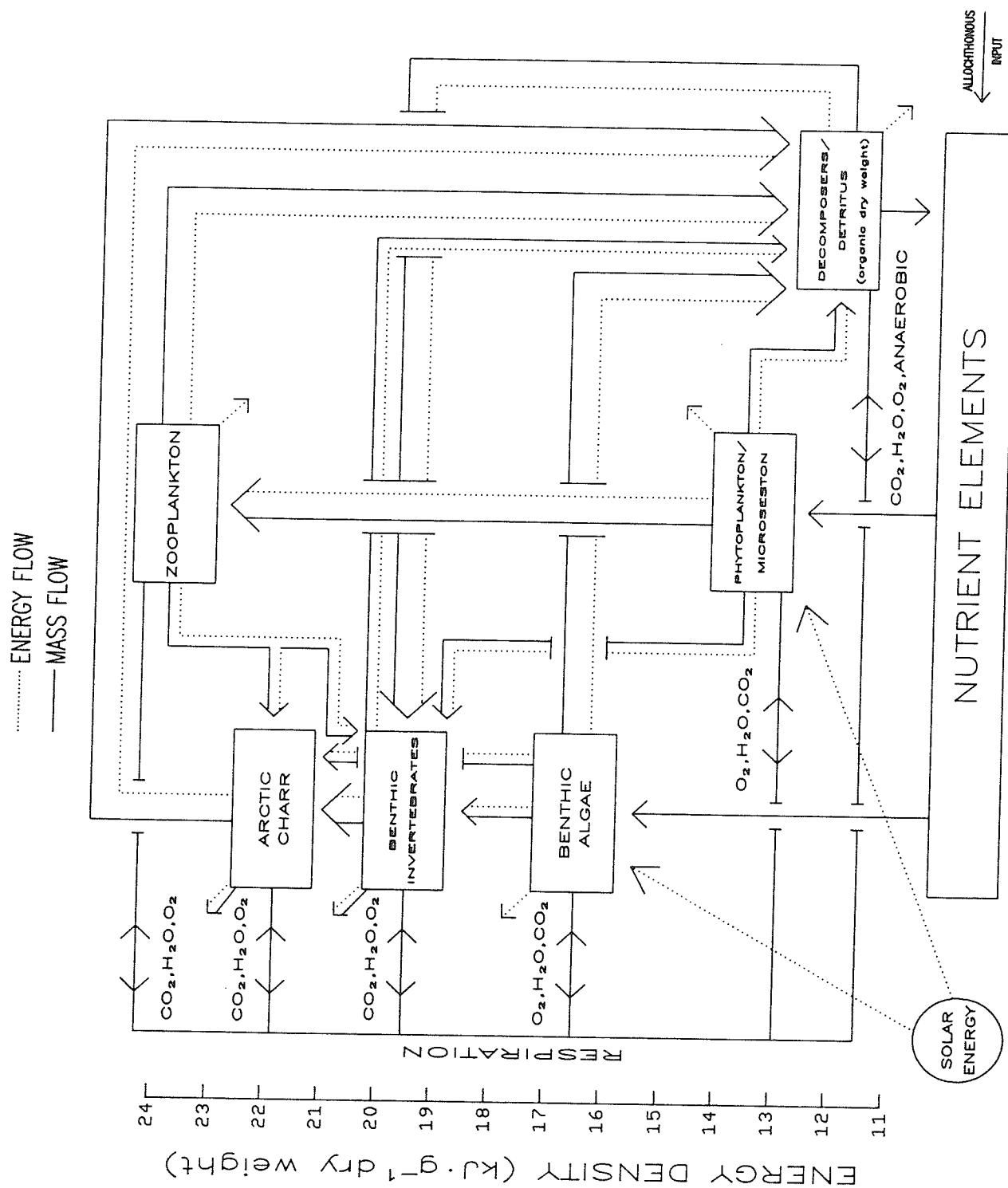
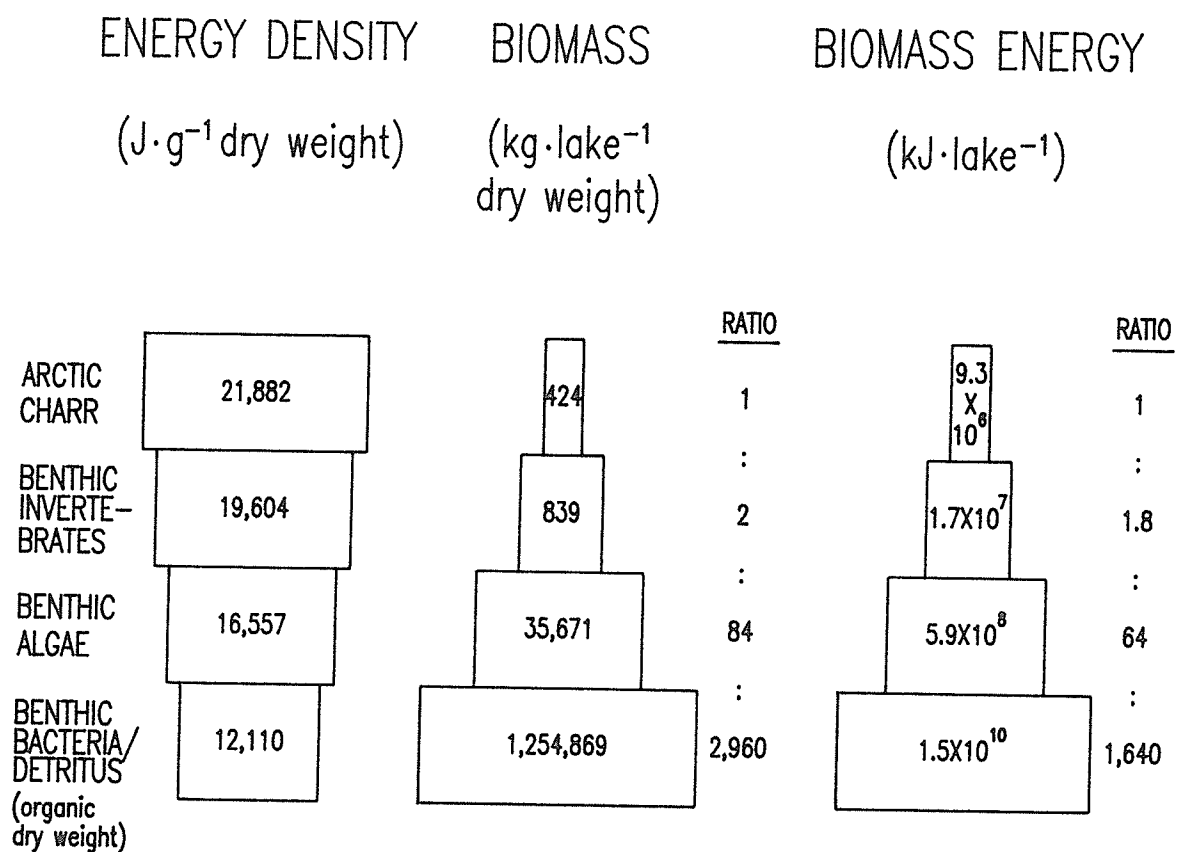


Figure 54. Eltonian Pyramids of energy density, biomass, and biomass energy of the main food chain in Keyhole Lake. Values represent the means of Periods I, II, and III, 1985. Weight of clamshells is excluded from the biomass of benthic invertebrates. Bars are not drawn to scale.



ratio will subsequently be referred to as the biomass trophic level (BTL) ratio. A pyramid showing the value of biomass energy (energy density times biomass) of each trophic level is also included in Figure 54, expressed in absolute values and as a ratio (biomass energy trophic level (BETL) ratio). The BTL ratio and BETL ratio are concordant; however, the magnitude of the BETL ratio decreases, compared to the BTL ratio, as one descends the food chain. This is because lower trophic levels exhibit lower energy densities. Since the biomass differences between trophic levels were proportionally higher than the differences in energy density between trophic levels the BETL ratio was predominantly influenced by the BTL values.

The biomass energy pyramid indicates that the direction of energy flow along the food chain is governed by biological temperature, not the total action of each trophic level. If the direction of energy flow was guided by an increase of total action along the food chain the biomass energy pyramid would have displayed an inverse configuration.

ENERGY DENSITY AND ECOSYSTEM STABILITY

The results of this study provide a remarkable verification of the hypothesis proposed in the introductory chapter: energy density increases with each succeeding link along the food chain.

Ulanowicz (1972) deduced from a simple straight-chain ecosystem model of three single species trophic levels that energy density should increase as one ascends the trophic ladder:

$$E\rho_3 > E\rho_2 > E\rho_1, \quad (24)$$

where $E\rho$ = energy density. May (1973) extended the model to n-trophic levels of a straight-chain closed ecosystem:

$$E\rho_n > E\rho_{n-1} > \dots > E\rho_3 > E\rho_2 > E\rho_1. \quad (25)$$

They concluded that a hierarchical energy density increase in a closed ecosystem is a necessary condition for the system to be stable. However, Hirata and Fukao (1977) found an error in the basic physics of the models of Ulanowicz (1972) and May (1973): mass circulated in the wrong direction under the stability condition of inequalities (24) and (25). This was corrected by Hirata and Fukao (1977) and the mathematical derivation of inequalities (24) and (25) are covered in-depth by these authors. Inequalities (24) and (25) can be written in terms of entropy production by reversing their direction. For example:

$$S_3 < S_2 < S_1, \quad (26)$$

where S = entropy production, and (26) is the analogue of (24).

From calorimetry results and the theoretical premise it is postulated that energy density is a determinant of the direction of energy flow in an ecosystem; energy flows from species of low energy density to species of high energy density.

The principal of most action, discussed in the introductory chapter, governs ecosystems over short time periods ("ecological time"). A product of most action—stability—is especially evident in autonomous ecosystems. Stabilization in ecosystems is induced by a decrease in energy flow; i.e. entropy production declines. Energy density, a component of biological action (formula (3)), increases along the food chain in accordance with a decline in entropy production. For an ecosystem to exist energy must accumulate faster than it is dissipated otherwise the system increases its entropy production and proceeds to instantaneous dissipation (Johnson in press b).

An energy density hierarchy is only one component that promotes energy to become more "concentrated" in ascending trophic levels. Others required for energy "concentrating" and thus the stabilization of an ecosystem

include, as previously discussed, increases in life span and increases in size along the food chain (Johnson in press b).

The energy density hierarchy along the food chain of Keyhole Lake refutes Nisbet and Gurney's (1976) conjecture that little or no significant differences exist between energy densities of different consumer levels in a closed ecosystem. Their findings were based on collections of energy density values of various animal species (from, for example, Morowitz (1968) and Odum (1971)) that did not specifically belong to a hierarchical food chain of an autonomous ecosystem. Non-autonomous hierarchical ecosystems probably do not display the distinct energy density hierarchy in the consumer levels as found in Keyhole Lake; although, for continued existence, the relationship must exist at a larger scale if the hypothesis is correct.

Non-autonomous ecosystems are frequently highly unstable especially with respect to external perturbation. For example, ecosystems of the Arctic tundra are relatively open; annual migrations by many of their components ensures a considerable removal of the systems' permanent residents. The loss of biomatter, in turn, induces an increase in the energy fluxes (Johnson 1981, 1983, 1988, in press a, b). The instability of such systems are exemplified by the oscillations of their lemming (*Lemmus lemmings*) populations (Huck 1987; Krebs 1987).

The stability of an ecosystem appears to depend primarily on its autonomy and not on the degree of its complexity (Tansley 1935; Johnson in press a). Johnson (in press b) contrasts two simple ecosystems: (1) a stable Arctic lake system, and (2) an unstable Arctic terrestrial system. Both differ markedly in their degree of autonomy. Although he acknowledges that part of the stability of an Arctic lake is due to the buffering capacity of aquatic systems to environmental fluctuations, due to the physical properties of water, their high degree of autonomy significantly contributes to their stability.

EPILOGUE

The effects of thermodynamic forces, in particular the dynamic counterpart of the first law—most action—, acting upon an ecosystem were illuminated. These forces do not appear to be restricted to biological systems. A river profile is analogous to an ecosystem in energetic terms; pools represent regions of reduced energy dissipation and riffles increase energy flow (Leopold and Langbein 1962). Thus pools behave like trophic levels and riffles are comparable to the high energy dissipation between trophic levels (Johnson in press b, in preparation). Even economic systems appear to have a correspondence: Adam Smith's "invisible hand" ensures that men's self-interest is transformed by the market mechanism into social well-being (Heilbroner 1975; Proops 1983; Wicken 1986; Dyke 1988).

Energy exchanges of varying magnitude occur between like (and frequently dissimilar) systems. This can be in the form of migrations between ecosystems, hydrological cycles between river profiles, and the transportation of goods between economic systems. These systems are ultimately bounded by Earth's resources. This ensures that only energy, but not matter, is exchanged with the universe and the aggregate of systems (actually sub-systems) function as a closed system. The principle of least action implements the second law by increasing entropy production. Given the antagonistic forces of most action and least action, for continuity, least action must always be supreme over long time periods (Johnson in press b).

The "action" principles encompass generally accepted biological relationships, which are usually thought of as being disparate. These include: the Production/Biomass ratio, the concept of r - and K -selection (MacArthur and Wilson 1967; Parry 1981), and the Power/Economy ratio (Gnaiger 1983, 1986). The P/B , r/K , and Power/Economy ratios are all equivalent measures of energy flow or biological temperature. Species low in the food chain have high r values and low K values. K -selected species are essentially dominant species. The more work an organism does the larger the Power/Economy ratio. In each case the numerator is a rate and the demoninator represents energy accumulation. They each represent measurements of energy

flow which can be explained and integrated by underlying thermodynamic processes (Johnson in press b). It is apparent that universal principles are governing the biological world. From these principles a unified theory of energy flow in biological systems is approaching maturity.

Ideally a series of mathematical expressions should be developed that unequivocally connect the biological principles and associated concepts governing ecosystems. The findings in this study indicate that this may be a realistic objective. Hirata and Ulanowicz (1986) congruently stated:

There is every reason to believe that individual processes actually change in nature as a result of their mutual interaction with other processes in the same community. Such circumstance would require that ecosystems be reviewed as a unit with identifiable properties which exhibit some macroscopic regularities. (Dare we say laws?)

On the evidence I think we dare.

NOTE

In physical thermodynamics the quantity $(\partial S/\partial E)_{n,\beta}$ is a potential that controls the tendency for energy to pass from one system to another. This "capturing tendency" is determined by the following relationship:

$$\left(\frac{\partial S_A}{\partial E_A} \right)_{n,\beta} > \left(\frac{\partial S_B}{\partial E_B} \right)_{n,\beta'} ,$$

where ∂ = small change, S = entropy, E = total energy of the system, n = number of particles, and β = number of constraints of n . If the value of the quantity $(\partial S/\partial E)_{n,\beta}$ for system A exceeds that of system B then energy passes from system B to system A. The reciprocal quantity $(\partial E/\partial S)_{n,\beta}$ is the "escaping tendency" which is equivalent to the temperature. It follows that "temperature" (T) (usually measured with the Kelvin scale) is:

$$T \equiv \left(\frac{\partial E}{\partial S} \right)_{n,\beta'} .$$

Thus the "escaping tendency" can be measured with T (Keenan et al. 1974).

Johnson (1981, in press b) applied the preceding to the biological situation as follows:

If . . . the rate of entropy production, which is equivalent to the annual production (P) in a steady state system is substituted for entropy (S) in the above relationship [the preceding formula], and biomass, B , is allowed to represent the total stored energy, then the biological temperature is equivalent to the biomass divided by the production (B/P). This is the Biomass Accumulation Ratio equivalent to the energy residence time (and the reciprocal of the P/B ratio).

Within an ecosystem, functioning as a partially closed system, the overall direction of energy flow is from species of low temperature (rapid turnover time) to species with high temperature (long turnover time) through the operation of an energy "pump" [*]. This is done by the performance of internal work. Between ecosystems energy flows in a general direction from ecosystems at high temperature to ecosystems at low temperature. Flow, in this case, is between open systems, allowing external work to be done.

(Johnson in press b)

(* i.e. Onsager's principle is equivalent to an "interference energy pump.")

REFERENCES

- Allen, W.T.R. 1971. River and lake ice, p. 13-14. In The national atlas of Canada. Department of Energy, Mines and Resources, Ottawa.
- Andrews, J.T. 1970. A geomorphological study of post-glacial uplift with particular reference to Arctic Canada. Institute of British Geographers Spec. Pub. 2: 156 p.
- Andrews, J.T. 1972. Post-glacial rebound, p. 35-36. In The national atlas of Canada. Department of Energy, Mines and Resources, Ottawa.
- Anonymous. 1985-86. Monthly record of meteorological observations. Environ. Can. Atmos. Environ. Serv., Meteorol. Branch, Ottawa.
- Atkinson, E.G., and J.W. Wacasey. 1983. Caloric equivalents for benthic marine organisms from the Canadian Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 1216: vii + 31 p.

- Banaszak, J. 1984. Density and biomass of benthic Chironomidae (Diptera) in a lake and melioration channel, situated in agricultural landscape. Pol. Arch. Hydrobiol. 31: 353-363.
- Banse, K., C.P. Falls, and L.A. Hobson. 1963. A gravimetric method for determining suspended matter in sea water using Millipore® filters. Deep-Sea Res. 10: 639-642.
- Barnes, R.D. 1980. Invertebrate zoology. Saunders College, Philadelphia. 1089 p.
- Bayly, I.A.E., and W.D. Williams. 1973. Inland waters and their ecology. Longman Australia Pty Ltd., Camberwell. 316 p.
- Berg, C.O. 1966. Middle Atlantic States, p. 191-237. In D.G. Frey [ed.] Limnology of North America. The University of Wisconsin Press, Madison.
- Berman, T., and U. Pollinger. 1974. Annual and seasonal variations of phytoplankton, chlorophyll, and photosynthesis in Lake Kinneret. Limnol. Oceanogr. 19: 31-54.

- Bird, J.B. 1980. The natural landscapes of Canada. John Wiley and Sons Canada Ltd., Toronto. 260 p.
- Bostock, H.S. 1970. Physiographic subdivisions of Canada, p. 11-30. In R.J.W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv. Can. Econ. Geol. Rep. 1.
- Bostock, H.S. 1972. Physiographic regions, p. 5-6. In The national atlas of Canada. Department of Energy, Mines and Resources, Ottawa.
- Boyd, W.L., and J.W. Boyd. 1963. A bacteriological study of an arctic coastal lake. Ecology 44: 705-710.
- Braaten, D.O. 1969. Robustness of the DeLury population estimator. J. Fish. Res. Board Can. 26: 339-355.
- Bray, J.R. 1961. Measurement of leaf utilization as an index of minimum level of primary consumption. Oikos 12: 70-74.
- Brewer, M. 1958. The thermal regime of an arctic lake. Trans. Am. Geophys. Union 39: 278-284.

- Brinkhurst, R.O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America. Can. Spec. Publ. Fish. Aquat. Sci. 84: 259 p.
- Brinkhurst, R.O., K.E. Chua, and E. Batoosingh. 1969. Modifications in sampling procedures as applied to studies on the bacteria and tubificid oligochaetes inhabiting aquatic sediments. J. Fish. Res. Board Can. 26: 2581-2593.
- Brinkhurst, R.O., and B.G.M. Jamieson. 1971. Aquatic Oligochaeta of the world. University of Toronto Press, Toronto. 860 p.
- Brinkhurst, R.O., and C.R. Kennedy. 1965. Studies on the biology of the Tubificidae (Annelida, Oligochaeta) in a polluted stream. J. Animal Ecol. 34: 429-443.
- Brooks, D.R., D.D. Cumming, and P.H. LeBlond. 1988. Dollo's law and the second law of thermodynamics: analogy or extension?, p. 189-224. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] Entropy, information, and evolution. MIT Press, Cambridge, MA.

- Brown, J.H., and B.A. Maurer. 1986. Body size, ecological dominance and Cope's rule. *Nature* 324: 248-250.
- Brylinsky, M. 1980. Estimating the productivity of lakes and reservoirs, p. 411-453. In E.D. Le Cren and R.H. Lowe-McConnell [eds.] *The functioning of freshwater ecosystems*. Cambridge University Press, Cambridge.
- Brylinsky, M., and K.H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnol. Oceanogr.* 18: 1-14.
- Carlander, K.D. 1955. The standing crop of fish in lakes. *J. Fish. Res. Board Can.* 12: 543-570.
- Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *Bio Science* 35: 634-639.
- Chitwood, B.G., and M.W. Allen. 1959. Keys and figures to the freshwater pseudocoelomates. *Nemata*, p. 368-401. In W.T. Edmondson, H.B. Ward, and G.C. Whipple [eds.] *Freshwater biology*. John Wiley and Sons, New York.

- Coffman, W.P. 1978. Chironomidae, p. 345-376. In R.W. Merritt and K.W. Cummins [eds.] An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque.
- Cole, G.A. 1983. Textbook of limnology. The C.V. Mosby Co., St. Louis. 401 p.
- Comita, G.W., and D.W. Schindler. 1963. Calorific values of microcrustacea. Science 140: 1394-1396.
- Clarke, A.H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacologia 13: 1-509.
- Clarke, A.H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, Ottawa. 446 p.
- Craig, J.F., M.J. Kenley, and J.F. Talling. 1978. Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. Freshwat. Biol. 8: 585-590.

- Crisp, D.J. 1971. Energy flow measurements, p. 197-279. In N.A. Holme and A.D. McIntyre [eds.] Methods for the study of marine benthos. IBP Handbook No. 16. Blackwell Scientific Publications, Oxford and Edinburgh.
- Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18: 1-158.
- Dale, N.G. 1974. Bacteria in intertidal sediments: Factors related to their distribution. Limnol. Oceanogr. 19: 509-518.
- Davies, P. 1980. Other worlds. Simon and Schuster, Inc., New York. 207 p.
- de Bernardi, R. 1984. Methods for the estimation of zooplankton abundance, p. 59-86. In J.A. Downing and F.H. Rigler [eds.] A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, 2nd ed. Blackwell Scientific Publications, Oxford.

- DeLury, D.B. 1947. On the estimation of biological populations. *Biometrics* 3: 145-167.
- DeLury, D.B. 1951. On the planning of experiments for the estimation of fish populations. *J. Fish. Res. Board Can.* 8: 281-307.
- Desortova, B. 1981. Relationships between chlorophyll- α concentration and phytoplankton biomass in several reservoirs in Czechoslovakia. *Int. Rev. ges. Hydrobiol.* 66: 153-169.
- Diaconis, P., and B. Efron. 1983. Computer-intensive methods in statistics. *Sci. Amer.* 248(5): 116-130.
- Dix, R.L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecology* 41: 49-56.
- Donald, G.L., and C.G. Paterson. 1977. Effect of preservation on wet weight biomass of chironomid larvae. *Hydrobiologia* 53: 75-80.

- Dunbar, M., and K.R. Greenaway. 1956. Arctic Canada from the air. Defence Res. Board Can., Ottawa. 541 p.
- Dutil, J.-D. 1982. Periodic changes in the condition of the arctic charr (Salvelinus alpinus) in the Nauyuk Lake system. Ph.D. thesis, University of Manitoba, Winnipeg. 149 p.
- Dyke, C. 1988. Cities as dissipative structures, p. 355-367. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] Entropy, information, and evolution. MIT Press, Cambridge, MA.
- Dyksterhuis, E.J., and E.M. Schmutz. 1947. Natural mulches or "litter" of grasslands: with kinds and amounts on a southern prairie. Ecology 28: 163-179.
- Eckert, R., and D.J. Randall. 1983. Animal physiology. W.H. Freeman and Company, San Francisco. 830 p.
- Efford, I.E. 1969. Energy transfer in Marion Lake, British Columbia, with particular reference to fish feeding. Verh. Internat. Verein. Limnol. 17: 104-108.

- Efford, I.E., and K.J. Hall. 1975. Marion Lake—an analysis of a lake ecosystem, p. 199-219. In T.W.M. Cameron and L.W. Billingsley [eds.] Energy flow—its biological dimensions. Royal Society of Canada, Ottawa.
- Efron, B. 1979a. Computers and the theory of statistics: Thinking the unthinkable. SIAM Rev. 21: 460-480.
- Efron, B. 1979b. Bootstrap methods: another look at the jackknife. Ann. Statist. 7: 1-26.
- Efron, B. 1981a. Nonparametric standard errors and confidence intervals. Canad. J. Statist. 9: 139-172.
- Efron, B. 1981b. Nonparametric estimates of standard error: the jackknife, the bootstrap and other methods. Biometrika 68: 589-599.
- Efron, B. 1984. Comparing non-nested linear models. J. Amer. Statist. Ass. 79: 791-803.
- Efron, B. 1985. Bootstrap confidence intervals for a class of parametric problems. Biometrika 72: 45-58.

- Efron, B. 1986. How biased is the apparent error rate of a prediction rule? J. Amer. Statist. Ass. 81: 461-470.
- Efron, B., and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statist. Sci. 1: 54-77.
- Ejsmont-Karabin, J. 1978. Studies on the usefulness of different mesh-size plankton nets for thickening zooplankton. Ekol. Pol. 26: 479-490.
- Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Pub. 25: 160 p.
- Elton, C.S. 1927. Animal ecology. Sidgwick & Jackson Ltd., London. 207 p.
- Federle, T.W., and D.C. White. 1982. Preservation of estuarine sediments for lipid analysis of biomass and community structure of microbiota. Appl. Environ. Microbiol. 44: 1166-1169.

- Feistel, R., and W. Ebeling. 1981. On the thermodynamics of irreversible processes in ecosystems. *Studia Biophysica* 86: 237-244.
- Feynman, R.P. 1963. The principle of least action, p. 19-1 to 19-14. In R.P. Feynman, R.B. Leighton, and M. Sands [eds.] *The Feynman lectures on physics*. Vol. 2. Addison-Wesley, Reading.
- Forbes, S.A. 1887. The lake as a microcosm. *Bull. Ill. Nat. Hist. Surv.* 15: 537-550.
- Forel, F.A. 1892. La thermique des lacs l'eau douce. *Verh. Schweiz. Naturforsch. Ges.* 75: 5-8.
- Freund, J.E. 1981. *Statistics: a first course*. Prentice-Hall, Inc., Englewood Cliffs. 466 p.
- Fry, J.C. 1982. Interactions between bacteria and benthic invertebrates, p. 171-201. In D.B. Nedwell and C.M. Brown [eds.] *Sediment microbiology*. Academic Press, London.

- Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. Anim. Ecol. 26: 263-286.
- Gates, M.A. 1984. Quantitative importance of ciliates in the planktonic biomass of lake ecosystems. Hydrobiologia 108: 233-238.
- Gates, M.A., and U.T. Lewg. 1984. Contribution of ciliated protozoa to the planktonic biomass in a series of Ontario lakes: quantitative estimates and dynamical relationships. J. Plankton Res. 6: 443-456.
- Gerking, S.D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. 32: 31-78.
- Gladyshev, G.P. 1978. On the thermodynamics of biological evolution. J. theor. Biol. 75: 425-441.
- Gladyshev, G.P. 1982. Classical thermodynamics, tandemism and biological evolution. J. theor. Biol. 94: 225-239.

- Gladyshev, G.P., and Yu.A. Ershov. 1982. Principles of the thermodynamics of biological systems. J. theor. Biol. 94: 301-343.
- Gladyshev, G.P., Yu.A. Ershov, and V.I. Loshchilov. 1980. Thermodynamic principles of the behavior of biological systems. J. theor. Biol. 83: 17-42.
- Glansdorff, P., and I. Prigogine. 1971. Thermodynamic theory of structure, stability and fluctuations. Wiley-Interscience, London. 306 p.
- Gnaiger, E. 1983. Heat dissipation and energetic efficiency in animal anoxibiosis: economy contra power. J. Exptl. Zool. 228: 471-490.
- Gnaiger, E. 1986. Optimum efficiencies of energy transformation in anoxic metabolism: the strategies of power and economy, p. 7-36. In P. Calow [ed.] Evolutionary physiological ecology. Cambridge University Press, Cambridge.
- Goldman, C.R. 1970. Antarctic freshwater ecosystems, p. 609-627. In M.W. Holdgate [ed.] Antarctic ecology. Vol. 2. Academic Press, London.

- Golley, F.B. 1961. Energy values of ecological materials. Ecology 42: 581-584.
- Górecki, A. 1975. Calorimetry in ecological studies, p. 275-281. In W. Grodzinski, R.Z. Klekowski, and A. Duncan [eds.] Methods for ecological bioenergetics. IBP Handbook No. 24. Blackwell Scientific Publications, Oxford.
- Graham, H.W. 1943. Chlorophyll-content of marine plankton. J. Mar. Res. 5: 153-160.
- Grainger, E.H. 1953. On the age, growth, migration, reproductive potential and feeding habits of arctic char. J. Fish. Res. Board Can. 10: 326-370.
- Hall, K.J., and K.D. Hyatt. 1974. Marion Lake (IBP)—from bacteria to fish. J. Fish. Res. Board Can. 31: 893-911.
- Harrison, L.G. 1988. Kinetic theory of living pattern and form and its possible relationship to evolution, p. 53-74. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] Entropy, information, and evolution. MIT Press, Cambridge, MA.

- Harvey, H.W. 1950. On the production of living matter in the sea off Plymouth. Journ. Mar. Biol. Assoc. 29: 7-137.
- Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (Coregonus clupeaformis) populations. Can. J. Fish. Aquat. Sci. 37: 255-267.
- Heath, W.A. 1985a. Analysis and processing of zoobenthos samples, p. 442-472. In sampling and analysis of the arctic marine benthic environment. Vol. 1. Review of methods. Environmental Protection Service, Yellowknife.
- Heath, W.A. 1985b. Methods for the study of marine macrobenthos, p. 51-92. In sampling and analysis in the arctic marine benthic environment. Vol. 2. Guide to practice. Environmental Protection Service, Yellowknife.
- Heilbroner, R.L. 1975. The making of economic society. Prentice-Hall, Inc., Englewood Cliffs. 299 p.

- Heinermann, P.H., and M.A. Ali. 1988. Seasonal changes in the underwater light climate of two Canadian shield lakes. *Hydrobiologia* 169: 107-121.
- Hirata, H. 1980. A model of hierarchical ecosystems with migration. *Bull. Math. Biol.* 42: 119-130.
- Hirata, H., and T. Fukao. 1977. A model of mass and energy flow in ecosystems. *Math. Biosci.* 33: 321-334.
- Hirata, H., and R.E. Ulanowicz. 1986. Large-scale system perspectives on ecological modelling and analysis. *Ecol. Modelling* 31: 79-104.
- Hoar, W.S. 1983. General and comparative physiology. Prentice-Hall, Inc., Englewood Cliffs. 851 p.
- Hobbie, J.E. 1973. Arctic limnology: a review, p. 127-168. In M.E. Britton [ed.] Alaskan Arctic tundra. Arct. Inst. N. Am. Tech. Pap. 25.

- Hobbie, J.E., R.J. Barsdate, V. Alexander, D.W. Stanley, C.P. McRoy, R.G. Stross, D.A. Bierle, R.D. Dillon, and M.C. Miller. 1972. Carbon flux through a tundra pond ecosystem at Barrow, Alaska. Tundra Biome Report 72-1: 28 p.
- Howmiller, R.P. 1972. Effects of preservatives on weights of some common macrobenthic invertebrates. Trans. Am. Fish. Soc. 101: 743-746.
- Huck, U.W. 1987. Lemming migrations, p. 656-657. In D.W. MacDonald [ed.] The encyclopedia of mammals. Facts On File Publications, New York.
- Hunt, G.W., and S.M. Chein. 1983. Seasonal distribution, composition and abundance of the planktonic Ciliata and Testacea of Cayuga Lake. Hydrobiologia 98: 257-266.
- Hunter, J.G. 1970. Production of arctic char (Salvelinus alpinus Linnaeus) in a small arctic lake. Fish. Res. Board Can. Tech. Rep. 231: 190 p.
- Huntsberger, D.V., and P. Billingsley. 1981. Elements of statistical inference. Allyn and Bacon, Inc., Boston. 505 p.

- Hutchinson, G.E. 1957. A treatise on limnology. Vol. 1. Geography, physics, and chemistry. John Wiley and Sons, Inc., New York. 1015 p.
- Johnson, L. 1962. The relict fauna of Greiner Lake, Victoria Island, N.W.T., Canada. J. Fish. Res. Board Can. 19: 1105-1120.
- Johnson, L. 1964a. Temperature regime of deep lakes. Science 144: 1336-1337.
- Johnson, L. 1964b. Marine-glacial relicts of the Canadian Arctic Islands. Syst. Zool. 13: 76-91.
- Johnson, L. 1966. Temperature of maximum density of fresh water and its effect on circulation in Great Bear Lake. J. Fish. Res. Board Can. 23: 963-973.
- Johnson, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. J. Fish. Res. Board Can. 29: 731-740.
- Johnson, L. 1973. Stock and recruitment in some unexploited Canadian Arctic lakes. Rapp. P. V. Reun. Cons. Int. Explor. Mer. 164: 219-227.

- Johnson, L. 1975a. Physical and chemical characteristics of Great Bear Lake, Northwest Territories. J. Fish. Res. Board Can. 32: 1971-1987.
- Johnson, L. 1975b. Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental conditions. J. Fish. Res. Board Can. 32: 1989-2004.
- Johnson, L. 1975c. The dynamics of Arctic fish populations, p. III 79 - III 90. In Proceedings Circumpolar Conference on Northern Ecology, Sept. 15-18, 1975. National Research Council, Ottawa.
- Johnson, L. 1976. Ecology of arctic populations of lake trout, Salvelinus namaycush, lake whitefish, Coregonus clupeaformis, arctic char, S. alpinus and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459-2488.
- Johnson, L. 1980. The arctic charr, Salvelinus alpinus, p. 15-98. In E.K. Balon [ed.] Charrs, Salmonid fishes of the genus Salvelinus. Dr. W. Junk bv Publishers, The Hague.

- Johnson, L. 1981. The thermodynamic origin of ecosystems. Can. J. Fish. Aquat. Sci. 38: 571-590.
- Johnson, L. 1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Can. J. Fish. Aquat. Sci. 40: 987-1024.
- Johnson, L. 1984. Hypothesis testing: Arctic charr, giant tortoises, marine and freshwater molluscs and tawny owls. Paper presented at the Third Meeting of the International Society of Arctic Charr Fanatics, Tromso, Norway, 1984. (MS).
- Johnson, L. 1987. Changes in the Arctic charr population of Keyhole Lake over a 25-year period, p. 73-87. In J. Hammar and L. Nyman [eds.] Proc. Fourth ISACF workshop on Arctic char, 1986. Institute of Freshwater Research, Drottningholm.
- Johnson, L. 1988. The thermodynamic origin of ecosystems: a tale of broken symmetry, p. 75-105. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] Entropy, information, and evolution. MIT Press, Cambridge, MA.

- Johnson, L. In press a. The far from equilibrium ecological hinterlands. In B.C. Patten and S.E. Jorgensen [eds.] Progress in systems ecology. Elsevier, Amsterdam.
- Johnson, L. In press b. The laws of nature in the living world: The physical basis of ecosystem structure. J. theor. Biol.
- Kajak, Z. 1963. Analysis of quantitative benthic methods. Ekol. Pol. Ser. A 11: 1-56.
- Kalff, J. 1968. Some physical and chemical characteristics of freshwaters in Alaska and northwestern Canada. J. Fish. Res. Board Can. 25: 2575-2587.
- Kalff, J. 1970. Arctic lake ecosystems, p. 651-663. In M.W. Holdgate [ed.] Antarctic ecology. Vol. 2. Academic Press, London.
- Keenan, J.H., G.N. Hatsopoulos, and E.P. Gyftopoulos. 1974. Thermodynamics, p. 290-315. In Encyclopaedia Britannica, 15th ed. Vol. 18. W. Benton and H.H. Benton, Chicago.

- Kelley, J.J., and D.F. Weaver. 1969. Physical processes at the surface of the arctic tundra. *Arctic* 22: 425-437.
- Kirchner, W.B. 1975. The effect of oxidized material on the vertical distribution of freshwater benthic fauna. *Freshwat. Biol.* 5: 423-429.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* 6: 315-353.
- Krebs, C.J. 1987. Voles and lemmings, p. 650-655. In D.W. MacDonald [ed.] *The encyclopedia of mammals*. Facts On File Publications, New York.
- Lee, R.E. 1980. *Phycology*. Cambridge University Press, Cambridge. 478 p.
- Leopold, L.B., and W.B. Langbein. 1962. The concept of entropy in landscape evolution. Geological Survey of the United States, Professional Paper 500-A. United States Government Printing Office, Washington.
- Leslie, P.H., and D.H.S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. *J. Animal Ecol.* 8: 94-113.

- Lindeman, R.L. 1941. Seasonal food-cycle dynamics in a senescent lake. *Amer. Midl. Nat.* 26: 636-673.
- Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.
- Livingstone, D.A. 1966. Alaska, Yukon, Northwest Territories, and Greenland, p. 559-574. In D.G. Frey [ed.] *Limnology of North America*. The University of Wisconsin Press, Madison.
- Livingstone, D.A., K. Bryan, Jr., and R.C. Leahy. 1958. Effects of an arctic environment on the origin and development of freshwater lakes. *Limnol. Oceanogr.* 3: 192-214.
- Lovegrove, T. 1960. An improved form of sedimentation apparatus for use with an inverted microscope. *Conseil Permanent Internat. Explor. Mer. Jour.* 25: 279-284.
- MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princetown University Press. Princetown Monogr. Popn. Biol. 1: 1-203.

- MacCallum, W.R., and H.A. Regier. 1984. The biology and bioenergetics of Arctic charr in Char lake, N.W.T., Canada, p. 329-340. In L. Johnson and B.L. Burns [eds.] Biology of the Arctic charr. University of Manitoba Press, Winnipeg.
- Maciolek, J.A. 1988. Tundra ponds of the Yukon Delta, Alaska, and their invertebrate communities. *Verh. Internat. Verein. Limnol.* 23: 212.
- Mann, K.H., and M. Brylinsky. 1975. IBP/PF synthesis—estimating the productivity of lakes and reservoirs, p. 221-226. In T.W.M. Cameron and L.W. Billingsley [eds.] Energy flow—its biological dimensions. Royal Society of Canada, Ottawa.
- Margalef, R. 1968. Perspectives in ecological theory. University of Chicago Press, Chicago. 111 p.
- Maxwell, J.B. 1980. The climate of the Canadian Arctic Islands and adjacent waters. Vol. 1. Climatological Studies 30. Atmospheric Environment Service, Toronto. 531 p.

- Maxwell, J.B. 1981. Climatic regions of the Canadian Arctic Islands. *Arctic* 34: 225-240.
- May, R.M. 1973. Mass and energy flow in closed ecosystems: a comment. *J. theor. Biol.* 39: 155-163.
- Melchiorri-Santolini, U., and J.W. Hopton [eds.]. 1972. Detritus and its role in aquatic ecosystems. *Proc. IBP-UNESCO Symp., Pallanza, Italy.* 540 p.
- Miller, Jr., A.T. 1968. Energy metabolism. F.A. Davis Co., Philadelphia. 186 p.
- Morowitz, H.J. 1968. Energy flow in biology. Academic Press, New York and London. 179 p.
- Morse, D.H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, MA, and London. 383 p.
- Nicolis, G., and I. Prigogine. 1977. Self-organization in nonequilibrium systems. Wiley-Interscience, New York. 492 p.

- Nisbet, R.M., and W.S.C. Gurney. 1976. Model of material cycling in a closed ecosystem. *Nature* 264: 633-634.
- Nordeng, H. 1961. On the biology of char (Salmo alpinus L.) in Salangen, North Norway. I. Age and spawning frequency determined from scales and otoliths. *Nytt. Mag. Zool.* 10: 67-123.
- Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. *Can. J. Fish. Aquat. Sci.* 45: 361-379.
- Oceviski, B. 1966. Microbiological investigations of the Balkan Lakes Ostrovo, Petersko, Rudnik and Zazercic. *Verh. Internat. Verein. Limnol.* 16: 1519-1525.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Odum, E.P. 1971. *Fundamentals of ecology.* W.B. Saunders Co., Philadelphia. 574 p.
- Odum, E.P., and A.A. de la Cruz. 1963. Detritus as a major component of ecosystems. *Am. Inst. Biol. Sci. Bull.* 13: 39-40.

- Oliver, D.R. 1968. Adaptations of arctic Chironomidae. Ann. Zool. Fenn. 5: 111-118.
- Oliver, D.R. 1971. Life history of the Chironomidae. Ann. Rev. Ent. 16: 211-230.
- Onsager, L. 1931. Reciprocal relations in irreversible processes. Phys. Rev. 37: 405-426.
- Pace, M.L, and J.D. Orcutt, Jr. 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol. Oceanogr. 26: 822-830.
- Page, L. 1958. Introduction to theoretical physics. D. van Nostrand Co., Inc., Princeton. 701 p.
- Paine, R.T. 1971. The measurement and application of the calorie to ecological problems. Ann. Rev. Ecol. Systematics 2: 145-164.
- Paloheimo, J.E., and L.M. Dickie. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23: 1209-1248.

- Parry, G.D. 1981. The meaning of r- and K-selection. *Oecologia* 48: 260-264.
- Patalas, K., and A. Salki. 1984. Effects of impoundment and diversion on the crustacean plankton of Southern Indian Lake. *Can. J. Fish. Aquat. Sci.* 41: 613-637.
- Paterson, C.G., and C.H. Fernando. 1971. A comparison of a simple corer and an Ekman grab for sampling shallow-water benthos. *J. Fish. Res. Board Can.* 28: 365-368.
- Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos* 15: 130-139.
- Pick, M.A. 1969. The specific heat of ice Ih, p. 344-347. In N. Riehl, B. Bullemer, and H. Engelhardt [eds.] *Physics of ice*. Plenum Press, New York.
- Pitt, V.H. [ed.]. 1983. *The Penguin dictionary of physics*. Penguin Books Ltd., Harmondsworth. 428 p.
- Platt, J.R. 1964. Strong inference. *Science* 146: 347-353.

- Pollard, J.H. 1977. A handbook of numerical and statistical techniques with examples mainly from the life sciences. Cambridge University Press, Cambridge. 349 p.
- Prest, V.K. 1973. Glacial retreat, p. 31-32. In The national atlas of Canada. Department of Energy, Mines and Resources, Ottawa.
- Prest, V.K., D.R. Grant, and V.N. Rampton. 1972. Glacial geology, p. 33-34. In The national atlas of Canada. Department of Energy, Mines and Resources, Ottawa.
- Pridmore, R.D., and J.E. Hewitt. 1984. Chlorophyll- α as an indicator of phytoplankton cell volume in 12 lakes, North Island, New Zealand. N.Z.J. Botany 22: 295-302.
- Prigogine, I. 1973. Irreversibility as a symmetry-breaking process. Nature 246: 67-71.
- Prigogine, I. 1978. Time, structure and fluctuations. Science 20: 777-785.

- Prigogine, I. 1980. From being to becoming. Freeman Publications, San Francisco. 272 p.
- Prigogine, I., and G. Nicolis. 1971. Biological order, structure and instabilities. Quart. Rev. Biophysics 4: 107-148.
- Prigogine, I., G. Nicolis, and A. Babloyantz. 1972. Thermodynamics of evolution. Physics Today. Nov. 1972, p. 23-28 and Dec. 1972, p. 38-44.
- Prigogine, I., and I. Stengers. 1984. Order out of chaos: Man's new dialogue with nature. Bantam Books, New York. 349 p.
- Proops, J.L.R. 1983. Organization and dissipation in economic systems. J. Soc. Biol. Str. 6: 353-366.
- Prus, T. 1975. Measurement of calorific value using Phillipson microbomb calorimeter, p. 149-160. In W. Grodzinski, R.Z. Klekowski, and A. Duncan [eds.] Methods for ecological bioenergetics. IBP Handbook No. 24. Blackwell Scientific Publications, Oxford.

- Reed, D.F., and E.B. Reed. 1970. Estimates of seston crops by filtration with glass fiber discs. J. Fish. Res. Board Can. 27: 180-185.
- Rheinheimer, G. 1974. Aquatic microbiology. Transl. from German by A. Mayr-Harting. Wiley-Interscience, London. 184 p.
- Riget, F.F., K.H. Nygaard, and B. Christensen. 1986. Population structure, ecological segregation, and reproduction in a population of Arctic char (Salvelinus alpinus) from Lake Tasersuaq, Greenland. Can. J. Fish. Aquat. Sci. 43: 985-992.
- Rigler, F.H. 1972. The Char Lake project. A study of energy flow in a high arctic lake, p. 287-300. In Z. Kajak and A. Hillbricht-Ilkowska [eds.] Productivity problems of freshwaters. Polish Scientific Publishers, Warszawa and Cracow.
- Rigler, F.H. 1975. The Char Lake project, p. 171-198. In T.W.M. Cameron and L.W. Billingsley [eds.] Energy flow—its biological dimensions. Royal Society of Canada, Ottawa.

- Rigler, F.H., M.E. MacCallum, and J.C. Roff. 1974. Production of zooplankton in Char Lake. J. Fish. Res. Board Can. 31: 637-646.
- Roulet, N.T., and M.K. Woo. 1986. Low arctic wetland hydrology. Can. Water Resour. Jour. 11: 69-75.
- Rublee, P., and B.E. Dornseif. 1978. Direct counts of bacteria in the sediments of a North Carolina salt marsh. Estuaries 1: 188-191.
- Rybak, J.I. 1969. Bottom sediments of the lakes of various trophic type. Ekol. Pol. Ser. A 17: 1-52.
- Saraceni, C., and D. Ruggiu. 1969. Techniques for sampling water and phytoplankton, p. 5-7. In R.A. Vollenweider [ed.] A manual on methods for measuring primary production in aquatic environments. IBP Handbook No. 12. Blackwell Scientific Publications, Oxford and Edinburgh.

- Saunders, G.W., K.W. Cummins, D.Z. Gak, E. Pieczyńska, V. Straškrabová, and R.G. Wetzel. 1980. Organic matter and decomposers, p. 341-392. In E.D. Le Cren and R.H. Lowe-McConnell [eds.] The functioning of freshwater ecosystems. Cambridge University Press, Cambridge.
- Schindler, D.W., A.S. Clark, and J.R. Gray. 1971. Seasonal calorific values of freshwater zooplankton, as determined with a Phillipson bomb calorimeter modified for small samples. J. Fish. Res. Board Can. 28: 559-564.
- Schindler, D.W., J. Kalff, H.E. Welch, G.J. Brunskill, H. Kling, and N. Krich. 1974b. Eutrophication in the high arctic—Meretta Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 647-662.
- Schindler, D.W., and N. Krich. 1972. Natural and cultural sources of nutrients and their effects on Char, Meretta and Resolute lakes, Cornwallis Island, p. 5-15. In Annual report on Char Lake Project, IBP. Dept. of Zoology, University of Toronto, Toronto.

- Schindler, D.W., H.E. Welch, J. Kalff, G.J. Brunskill, and N. Kritsch. 1974a. Physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 585-607.
- Schneider, E.D. 1988. Thermodynamics, ecological succession, and natural selection: a common thread, p. 107-138. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] Entropy, information, and evolution. MIT Press, Cambridge, MA.
- Seyfried, P.L, and A.R.G. Owen. 1979. Evaluation of the most probable number technique for the enumeration of fecal coliforms and Pseudomonas aeruginosa in sediment, p. 52-63. In C.D. Litchfield and P.L. Seyfried [eds.] Methodology for biomass determinations and microbial activities in sediments. American Society for Testing and Materials Spec. Tech. Publ. 673.
- Shimada, B.M. 1958. Diurnal fluctuations in photosynthetic rate and chlorophyll content of phytoplankton from eastern Pacific waters. Limnol. Oceanogr. 3: 336-339.

- Shiozawa, D.K., and J.R. Barnes. 1977. The microdistribution and population trends of larval Tanypus stellatus (Coquellet) and Chironomus frommeri (Atchley & Martin) (Diptera: Chironomidae) in Utah Lake, Utah. Ecology 58: 610-618.
- Slack, K.V., R.C. Averett, P.E. Greeson, and R.G. Lipscomb. 1973. Methods for collection and analysis of aquatic biological and microbiological samples. Chapter A4, book 5, p 1-165. In Techniques of water-resources investigations of the United States Geological Survey. United States Government Printing Office, Washington.
- Slobodkin, L.B., and S. Richman. 1960. The availability of a miniature bomb calorimeter for ecology. Ecology 41: 784.
- Smith, R.L. 1980. Ecology and field biology. Harper and Row, Publishers, New York. 835 p.
- Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. The Iowa State University Press, Ames. 507 p.

- Soodak, H., and A. Iberall. 1978. Homeokinetics: a physical science for complex systems. *Science* 201: 579-582.
- Sprules, W.G. 1988. Effects of trophic interactions on the shape of pelagic size spectra. *Verh. Internat. Verein. Limnol.* 23: 234-240.
- Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of fresh water. *Can. Fish. Mar. Serv. Misc. Spec. Publ.* 25: 180 p.
- Stanford, J.A. 1973. A centrifuge method for determining live weights of aquatic insect larvae, with a note on weight loss in preservative. *Ecology* 54: 449-451.
- Stewart, D.B., and L.M.J. Bernier. 1982. An aquatic resource survey of the islands bordering Viscount Melville Sound, District of Franklin, Northwest Territories. Lands Directorate of Environment Canada, and Northern Environment Directorate of Indian and Northern Affairs, Northern Land Use Information Series, Background Report No. 2. 110 p.

- Stewart, D.B, and L.M.J. Bernier. 1983. An aquatic resource survey of Victoria and King William Islands and the northeastern District of Keewatin, Northwest Territories. Lands Directorate of Environment Canada, and Northern Environment Directorate of Indian and Northern Affairs, Northern Land Use Information Series, Background Report No. 3. 124 p.
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.
- Thorsteinsson, R., and E.T. Tozer. 1962. Banks, Victoria, and Stefansson islands, Arctic Archipelago. Geol. Surv. Can. Mem. 330: 85 p.
- Thorsteinsson, R., and E.T. Tozer. 1970. Geology of the Arctic Archipelago, p. 549-590. In R.J.W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv. Can. Econ. Geol. Rep. 1.
- Tonolli, V. 1971. Methods of collection. Zooplankton, p. 1-14. In W.T. Edmondson and G.G. Winberg [eds.] A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, 1st ed. Blackwell Scientific Publications, Oxford and Edinburgh.

- Trincher, K.S. 1965. Biology and information: Elements of biological thermodynamics. Transl. from Russian by E.S. Spiegelthal. Consultants Bureau, New York.
- Tucker, A. 1949. Pigment extractions as a method of quantitative analysis of phytoplankton. Trans. Amer. micr. Soc. 68: 21-33.
- Ulanowicz, R.E. 1972. Mass and energy flow in closed ecosystems. J. theor. Biol. 34: 239-253.
- Ulanowicz, R.E. 1980. A hypothesis on the development of natural communities. J. theor. Biol. 85: 223-245.
- Watson, A. 1986. Physics—were the action is. New Scient. 109: 42-44.
- Welch, H.E., and J. Kalff. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609-620.
- Wetzel, R.G. 1983. Limnology. CBS College Publishing, Philadelphia. 767 p.

- White, D.C. 1983. Analysis of microorganisms in terms of quantity and activity in natural environments, p. 37-66. In J.H. Slater, R. Whittenbury, and J.W.I. Wimpenny [eds.] Microbes in their natural environments. Cambridge University Press, Cambridge.
- White, E., G. Payne, and S. Pickmere. 1988. A limitation to the usefulness of chlorophyll as a biomass indicator in eutrophication studies. Verh. Internat. Verein. Limnol. 23: 598-601.
- Wicken, J.S. 1979. The generation of complexity in evolution: a thermodynamic and information-theoretical discussion. J. theor. Biol. 77: 349-365.
- Wicken, J.S. 1980. A thermodynamic theory of evolution. J. theor. Biol. 87: 9-23.
- Wicken, J.S. 1981. Evolutionary self-organization and the entropy principle. Nature and System 3: 129-141.
- Wicken, J.S. 1983. Entropy, information and nonequilibrium evolution. Syst. Zool. 32: 438-443.

- Wicken, J.S. 1985. Thermodynamics and the conceptual structure of evolutionary theory. *J. theor. Biol.* 117: 363-383.
- Wicken, J.S. 1986. Evolutionary self-organization and entropic dissipation in biological and socioeconomic systems. *J. Soc. Biol. Str.* 9: 261-273.
- Wicken, J.S. 1988. Thermodynamics, evolution, and emergence: ingredients for a new synthesis, p. 139-169. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] *Entropy, information, and evolution*. MIT Press, Cambridge, MA.
- Wiggins, G.B. 1978. Trichoptera, p. 147-185. In R.W. Merritt and K.W. Cummins [eds.] *An introduction to the aquatic insects of North America*. Kendall/Hunt Publishing Co., Dubuque.
- Wiley, E.O. 1988. Entropy and evolution, p. 173-188. In B.H. Weber, D.J. Depew, and J.D. Smith [eds.] *Entropy, information, and evolution*. MIT Press, Cambridge, MA.

- Wiley, E.O., and D.R. Brooks. 1982. Victims of history—a nonequilibrium approach to evolution. *Syst. Zool.* 31: 1-24.
- Wiley, E.O., and D.R. Brooks. 1983. Nonequilibrium thermodynamics and evolution: a response to Løvtrup. *Syst. Zool.* 32: 209-219.
- Wilson, J.A. 1968. Increasing entropy of biological systems. *Nature* 219: 534-535.
- Winberg, G.G. [ed.]. 1971. Methods for the estimation of production of aquatic animals. Transl. from Russian by A. Duncan. Academic Press, London and New York. 175 p.
- Winberg, G.G. 1972. Études sur le bilan biologique energetique et la productivité des lacs en Union Soviétique. *Verh. Internat. Verein. Limnol.* 18: 39-64.

- Winberg, G.G., V.A. Babitsky, S.I. Gavrilov, G.V. Gladky, I.S. Zakharenkov, R.Z. Kovalevskaya, T.M. Mikheeva, P.S. Nevyadomskaya, A.P. Ostapenya, P.G. Petrovich, J.S. Potaenko, and O.F. Yakushko. 1972. Biological productivity of different types of lakes, p. 383-404. In Z. Kajak and A. Hillbricht-Ilkowska [eds.] Productivity problems of freshwaters. Polish Scientific Publishers, Warszawa and Cracow.
- Wittaker, R.H., and G.M. Woodwell, 1972. Evolution of natural communities, p. 137-159. In J.A. Wiens [ed.] Ecosystem structure and function. Proc. 31st Ann. Biol. Colloquium, Oregon State University Press, Corvallis.
- Woolhouse, H.W. 1967. Entropy and evolution. Nature 216: 200.
- Yentsch, C.S., and J.H. Ryther. 1957. Short-term variations in phytoplankton chlorophyll and their significance. Limnol. Oceanogr. 2: 140-142.

PERSONAL COMMUNICATIONS

- Johnson, L. Department of Fisheries and Oceans, 501
University Cr., Winnipeg, Manitoba, R3T 2N6.
- Kling, H. Department of Fisheries and Oceans, 501
Universtiy Cr., Winnipeg, Manitoba, R3T 2N6.
- Salki, A. Department of Fisheries and Oceans, 501
University Cr., Winnipeg, Manitoba, R3T 2N6.
- Stainton, M.P. Department of Fisheries and Oceans, 501
University Cr., Winnipeg, Manitoba, R3T 2N6.
- Tabisz, G.C. Department of Physics, University of Manitoba,
Winnipeg, Manitoba, R3T 2N2.
- Warwick, W. National Hydrology Research Institute, 11
Innovation Blvd., Saskatoon, Saskatchewan, S7N 3H5.

APPENDIX A

MORPHOMETRIC FORMULAE AND DATA

Table A1. Description of morphometric formulae (after Cole 1983 and Wetzel 1983).

Morphometric Formulae

1. Shoreline development (D_L) =

$$\frac{L}{2\sqrt{\pi A_0}}, \quad (A1)$$

where L = length of shoreline, and A_0 = surface area of lake.

2. Mean depth ($\bar{Z}$) =

$$\frac{V}{A_0}, \quad (A2)$$

where V = lake volume, and A_0 = surface area of lake.

3. Relative depth (Z_r) =

$$\frac{50Z_m\sqrt{\pi}}{\sqrt{A_0}}, \quad (A3)$$

where Z_m = maximum depth, and A_0 = surface area of lake.

4. Lake volume (V) =

$$\sum \frac{1}{3} (A_{Z_n} + A_{Z_{n+1}} + \sqrt{A_{Z_n}A_{Z_{n+1}}}) (Z_{n+1} - Z_n), \quad (A4)$$

where Z_n = depth at contour line n , $Z_{n+1} - Z_n$ = vertical contour interval, and A_{Z_n} = area limited by the Z_n contour line.

Continued

Morphometric Formulae

5. Volume development (D_v) =

$$3 \frac{\bar{Z}}{Z_m}, \quad (A5)$$

where $\bar{Z}$ = mean depth, and Z_m = maximum depth.

6. Basin slope between contours =

$$\left(\frac{L_{Z_1} + L_{Z_2}}{2} \right) \left(\frac{Z_2 - Z_1}{A_{Z_1} - A_{Z_2}} \right), \quad (A6)$$

where L_{Z_1} = upper contour length, L_{Z_2} = lower contour length, $A_{Z_1} - A_{Z_2}$ = area enclosed by the two contours, and $Z_2 - Z_1$ = vertical contour interval.

7. Mean basin slope =

$$\frac{(\frac{1}{2}L_{Z_0} + L_{Z_1} + L_{Z_2} + L_{Z_3} \dots L_{Z_{n-1}} + \frac{1}{2}L_{Z_n}) Z_m}{nA_0}, \quad (A7)$$

where L_z = contour length, n = total number of contours, Z_m = maximum depth, and A_0 = surface area of lake.

Continued

Morphometric Formulae

8. Results in (A6) and (A7) were converted to degrees with the following formula:

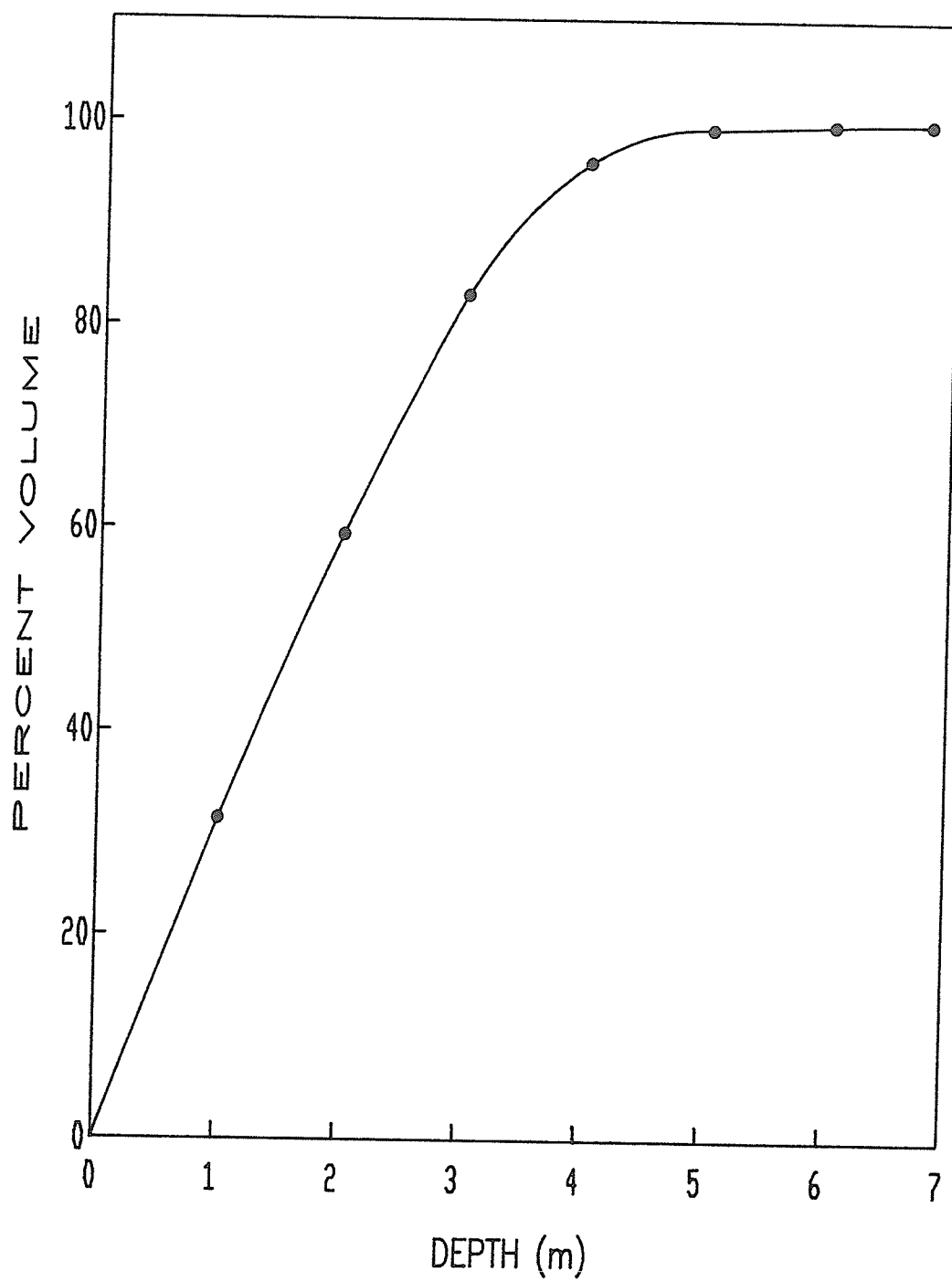
$$\cos^{-1} (\sqrt{1 + B_S^2})^{-1}, \quad (A8)$$

where B_S = basin slope.

Table A2. Comparison of area, volume, percent volume, and slope between contours, at 1 m depth intervals.

Depth range (m)	Area of upper surface (m ²)	Volume (m ³)	Percent volume	Slope between isobaths
0 - 1	486,312	461,226	31.50	3° 32'
1 - 2	436,586	411,048	28.07	3° 06'
2 - 3	386,028	342,991	23.43	1° 33'
3 - 4	301,685	193,813	13.24	0° 22'
4 - 5	97,786	45,520	3.11	0° 15'
5 - 6	14,513	8,202	0.56	0° 23'
6 - 6.8	4,996	1,332	0.09	0° 09'

Figure A1. Percent volume hypsographic curve for Keyhole Lake. The curve indicates that the deeper regions of the lake contribute relatively little to the total lake volume.



APPENDIX B

TEMPERATURES

MATERIALS AND METHODS, AND DATA

WATER TEMPERATURE

Materials and Methods

In 1985 surface and subsurface water temperatures were read with a calibrated standard laboratory thermometer. Subsurface water samples were collected at predetermined depth intervals and at the bottom with water-sampling bottles (described in "Materials and Methods" under "Field work—Phytoplankton, other microseston, and chlorophyll"). The water samples were rapidly brought to the surface and a standard laboratory thermometer was immediately placed in them. In 1986 surface and subsurface water temperatures were obtained with a Yellow Springs Instrument Co., Inc. Tele-thermometer (Model 43TD).

Figure B1. Daily maximum and minimum air temperatures recorded at Cambridge Bay from June to September, 1985.

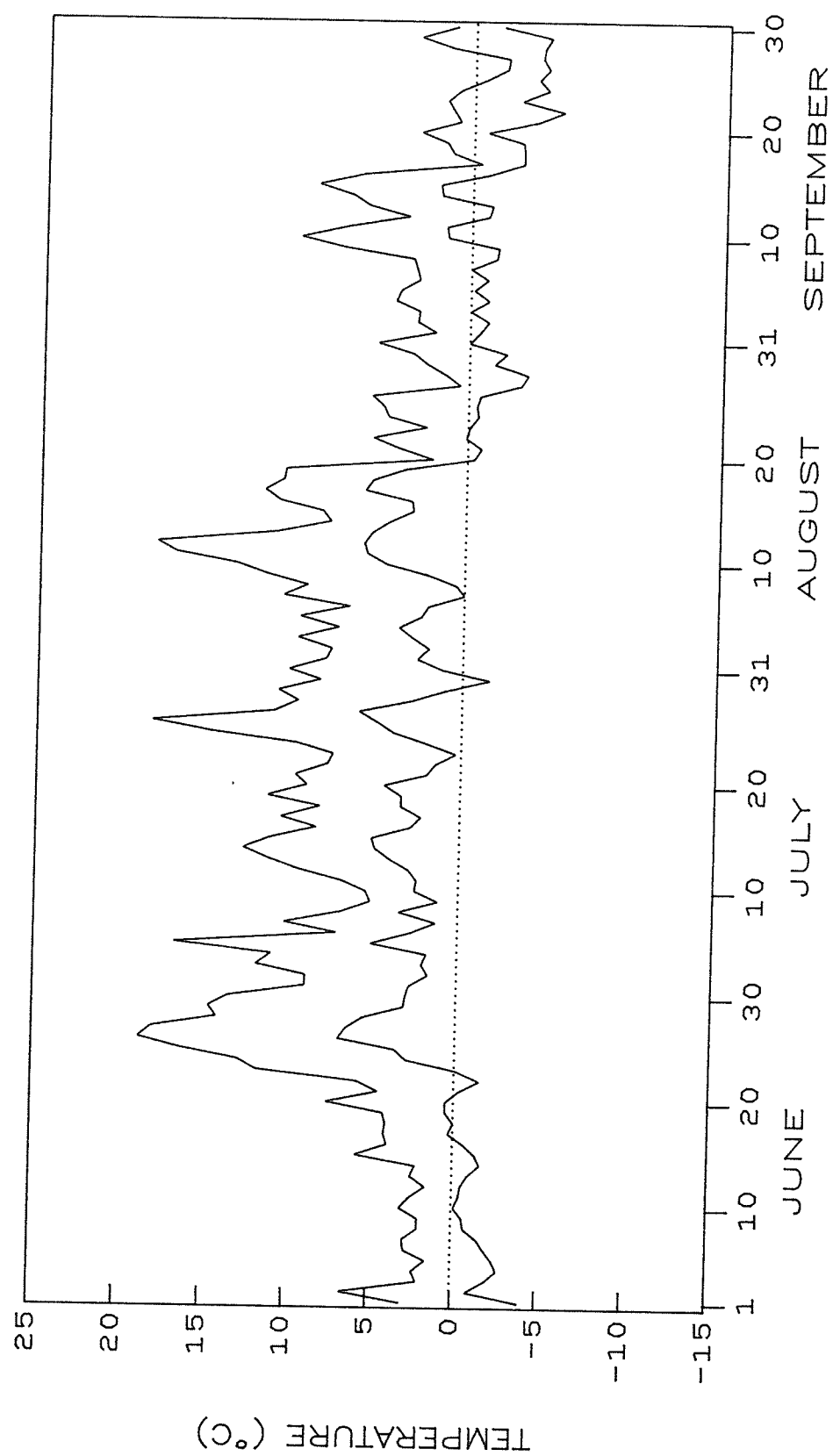


Figure B2. Daily maximum and minimum air temperatures recorded at Cambridge Bay from June to September, 1986.

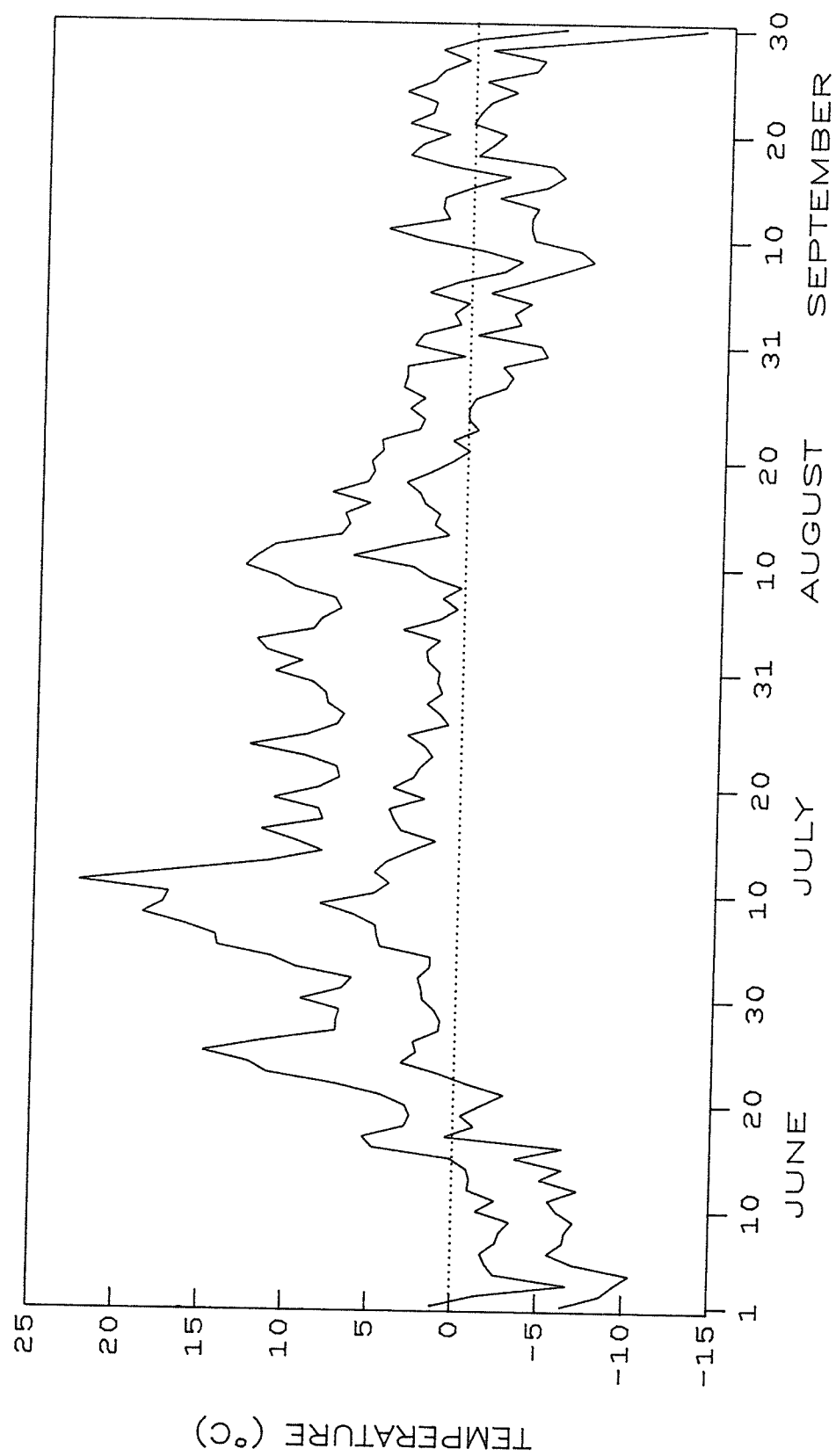
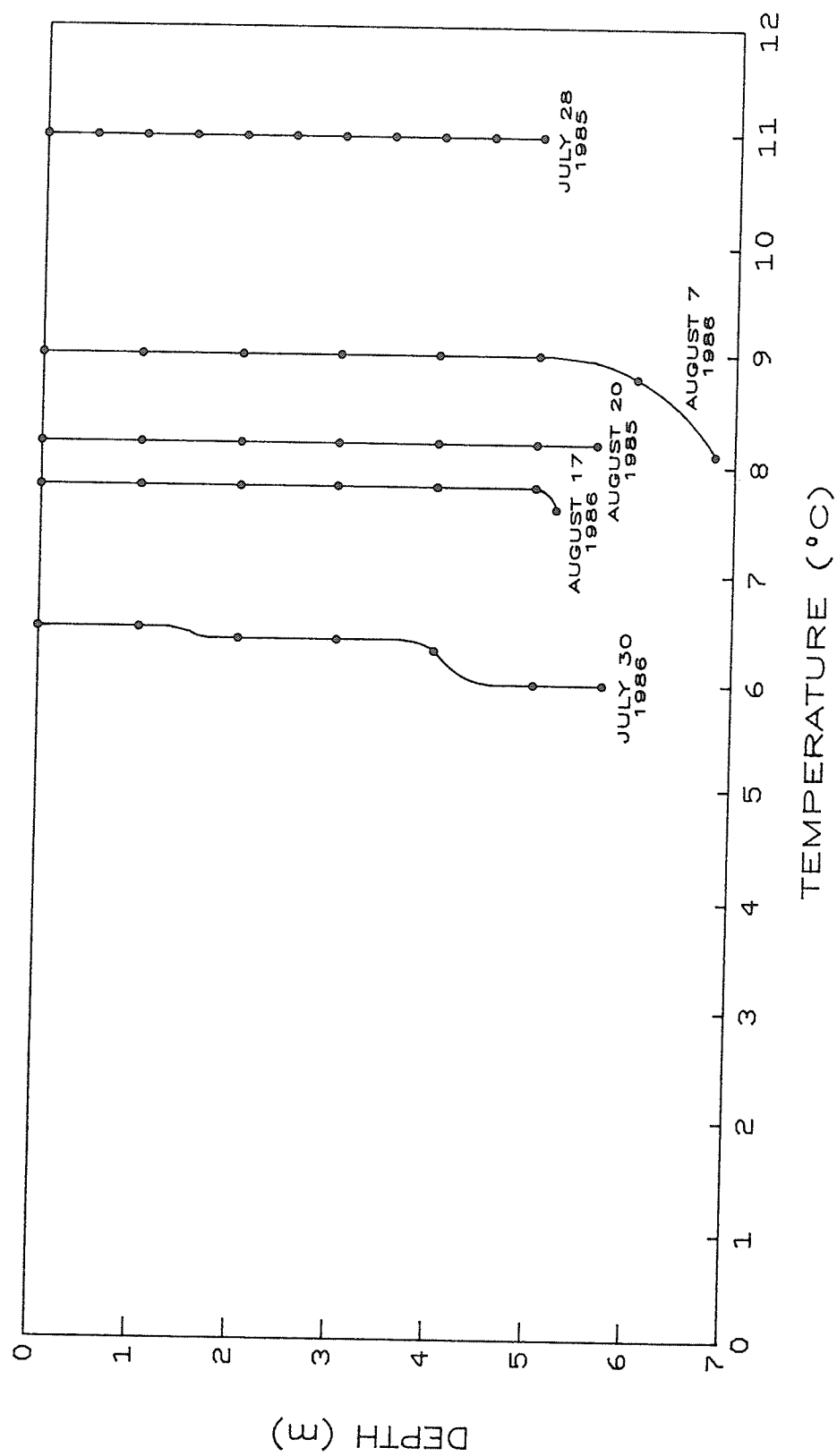


Figure B3. Water temperature profiles for Keyhole Lake.



APPENDIX C

WATER TRANSPARENCY MATERIALS AND METHODS, FORMULAE, AND DATA

DOWNWELLING VISIBLE IRRADIANCE

Materials and Methods

Unpublished data on downwelling light quanta, quanta frequency distribution at various wave lengths, and vertical absorption coefficient for Keyhole Lake were provided by P.H. Heinermann, Department of Biological Sciences, University of Montreal. Downwelling quanta in the visible portion of the spectrum were measured with an underwater spectroradiometer. See Heinermann and Ali (1988) for a complete description of this instrument. Measurements were taken above the water surface and from 0 to 5 m below the surface. Data was collected at approximate hourly intervals spanning a 24 hour period during July 24 to 25, 1985. On July 22 and 30, 1985 measurements were taken on quanta frequency distribution at a spectral band of 400 to 640 nm, at 20 nm intervals. Recordings were made with an underwater spectroradiometer at the same station and vertical intervals as downwelling quanta measurements. Ideally quanta frequency distribution is determined at the photosynthetically active spectral band of 380 to 720 nm (Cole 1983). However, sufficient information was provided for a reasonable approximation of energy in downwelling visible irradiance. Data on quanta frequency distribution per wavelength interval were pooled for the two recording dates except for measurements above the water surface; these

were only recorded on July 22, 1985. See this appendix for quanta to joules conversion and vertical absorption coefficient formulae (Table C1).

Table C1. Quanta to joules conversion and vertical absorption coefficient formulae (after Cole 1983 and Wetzel 1983).

Quanta to joules conversion and vertical
absorption coefficient formulae

1. Quanta to joules:

$$E = 1 \times 10^4 \frac{Q_T h c}{Q_T \lambda} \sum_{i=1}^n \frac{Q \lambda_i}{\lambda_i}, \quad (C1)$$

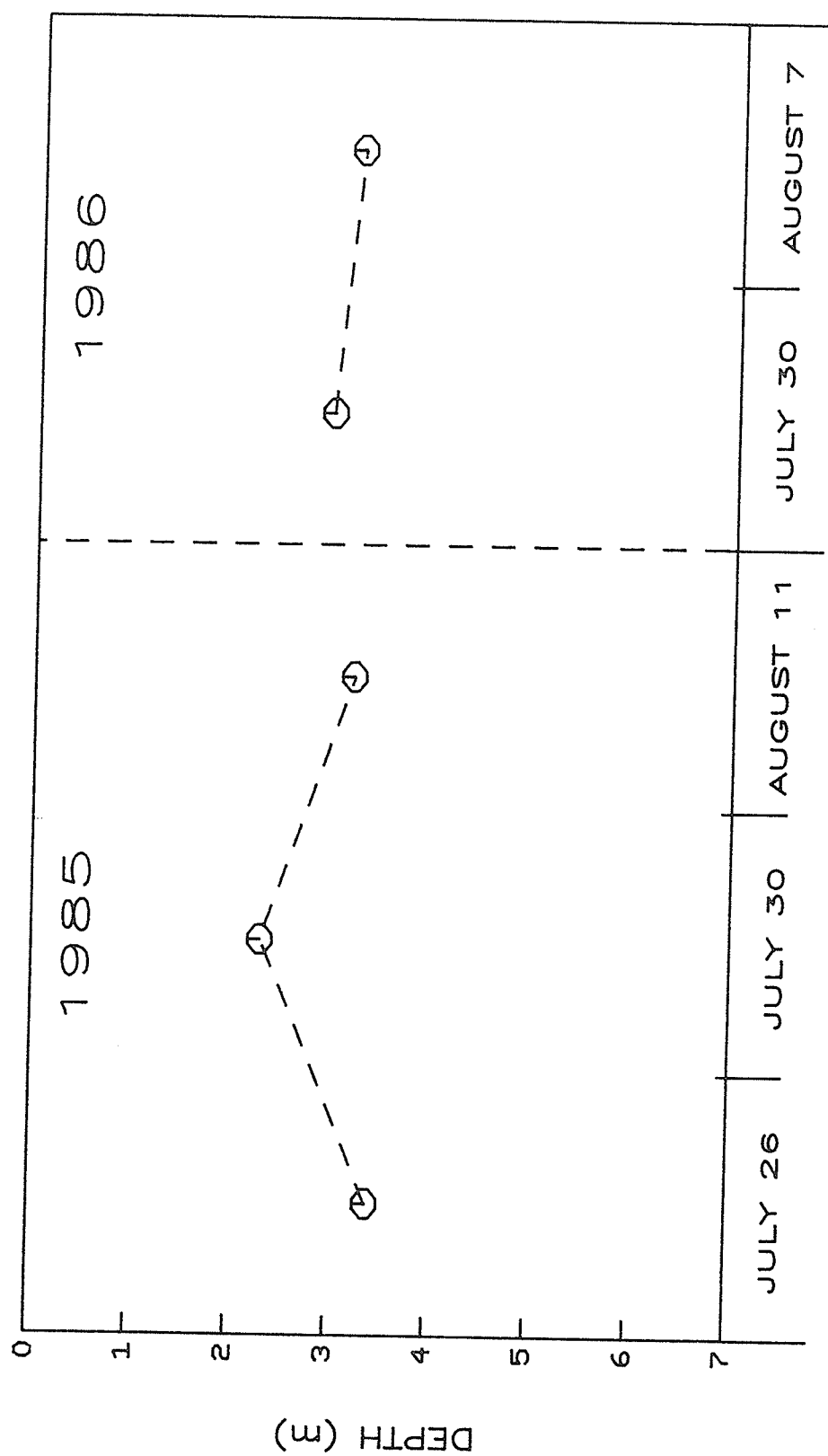
where E = energy in $J \cdot m^{-2} \cdot sec^{-1}$, Q_T = total downwelling quanta $\cdot cm^{-2} \cdot sec^{-1}$, $Q_T \lambda$ = total downwelling quanta $\cdot cm^{-2} \cdot sec^{-1}$ of wave length profile, λ = wave length in m, $Q \lambda$ = downwelling quanta $\cdot cm^{-2} \cdot sec^{-1}$ at λ , c = speed of light in $m \cdot sec^{-1}$, and h = Planck's constant in $J \cdot sec^{-1}$.

2. Vertical absorption coefficient (k) =

$$\frac{\ln I_0 - \ln I_z}{Z}, \quad (C2)$$

where I_0 = light intensity at water surface, I_z = remaining light intensity after having passed through water of thickness Z (in m).

Figure C1. Secchi disc measurements in Keyhole Lake.



APPENDIX D

WATER CHEMISTRY MATERIALS AND METHODS, AND DISCUSSION

WATER CHEMISTRY

Materials and Methods

Water samples for chemical analyses were collected at four stations during each sampling period (one station per lake quadrant—discussed in "Materials and methods" under "Field work—Sampling location selection for biomass estimation"). Samples were obtained at 0.5 m with water-sampling bottles (described in "Materials and methods" under "Field work—Phytoplankton, other microseston, and chlorophyll") in 1985 on July 28-29, August 14, and 26-27, and in 1986 on July 27-28, and August 17. Sampling at different depths was unnecessary due to the complete mixing of the lake during the summer. Water chemistry data of Keyhole Lake in Hunter (1970) indicates very little or no change at different depths once isothermal conditions became established. Schindler et al. (1974a, 1974b) found surface samples to represent the chemistry of monomictic Arctic lakes in the summer.

Dissolved organic carbon, suspended phosphorus, chloride, sulphate, calcium, iron, magnesium, manganese, potassium, sodium, some soluble reactive silicon, and some specific conductance samples were treated and stored as per Stainton et al. (1977). Organic acid samples were handled and stored identically to dissolved organic carbon in

Stainton et al. (1977). Water samples (100 ml minimum) for alkalinity determination were collected in polyethylene bottles and stored (Stainton pers. comm.). Handling and/or storing of dissolved inorganic carbon, suspended carbon, suspended nitrogen, total dissolved nitrogen, total dissolved phosphorus, some soluble reactive silicon, some specific conductance, and pH samples deviated in varying degrees from the guidelines in Stainton et al. (1977). Usually the remoteness of Keyhole Lake prevented freezing and/or rapid transportation to Winnipeg for analysis.

Dissolved inorganic carbon samples were stored longer (by 6 to 19 days) than the suggested 24 hours in Stainton et al. (1977). This may not have altered the samples markedly (Stainton pers. comm.). Suspended carbon and suspended nitrogen samples, after collection on glass fiber filters, were not stored at the recommended -10°C but at approximately 5°C . The higher storage temperature may have degraded the samples (Stainton pers. comm.). This suggests that the analytical results should be accepted with caution. Total dissolved nitrogen and total dissolved phosphorus samples received UV photocombustion after 6 to 19 days instead of the recommended 48 hour constraint. These samples, according to Stainton (pers. comm.), probably were not affected by this time-delay. The recommended maximum 24 hour storage period for pH samples was exceeded by 5 to 18 days. This deviation prevents detection of short-term pH

changes. The analytical data therefore depicts the long-term equilibrate condition of the lake (Stainton pers. comm.). Some soluble reactive silicon and specific conductance samples were stored in excess (by 1 to 12 days) of the suggested 7 days. This brief extension of the recommended storage period probably did not affect the samples (Stainton pers. comm.).

Analyses were performed by the Analytical Chemistry Unit at the Freshwater Institute, Department of Fisheries and Oceans, Winnipeg. Most analyses were performed according to procedures in Stainton et al. (1977). The following exceptions were noted: dissolved inorganic carbon and dissolved organic carbon analyses with a commercial automated infrared detector, and the employment of an ion chromatograph in the analyses of chloride and sulphate. Analytical methods for organic acids and alkalinity are not described in Stainton et al. (1977) and were performed with ion chromatography (unpublished) and Gran titration (0.01 N hydrochloric acid), respectively (Stainton pers. comm.).

Means and 95% confidence intervals for each field season were calculated according to standard statistical procedures (Table 1). Sampling period means are used in the following discussion.

Results and Discussion

NUTRIENT ELEMENTS

Dissolved inorganic carbon levels ranged from 1,425 to 1,600 $\mu\text{mole}\cdot\text{l}^{-1}$ in 1985. During the following field season concentrations were lower and remained relatively stationary varying from 1,193 to 1,210 $\mu\text{mole}\cdot\text{l}^{-1}$.

Concentrations of dissolved organic carbon were distinctly lower than dissolved inorganic carbon levels and ranged from 395 to 503 $\mu\text{mole}\cdot\text{l}^{-1}$ in 1985, and from 315 to 348 $\mu\text{mole}\cdot\text{l}^{-1}$ in 1986. Dissolved organic carbon content varied from 130 to 420 $\mu\text{mole}\cdot\text{l}^{-1}$ in seven other Victoria Island lakes (Stewart and Bernier 1982). Due to low concentrations ($< 90 \mu\text{g}\cdot\text{l}^{-1}$ or approximately less than 7.5 $\mu\text{mole}\cdot\text{l}^{-1}$) Schindler et al. (1974a) experienced difficulties in measuring dissolved organic carbon in Char Lake. For oligotrophic temperate lakes Hobbie (1973) noted a range of 3 to 4 $\text{mg}\cdot\text{l}^{-1}$ (approximately 250 to 333 $\mu\text{mole}\cdot\text{l}^{-1}$).

Values for suspended carbon ranged from 600 to 1,163 $\mu\text{g}\cdot\text{l}^{-1}$ during the 1985 sampling periods, and from 478 to 545 $\mu\text{g}\cdot\text{l}^{-1}$ in 1986. This is markedly higher than an annual mean of 172 $\mu\text{g}\cdot\text{l}^{-1}$ (range is less than 100 to 300 $\mu\text{g}\cdot\text{l}^{-1}$) reported for Char Lake by Schindler et al. (1974a). Stewart and Bernier (1982, 1983), during a survey of eighteen Victoria Island lakes, measured a suspended carbon range from 220 to 940 $\mu\text{g}\cdot\text{l}^{-1}$, with the exception of one shallow turbid lake that had a concentration of 2,530 $\mu\text{g}\cdot\text{l}^{-1}$.

Suspended nitrogen values generally declined after the first sampling period in 1985; during 1986 this trend was reversed. In 1985 levels ranged from 79 to 158 $\mu\text{g}\cdot\text{l}^{-1}$ but was lower (44 to 62 $\mu\text{g}\cdot\text{l}^{-1}$) in 1986. Schindler et al. (1974a) reported a much lower range of 7 to 27 $\mu\text{g}\cdot\text{l}^{-1}$ for Char Lake. In most Victoria Island lakes sampled by Stewart and Bernier (1982, 1983) the suspended nitrogen content varied from 21 to 102 $\mu\text{g}\cdot\text{l}^{-1}$, but one lake contained 270 $\mu\text{g}\cdot\text{l}^{-1}$.

Total dissolved nitrogen concentrations fluctuated a little in 1985 (325 to 440 $\mu\text{g}\cdot\text{l}^{-1}$) and remained almost constant in 1986 (305 to 313 $\mu\text{g}\cdot\text{l}^{-1}$). Other Victoria Island lakes exhibited a range from 90 to 745 $\mu\text{g}\cdot\text{l}^{-1}$ (Stewart and Bernier 1982, 1983). For Char Lake an annual average of 75 $\mu\text{g}\cdot\text{l}^{-1}$ was measured by Schindler et al. (1974a).

Total dissolved phosphorus concentrations varied markedly for 1985 (13.5 to 32.3 $\mu\text{g}\cdot\text{l}^{-1}$) but remained almost stationary in 1986 (16.0 to 16.5 $\mu\text{g}\cdot\text{l}^{-1}$). Stewart and Bernier (1982, 1983) measured a range of 6 to 18 $\mu\text{g}\cdot\text{l}^{-1}$ in eighteen Victoria Island lakes. Schindler et al. (1974a) reported annual averages of only 2 $\mu\text{g}\cdot\text{l}^{-1}$ for Char Lake.

The pattern for suspended phosphorus was similar to total dissolved phosphorus; it ranged from 7.0 to 12.8 $\mu\text{g}\cdot\text{l}^{-1}$ in 1985 and was stationary at 4.5 $\mu\text{g}\cdot\text{l}^{-1}$ in 1986. The Victoria Island lakes surveyed by Stewart and Bernier

(1982, 1983) had a suspended phosphorus range from 2 to 12 $\mu\text{g}\cdot\text{l}^{-1}$, except for one shallow silty lake that contained 82 $\mu\text{g}\cdot\text{l}^{-1}$. In Char Lake values varied from 1 to 5 $\mu\text{g}\cdot\text{l}^{-1}$ (Schindler et al. 1974a).

Soluble reactive silicon displayed pronounced fluctuations during the first two field seasons, when samples were collected. Concentrations ranged from 68 to 148 $\mu\text{g}\cdot\text{l}^{-1}$ in 1985 and from 59 to 173 $\mu\text{g}\cdot\text{l}^{-1}$ in 1986. Larger seasonal variations were noted for Char Lake; 100 $\mu\text{g}\cdot\text{l}^{-1}$, directly below a melting ice cover, to 800 $\mu\text{g}\cdot\text{l}^{-1}$ (Schindler et al. 1974a).

MAJOR ANIONS

Chloride values in both years increased as the season progressed. Concentration varied from 22.5 to 25.3 $\text{mg}\cdot\text{l}^{-1}$ in 1985. For 1986 the values were slightly lower ranging from 19.0 to 21.8 $\text{mg}\cdot\text{l}^{-1}$. Hunter (1970) listed comparable values (19.5 to 20.0 $\text{mg}\cdot\text{l}^{-1}$) for Keyhole Lake during August 1965. Johnson (1964b) analysed water samples from three Victoria Island lakes and reported chloride levels of 2.7, 4.7, and 11.0 $\text{mg}\cdot\text{l}^{-1}$. Stewart and Bernier (1982, 1983) measured a wide variation in Victoria Island lakes (1.0 to 50.5 $\text{mg}\cdot\text{l}^{-1}$). Char Lake chloride concentrations varied from 5 $\text{mg}\cdot\text{l}^{-1}$ near a thawing ice cover to 12 $\text{mg}\cdot\text{l}^{-1}$ (Schindler et al. 1974a), and Kalff (1968) reported a range of 1.7 to 24.2 $\text{mg}\cdot\text{l}^{-1}$ in nine northern lakes.

Sulphate concentrations varied from 5.5 to 7.3 $\text{mg}\cdot\text{l}^{-1}$ in 1985 and from 5.1 to 5.4 $\text{mg}\cdot\text{l}^{-1}$ in 1986. Other Victoria Island lakes ranged from 0.8 to 12.0 $\text{mg}\cdot\text{l}^{-1}$ (Johnson 1964b; Stewart and Bernier 1982, 1983). In Char Lake sulphate levels during the winter varied from 8 to 14 $\text{mg}\cdot\text{l}^{-1}$ (Schindler et al. 1974a). Ions are usually more concentrated in the winter due to freezing out (Livingstone 1966). Kalff (1968) surveyed fourteen northern lakes for sulphate and found concentrations ranging from 0.0 to 18.0 $\text{mg}\cdot\text{l}^{-1}$.

MAJOR CATIONS

Calcium concentrations increased during the progression of the sampling periods in both years. In 1985 the samples contained from 13.5 to 14.8 $\text{mg}\cdot\text{l}^{-1}$ calcium and ranged from 13.6 to 15.2 $\text{mg}\cdot\text{l}^{-1}$ in the following year. These values are higher than 9.1 to 9.8 $\text{mg}\cdot\text{l}^{-1}$ reported by Hunter (1970) for Keyhole Lake during August, 1965. In other lakes on Victoria Island concentrations from 8.8 to 18.2 $\text{mg}\cdot\text{l}^{-1}$ (Johnson 1964b) and 5.98 to 31.4 $\text{mg}\cdot\text{l}^{-1}$ (Stewart and Bernier 1982, 1983) were measured. Schindler and Kritsch (1972) recorded a range of 34 to 37 $\text{mg}\cdot\text{l}^{-1}$ for Char Lake and surveys of northern lakes by Kalff (1968) and Livingstone (1966) found calcium ranges of 3.0 to 34.6 $\text{mg}\cdot\text{l}^{-1}$ and 3.1 to 31.0 $\text{mg}\cdot\text{l}^{-1}$, respectively.

Iron concentrations slightly increased from July to August, 1985 (40 to 55 $\mu\text{g}\cdot\text{l}^{-1}$) but decreased during the same period in 1986 (80 to 40 $\mu\text{g}\cdot\text{l}^{-1}$). Johnson (1964b) reported only traces of iron in three other Victoria Island lakes. Dissolved iron in Char Lake was undetectable ($< 1 \mu\text{g}\cdot\text{l}^{-1}$) (Schindler et al. 1974a). Hobbie (1973) quoted a range of 15 to 138 $\mu\text{g}\cdot\text{l}^{-1}$ dissolved iron for lakes in northern Alaska. Surveys by Livingstone et al. (1958) and Kalff (1968) indicated iron concentrations from 10 to 180 $\mu\text{g}\cdot\text{l}^{-1}$ in northern lakes.

Magnesium levels remained relatively stationary in 1985 (9.4 to 9.8 $\text{mg}\cdot\text{l}^{-1}$) and increased slightly from 8.9 to 10.3 $\text{mg}\cdot\text{l}^{-1}$ in 1986. Hunter (1970) measured lower values of 7.1 to 7.4 $\text{mg}\cdot\text{l}^{-1}$ during August 1965 in Keyhole Lake. Levels in other Victoria Island Lakes varied from 2.73 to 27.5 $\text{mg}\cdot\text{l}^{-1}$ (Johnson 1964b; Stewart and Bernier 1982, 1983). Magnesium concentrations in Char Lake ranged from 5.0 to 7.0 $\text{mg}\cdot\text{l}^{-1}$ (Schindler and Kritsch 1972; Schindler et al. 1974a). Livingstone (1966) and Kalff (1968) reported magnesium ranges of 1.8 to 9.4 $\text{mg}\cdot\text{l}^{-1}$ and 0.7 to 18.7 $\text{mg}\cdot\text{l}^{-1}$, respectively, for northern lakes.

Manganese levels were low; less than 10 to below 20 $\mu\text{g}\cdot\text{l}^{-1}$ in 1985 and below 10 $\mu\text{g}\cdot\text{l}^{-1}$ in 1986. Livingstone et al. (1958) reported no measurable manganese in two northern Alaskan lakes and Hobbie (1973) quoted ranges of 1.0 to 1.7 $\mu\text{g}\cdot\text{l}^{-1}$ for some northern Alaska lakes.

Potassium concentrations remained relatively stationary during the first two field seasons, when samples were collected. Values ranged from 1.10 to 1.19 $\text{mg}\cdot\text{l}^{-1}$ in 1985, and 1.07 to 1.09 $\text{mg}\cdot\text{l}^{-1}$ in 1986. Hunter (1970) measured similar concentrations (0.9 to 1.3 $\text{mg}\cdot\text{l}^{-1}$) in Keyhole Lake during August 1965. During surveys of Victoria Island lakes potassium level ranges from 0.3 to 0.8 $\text{mg}\cdot\text{l}^{-1}$ (Johnson 1964b) and 0.13 to 1.27 $\text{mg}\cdot\text{l}^{-1}$ (Stewart and Bernier 1982, 1983) were reported. Values for Char Lake varied from 0.2 $\text{mg}\cdot\text{l}^{-1}$ near a receding ice cover to over 0.7 $\text{mg}\cdot\text{l}^{-1}$ (Schindler et al. 1974a). Lake Peters, in the Brooks Range of Alaska, contained 0.1 $\text{mg}\cdot\text{l}^{-1}$ (Hobbie in Livingstone 1966) and 0.3 $\text{mg}\cdot\text{l}^{-1}$ potassium (Rainwater and Guy in Hobbie 1973).

Sodium concentrations rose during both years' sampling periods. Values increased from 12.3 to 13.9 $\text{mg}\cdot\text{l}^{-1}$ in 1985, and 9.6 to 10.9 $\text{mg}\cdot\text{l}^{-1}$ in 1986. Similar values (9.3 to 11.0 $\text{mg}\cdot\text{l}^{-1}$) were reported by Hunter (1970) for this lake during August, 1965. In Victoria Island lakes sampled by Stewart and Bernier (1982, 1983) sodium levels ranged from 0.62 to 25.2 $\text{mg}\cdot\text{l}^{-1}$. Johnson (1964b) measured concentrations from 0.9 to 6.0 $\text{mg}\cdot\text{l}^{-1}$ in lakes on the same island. Char Lake sodium levels varied from 1.0 $\text{mg}\cdot\text{l}^{-1}$ directly under a thawing ice cover to 6.5 $\text{mg}\cdot\text{l}^{-1}$ (Schindler et al. 1974a). Livingstone (1966) reported a range of 0.2 to 18.0 $\text{mg}\cdot\text{l}^{-1}$ in Alaskan and Northwest Territorial lakes.

MISCELLANEOUS WATER QUALITY MEASUREMENTS

Organic acid concentrations initially increased but declined after the penultimate sampling period in 1985; values ranged from 12.3 to 42.5 $\mu\text{eq}\cdot\text{l}^{-1}$. In 1986 a concentration of 31.0 $\mu\text{eq}\cdot\text{l}^{-1}$ decreased to below 1.0 $\mu\text{eq}\cdot\text{l}^{-1}$ in approximately three weeks.

Alkalinity increased during the sampling periods of both years. In 1985 values ranged from 1,330 to 1,470 $\mu\text{eq}\cdot\text{l}^{-1}$, and in 1986 from 1,215 to 1,299 $\mu\text{eq}\cdot\text{l}^{-1}$. During August 1965 Hunter (1970) measured slightly lower levels varying from 1,064 to 1,112 $\mu\text{eq}\cdot\text{l}^{-1}$ (CaCO_3 alkalinity converted by formulae in Cole (1983) and Wetzel (1983)). Johnson (1964b) reported a range of 1,416 to 1,942 $\mu\text{eq}\cdot\text{l}^{-1}$ (CaCO_3 alkalinity converted) from a survey of three Victoria Island lakes. Char Lake displayed an alkalinity range of 1,477 to 2,510 $\mu\text{eq}\cdot\text{l}^{-1}$ (HCO_3^- alkalinity converted by formulae in Cole (1983)) (Schindler and Kritsch 1972). Kalff (1968) measured an alkalinity range of 160 to 2,760 $\mu\text{eq}\cdot\text{l}^{-1}$ (CaCO_3 alkalinity converted) in northern lakes. Livingstone's (1966) survey of subarctic and Arctic lakes indicated an alkalinity variation of 197 to 1,829 $\mu\text{eq}\cdot\text{l}^{-1}$ (HCO_3^- alkalinity converted).

Specific conductance increased during the field seasons of both years but was markedly higher in 1985. Values ranged from 215 to 234 $\mu\text{S}\cdot\text{cm}^{-1}$ (at 25°C) in 1985, and

from 192 to 206 $\mu\text{S}\cdot\text{cm}^{-1}$ (at 25°C) in 1986. Hunter (1970) listed lower values (153 to 177 $\mu\text{S}\cdot\text{cm}^{-1}$ at 25°C) for Keyhole Lake during August 1965. Char Lake data averaged slightly higher than Keyhole Lake ranging from 200 to 280 $\mu\text{S}\cdot\text{cm}^{-1}$ (at 25°C) (Schindler et al. 1974a). Stewart and Bernier (1982, 1983) measured a variation from 60 to 380 $\mu\text{S}\cdot\text{cm}^{-1}$ (at 25°C) in eighteen Victoria Island lakes. Kalff (1968) reported a specific conductance range of 20 to 288 $\mu\text{S}\cdot\text{cm}^{-1}$ (at 25°C) for fourteen lakes in northern North America.

The pH values, measured in July and August, varied little for 1985 (7.94 to 8.10) and even less for 1986 (8.12 to 8.15). For the same period in 1965 Hunter (1970) measured lower pH values ranging between 6.4 and 7.9. Other Victoria Island lakes had pH values varying from 7.13 to 8.20 (Johnson 1964b; Stewart and Bernier 1982, 1983). In Char Lake pH values ranged from 7.6 to over 8.0 during 1971 (Schindler et al. 1974a). Kalff (1968) measured a pH range of 6.7 to 8.4 for lakes in the Arctic Slope of Alaska and the northern Canadian mainland.

No measurements were taken for dissolved oxygen concentrations. Hunter (1970) measured concentrations from 7.28 to 17.77 $\text{mg}\cdot\text{l}^{-1}$ (converted from $\text{cc}\cdot\text{l}^{-1}$ by conversion factor in Cole (1983)) at Keyhole Lake during June 18 to September 3, 1965. Supersaturated conditions persisted after July 5 of that year. In Char Lake Schindler et al. (1974a) recorded a large vertical oxygen concentration

change during late May in 1970. Concentrations ranged from 2.5 $\text{mg}\cdot\text{l}^{-1}$ near the deepest region of the lake to 15.5 $\text{mg}\cdot\text{l}^{-1}$ proximate to the ice cover. During the fall turnover period dissolved oxygen concentrations approached saturation. Hobbie (1973) noted that ice-free Arctic lakes are usually close to complete oxygen saturation. Johnson (1975a) measured dissolved oxygen concentrations of 12.42 to 14.40 $\text{mg}\cdot\text{l}^{-1}$ in Great Bear Lake; the lake was close to saturation during the whole year and throughout the water column.

APPENDIX E

TAXA IDENTIFICATION

Table E1. Phytoplankton taxa in Keyhole Lake from water samples collected in 1986 (identified by H. Kling). Plus sign (+) indicates most abundant taxa.

Class	Taxon	Period present		
		I	II	III
Cyanophyceae	<u>Anabaena</u> sp.		*	
	<u>Aphanizomenon</u> sp.			*
	<u>Aphanocapsa elachista</u>	*		
	<u>Gloeotheca linearis</u>		*	
	<u>Merismopedia tenuissima</u>	*		
	<u>Microcystis incerta</u>			*
	<u>Oscillatoria limnetica</u>	*		
Dinophyceae	<u>Glenodinium</u> cf. <u>edax</u>	*		
	<u>Gymnodinium helveticum</u>		*	
	<u>Gymnodinium uberimum</u>	*		
	<u>Peridinium aciculiferum</u>	*		
	<u>Peridinium inconspicuum</u>		*	
Cryptophyceae	<u>Cryptomonas marssonii</u>	*		
	<u>Katablepharis ovalis</u>	*	*	*
	<u>Rhodomonas lacustris</u>	*		
	<u>Rhodomonas minuta</u>		*	
	<u>Rhodomonas minuta</u> v. <u>nanoplanctica</u>	*	*	
Chrysophyceae	<u>Aulomonas perdyi</u>	*	*	
	<u>Chromulina</u> sp.		*	
	<u>Chrysolykos planktonicus</u>	*	*	

Continued

Class	Taxon	Period present		
		I	II	III
Chrysophyceae (continued)	<u>Dinobryon bavaricum</u> v. <u>bavaricum</u>		*	*
	<u>Dinobryon bavaricum</u> v. <u>van hoffeni</u>	*	*	
	<u>Dinobryon borgei</u>		*	
	<u>Dinobryon cylindricum</u>	++	*	*
	<u>Dinobryon divergens</u>	*	*	
	<u>Dinobryon sociale</u>	*	*	*
	<u>Dinobryon sociale</u> v. <u>stipitatum</u>	*	*	*
	<u>Epiphyxis</u> sp.		*	
	<u>Kephyrion</u> sp.		*	
	<u>Mallomonas</u> sp.	*		*
	<u>Mallomonas akrokomos</u>	*		
	<u>Pedinella</u> sp.			*
	<u>Spiniferomonas</u> sp.	*		
	<u>Stichogloea</u> sp.	*		*
	<u>Synura</u> sp.	*		
	<u>Uroglena</u> cf. <u>americanum</u>		*	
Bacillariophyceae	<u>Achnanthes</u> cf. <u>minutissima</u>	*		
	<u>Asterionella formosa</u>	++	*	*
	<u>Cyclotella</u> sp. (1) <4 μ m	*		

Continued

Class	Taxon	Period present		
		I	II	III
Bacillariophyceae (continued)	<u>Cyclotella</u> sp. (2) 21 μ m			*
	<u>Cyclotella bodanica</u> v. <u>affinis</u>		*	
	<u>Diatoma elongatum</u>	*+	*	*
	<u>Eunotia (Asterionella)</u> <u>zasumensis</u>		*+	*
	<u>Melosira distens</u>	*		
	<u>Nitzschia</u> sp. (1) 28 μ m		*	
	<u>Nitzschia</u> sp. (2) 44.8 μ m		*	
	<u>Nitzschia acicularis</u>	*		*
	<u>Nitzschia palea</u>			*
	<u>Rhizosolenia erienne</u>			*
	<u>Rhizosolenia longiseta</u>	*		*
	<u>Stephanodiscus</u> sp.	*	*	*
	<u>Synedra acus</u>		*	*
	<u>Synedra nana</u>		*	
	<u>Tabellaria fenestrata</u>	*	*	*
	<u>Tabellaria flocculosa</u>		*	
Chlorophyceae	<u>Ankistrodesmus falcatus</u>			*
	<u>Chlamydomonas</u> sp.	*		
	<u>Coenocystis hindaki</u>	*		

Continued

Class	Taxon	Period present		
		I	II	III
Chlorophyceae (continued)	<u>Dictyosphaerium</u> <u>ehrenbergiana</u>			*
	<u>Nephrocytium</u> <u>aghardianum</u>	*		
	<u>Oocystis</u> sp.		*	
	<u>Oocystis</u> cf. <u>submarina</u>	*		
	<u>Quadriqula</u> sp.		*	
	<u>Scenedesmus</u> cf. <u>quadricauda</u>		*	
	<u>Spondylosium</u> <u>planum</u>	*		
	<u>Tetraedron</u> <u>minimum</u>			*
	<u>Tetraedron</u> <u>minimum</u> v. <u>tetralobulatum</u>	*	*	

Table E2. Protozoa taxa in Keyhole Lake from water samples collected in 1986 (identified by H. Kling).

Phylum	Taxon	Period present		
		I	II	III
Sarcodina	<u>Raphidocystis tubifera</u>	*	*	*
Ciliophora	<u>Askenasia</u> sp.		*	
	<u>Strobilidium</u> sp.			*
	<u>Strombidium</u> sp.	*		*
	<u>Urotricha</u> sp.	*	*	*

Table E3. Zooplankton taxa in Keyhole Lake from water samples collected in 1985 (identified by Dr. B.J. Hann). Most abundant and next most abundant taxa are indicated with (++) and (+), respectively.

Taxon	Period present	
	I	III
<u>Alona circumfimbriata</u>	*	
<u>Bosmina</u> sp.		*
<u>Chydorus brevilabris</u>	*	*
<u>Chydorus</u> cf. <u>ovalis</u>	*	
<u>Cyclops scutifer</u>	+++	++
<u>Daphnia longiremis</u>	++	*
<u>Diaptomus tyrelli</u>		+++
Calanoida nauplii	*	
Rotifera	*	*

APPENDIX F

APPLICATION OF THE LESLIE-DELURY METHOD OF POPULATION
ESTIMATION TO THE ARCTIC CHARR FISHERY OF KEYHOLE LAKE

Figure F1. Weight per unit of effort decline of all Arctic charr sizes during the 1985-86 fishery.

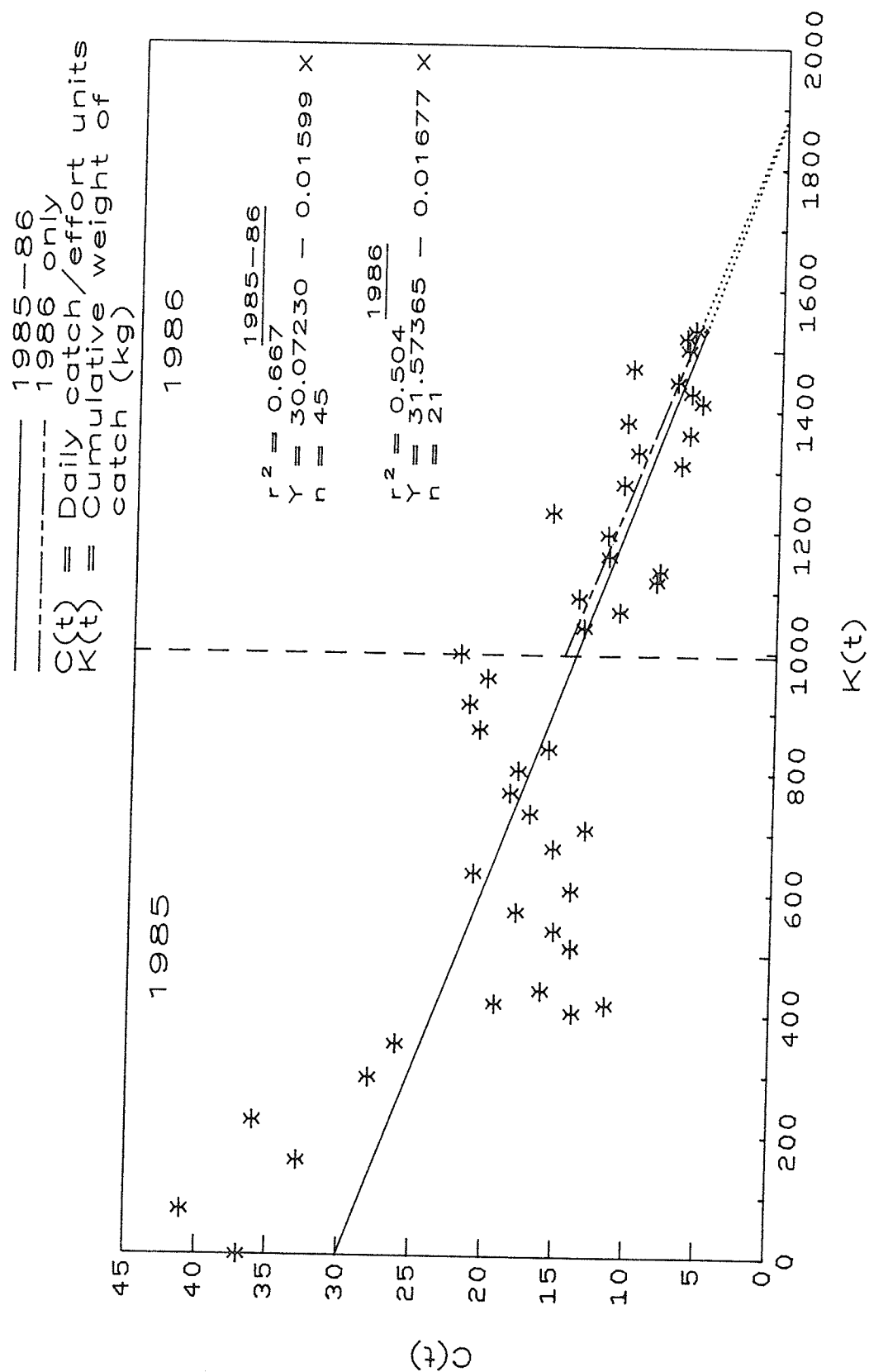
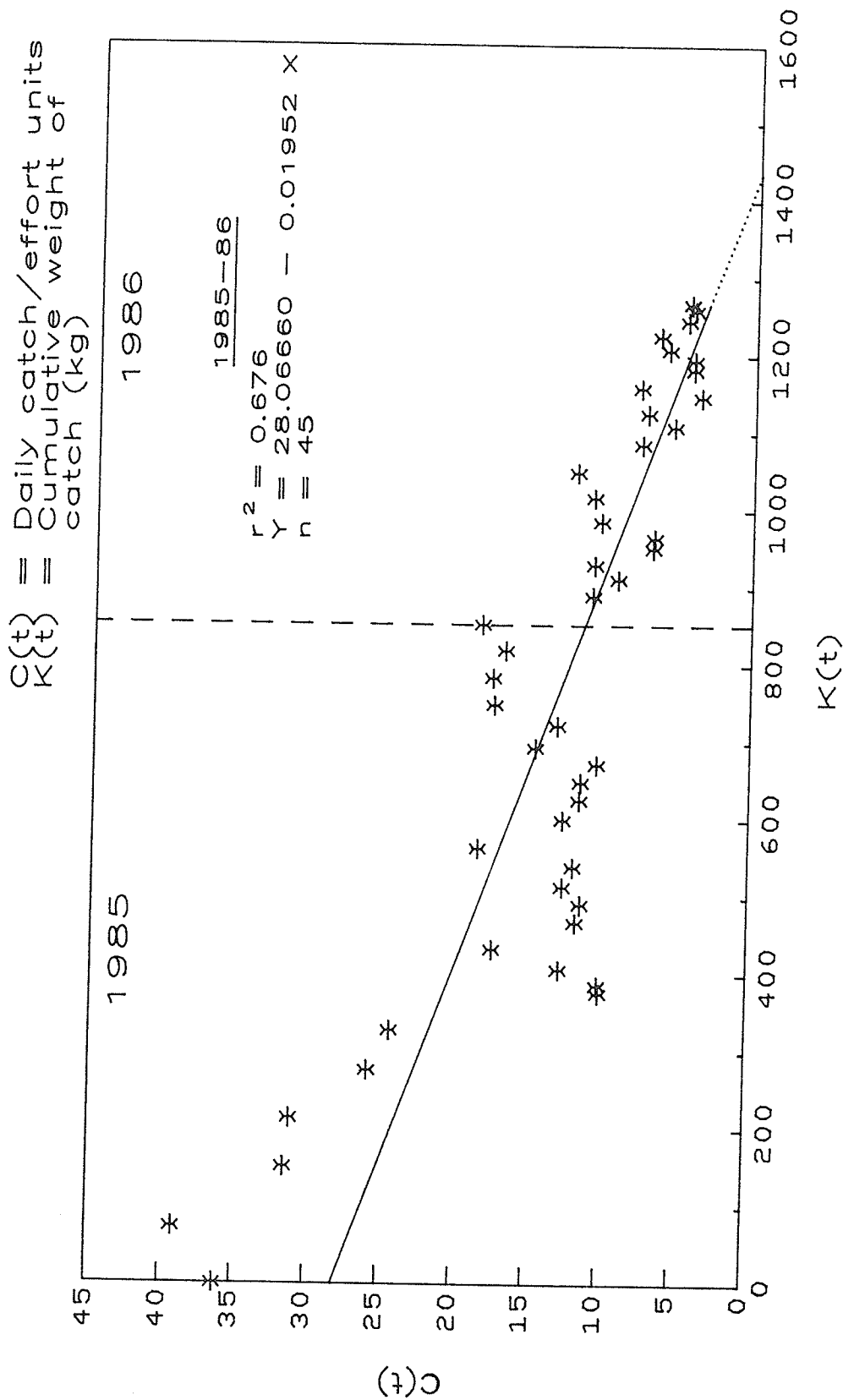


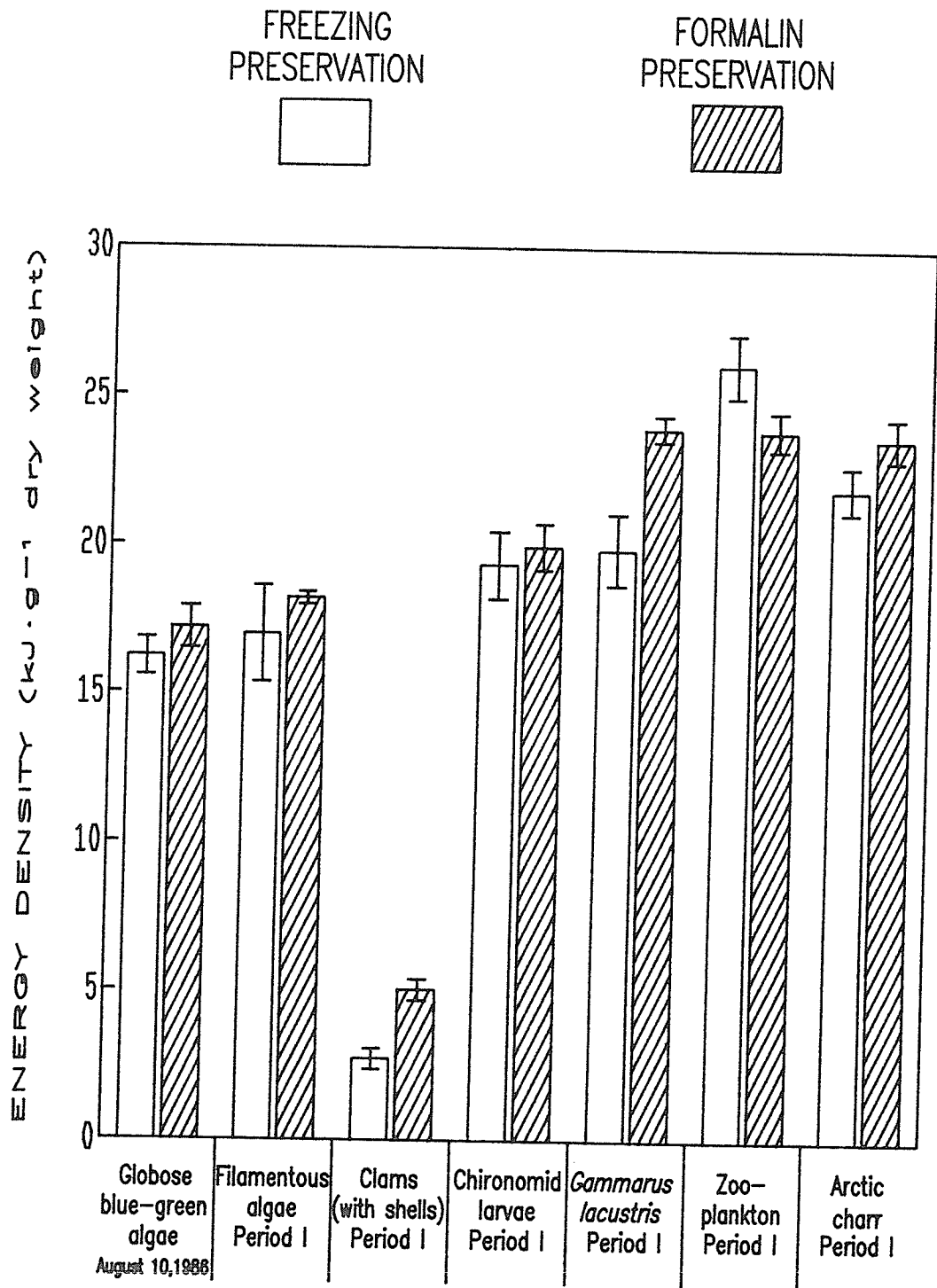
Figure F2. Weight per unit of effort decline of Arctic charr 30 cm or larger during the 1985-86 fishery.



APPENDIX G

COMPARISON OF ENERGY DENSITY BETWEEN DIFFERENT PRESERVING METHODS

Figure G1. Comparison of energy densities between freezing and formalin preservation of similar samples. All samples collected in 1985 unless noted otherwise (95% confidence intervals).



APPENDIX H

BIOMASS ESTIMATES OF TROPHIC LEVELS AND TAXA WITHIN
TROPHIC LEVELS IN KEYHOLE LAKE IN WET WEIGHT,
NUMERICAL ESTIMATES OF BENTHIC INVERTEBRATES,
AND WET TO DRY WEIGHT CONVERSION FACTORS

Table H1. Biomass estimates of trophic levels and taxa within trophic levels in $\text{kg} \cdot \text{lake}^{-1}$ wet weight in Keyhole Lake for 1985 (95% confidence intervals). Wet weight estimates were derived from samples preserved in formalin except for Arctic charr which were weighed in the field.

Trophic Level	Taxon	Period I	Period II
Benthic algae	Globose blue-green algae Filamentous algae	120,572.13 ± 84,928.85 188,716.88 ± 78,066.69 309,289.00 ± 116,782.16	155,389.75 ± 44,723.50 161,023.37 ± 46,991.89 316,413.12 ± 63,355.71
Benthic algae total			
Benthic invertebrates	Chironomid larvae Chironomid pupae Gammarus lacustris Clams (with shells) Caddisfly larvae Caddisfly pupae Oligochaetes	2,466.85 ± 1,290.81 162.70 ± 80.29 937.45 ± 1,023.41 5,083.26 ± 1,506.86 143.49 ± 166.70 0 1,053.99 ± 407.12	2,376.93 ± 887.83 6.51 ± 5.72 875.67 ± 677.29 6,282.30 ± 1,226.97 41.89 ± 74.97 0 1,042.25 ± 387.21
Benthic invertebrates total (with clams—shells included)			
Zooplankton		9,850.09 ± 3,028.49	10,625.54 ± 2,069.43
Arctic charr		1,225.95 ± 153.59 1,920.16 ± 300.42 200.35	1,375.91 ± 170.39 1,920.16 ± 300.42 200.35

Continued

Trophic Level	Taxon	Period III	Periods $\bar{x}$
Benthic algae	Globose blue-green algae Filamentous algae	73,897.05 $\pm$ 21,435.88 172,232.91 $\pm$ 67,671.28 246,129.96 $\pm$ 66,785.53	116,619.64 $\pm$ 33,546.35 173,991.05 $\pm$ 35,960.44 290,610.69 $\pm$ 47,761.55
Benthic algae total			
Benthic invertebrates	Chironomid larvae Chironomid pupae Gammarus lacustris Clams (with shells) Caddisfly larvae Caddisfly pupae Oligochaetes	2,483.04 $\pm$ 945.09 0 $\pm$ — 1,862.30 $\pm$ 1,677.72 5,774.67 $\pm$ 2,024.93 39.95 $\pm$ 59.47 152.32 $\pm$ 185.10 1,324.21 $\pm$ 724.69	2,442.27 $\pm$ 550.29 56.40 $\pm$ 30.66 1,225.14 $\pm$ 656.75 5,713.41 $\pm$ 904.21 75.11 $\pm$ 58.53 50.77 $\pm$ 64.09 1,140.15 $\pm$ 292.42
Benthic invertebrates total (with clams—shells included)			
Zooplankton		11,637.21 $\pm$ 3,518.16	10,704.28 $\pm$ 1,604.79
Arctic charr		1,497.28 $\pm$ 247.83	1,361.47 $\pm$ 112.90
		1,920.16 $\pm$ 300.42 — 200.35	1,920.16 $\pm$ 300.42 — 200.35

Table H2. Estimated number of benthic invertebrates contained in Keyhole Lake in 1985 and mean dry weight per organism (95% confidence intervals).

Taxon/trophic level	Unit	Period I		Period II	
Chironomid larvae	Number·lake ⁻¹ mg·organism ⁻¹	8.701 X 10 ⁸ 0.466	± 3.067 X 10 ⁸ ± 0.164	8.282 X 10 ⁸ 0.466	± 2.382 X 10 ⁸ ± 0.134
Chironomid pupae	Number·lake ⁻¹ mg·organism ⁻¹	8.053 X 10 ⁷ 0.282	± 3.101 X 10 ⁷ ± 0.109	3.733 X 10 ⁶ 0.126	± 3.034 X 10 ⁶ ± 0.103
<u>Gammarus lacustris</u>	Number·lake ⁻¹ mg·organism ⁻¹	5.419 X 10 ⁷ 1.676	± 6.671 X 10 ⁷ ± 2.063	4.310 X 10 ⁷ 2.281	± 3.543 X 10 ⁷ ± 1.875
Clams (with shells)	Number·lake ⁻¹ mg·organism ⁻¹	9.356 X 10 ⁸ 1.401	± 2.987 X 10 ⁸ ± 0.447	9.249 X 10 ⁸ 1.315	± 1.762 X 10 ⁸ ± 0.251
Caddisfly larvae	Number·lake ⁻¹ mg·organism ⁻¹	4.410 X 10 ⁶ 6.417	± 5.223 X 10 ⁶ ± 7.559	3.697 X 10 ⁶ 1.414	± 6.234 X 10 ⁶ ± 2.384
Caddisfly pupae	Number·lake ⁻¹ mg·organism ⁻¹	0 0	± ±	0 0	± ±
Oligochaetes	Number·lake ⁻¹ mg·organism ⁻¹	9.071 X 10 ⁷ 1.329	± 3.274 X 10 ⁷ ± 0.480	9.609 X 10 ⁷ 1.231	± 3.339 X 10 ⁷ ± 0.428
Nematodes (free-living)	Number·lake ⁻¹ mg·organism ⁻¹	5.891 X 10 ⁶ 0.176	± 3.395 X 10 ⁶ ± 0.101	0 0	± ±
Benthic invertebrates total	Number·lake ⁻¹	2.041 X 10 ⁹	± 5.987 X 10 ⁸	1.900 X 10 ⁹	± 3.478 X 10 ⁸

Continued

Taxon/trophic level	Unit	Period III			Periods $\bar{x}$		
Chironomid larvae	Number·lake ⁻¹ mg·organism ⁻¹	9.217 X 10 ⁸ ± 0.446	3.398 X 10 ⁸ ± 0.165		8.733 X 10 ⁸ ± 0.459	1.600 X 10 ⁸ ± 0.084	
Chironomid pupae	Number·lake ⁻¹ mg·organism ⁻¹	0 0	± ±	— —	2.809 X 10 ⁷ ± 0.275	1.281 X 10 ⁷ ± 0.125	
<u>Gammarus lacustris</u>	Number·lake ⁻¹ mg·organism ⁻¹	9.965 X 10 ⁷ ± 2.381	9.884 X 10 ⁷ ± 2.362		6.565 X 10 ⁷ ± 2.165	3.899 X 10 ⁷ ± 1.286	
Clams (with shells)	Number·lake ⁻¹ mg·organism ⁻¹	8.880 X 10 ⁸ ± 1.273	3.185 X 10 ⁸ ± 0.457		9.162 X 10 ⁸ ± 1.331	1.519 X 10 ⁸ ± 0.221	
Caddisfly larvae	Number·lake ⁻¹ mg·organism ⁻¹	4.437 X 10 ⁶ ± 1.005	6.763 X 10 ⁶ ± 1.532		4.181 X 10 ⁶ ± 3.028	3.032 X 10 ⁶ ± 2.196	
Caddisfly pupae	Number·lake ⁻¹ mg·organism ⁻¹	3.685 X 10 ⁶ ± 8.203	4.655 X 10 ⁶ ± 10.362		1.228 X 10 ⁶ ± 8.203	1.593 X 10 ⁶ ± 10.638	
Oligochaetes	Number·lake ⁻¹ mg·organism ⁻¹	1.121 X 10 ⁸ ± 1.309	5.556 X 10 ⁷ ± 0.649		9.964 X 10 ⁷ ± 1.290	2.251 X 10 ⁷ ± 0.291	
Nematodes (free-living)	Number·lake ⁻¹ mg·organism ⁻¹	2.919 X 10 ⁶ ± 0.055	3.652 X 10 ⁶ ± 0.068		2.937 X 10 ⁶ ± 0.136	1.725 X 10 ⁶ ± 0.080	
Benthic invertebrates total	Number·lake ⁻¹	2.032 X 10 ⁹ ±	5.407 X 10 ⁸		1.991 X 10 ⁹ ±	2.748 X 10 ⁸	

Table H3. Wet weight to dry weight conversion factors for trophic levels and taxa within trophic levels (95% confidence intervals). Data obtained from samples collected in Keyhole Lake in 1985.

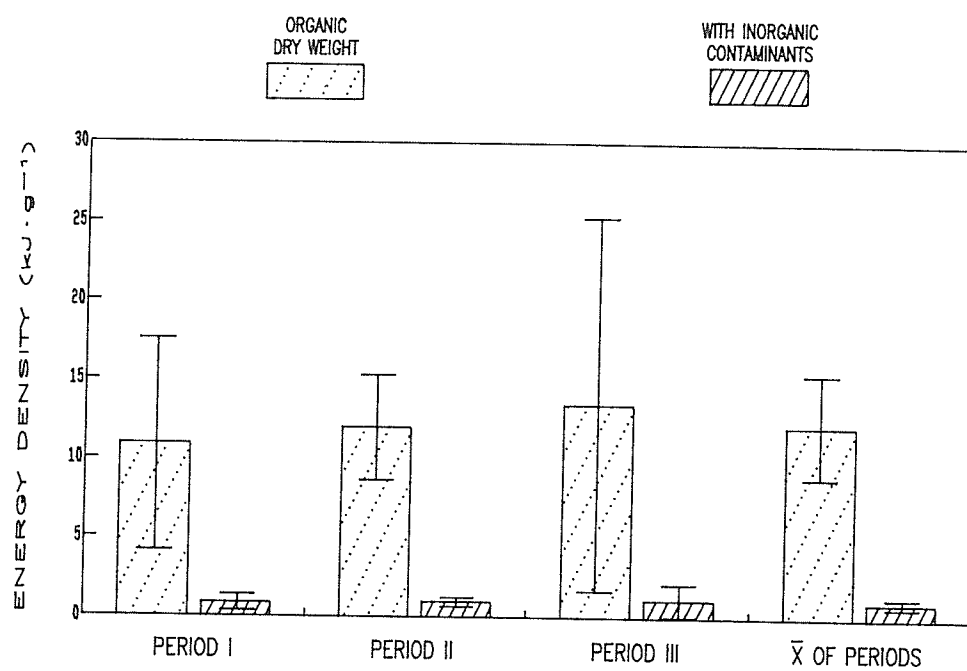
Taxon/trophic level	Percent dry weight of wet weight
Globose blue-green algae	2.38 ± 0.11
Filamentous algae	20.06 ± 1.24
Chironomid larvae	15.44 ± 0.68
Chironomid pupae	14.06 ± 1.70
<u>Gammarus lacustris</u>	11.60 ± 0.91
Clams (soft tissue only)	11.77 ± 1.57
Clams (with shells)	22.76 ± 1.28
Caddis fly larvae	12.50 ± 2.94
Caddis fly pupae	19.94 ± 0.56
Oligochaetes	11.51 ± 0.69
Zooplankton	9.05 ± 0.36
Arctic charr	22.06 ± 0.88

APPENDIX I

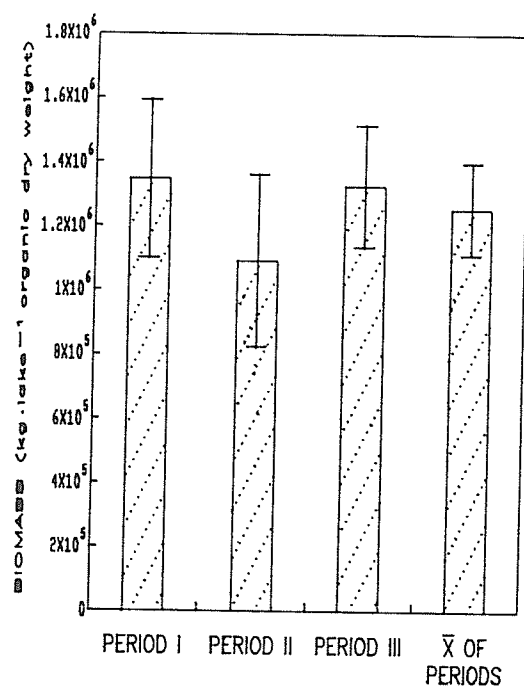
COMPREHENSIVE TROPHIC LEVEL COMPARISONS

Figure I1. Benthic bacteria and detritus (1985); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

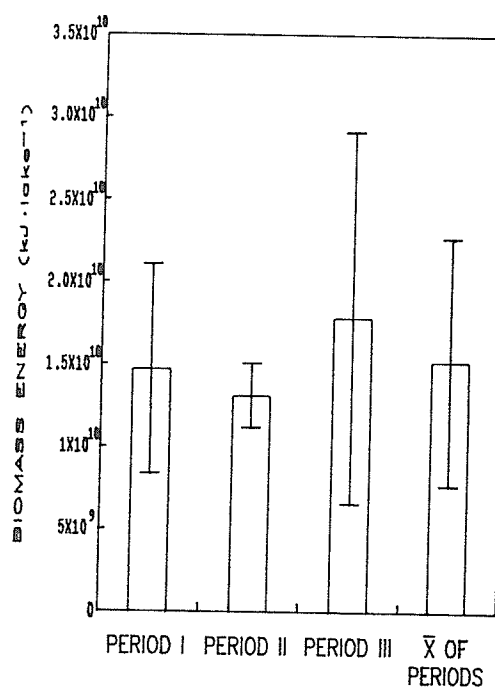
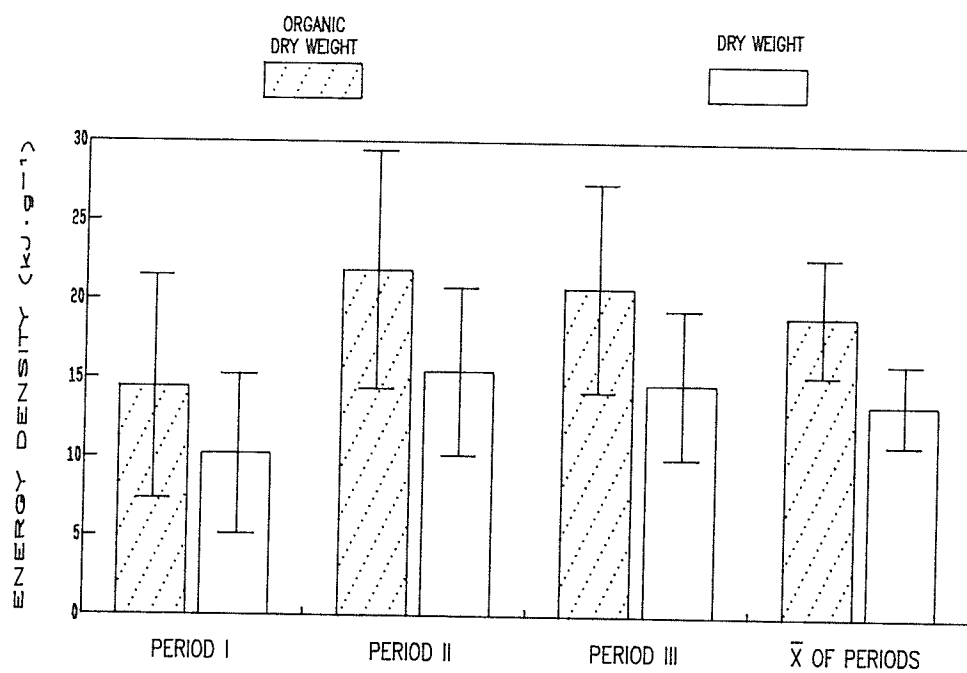
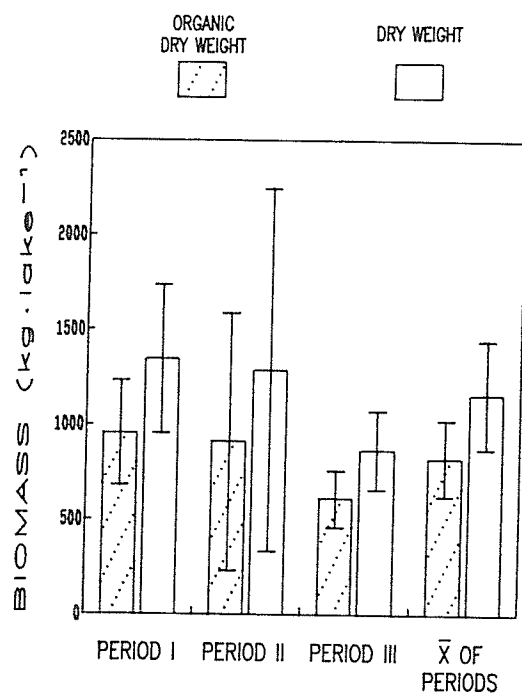


Figure I2. Phytoplankton and other microseston (1986); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

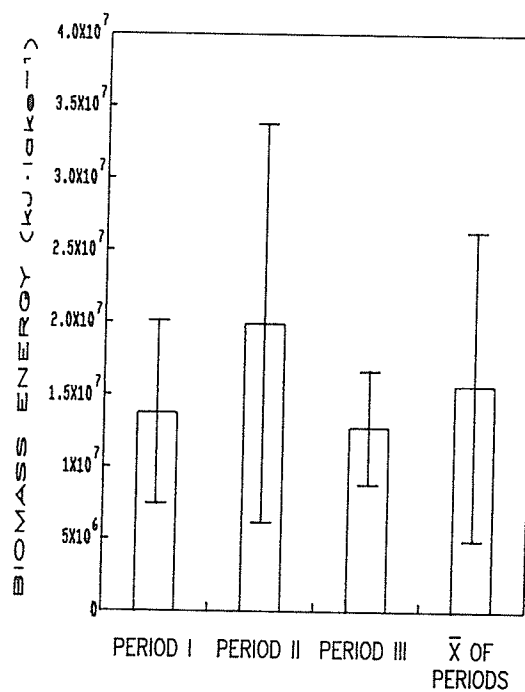
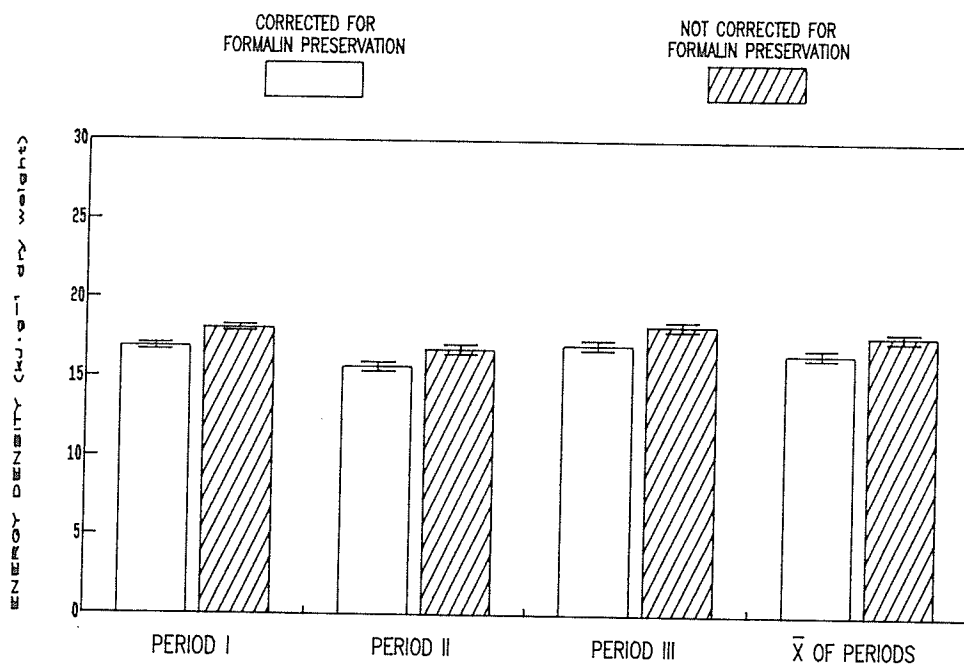
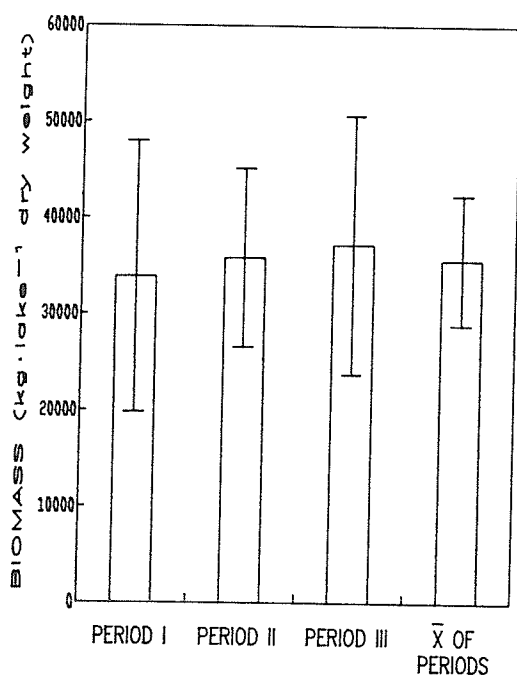


Figure I3. Benthic algae (1985); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

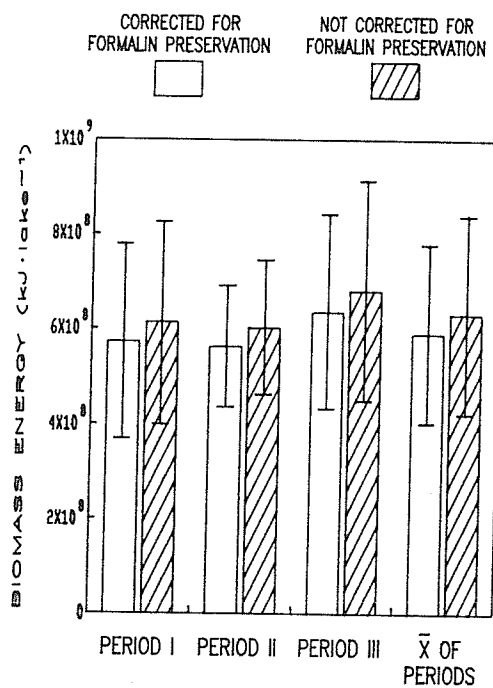
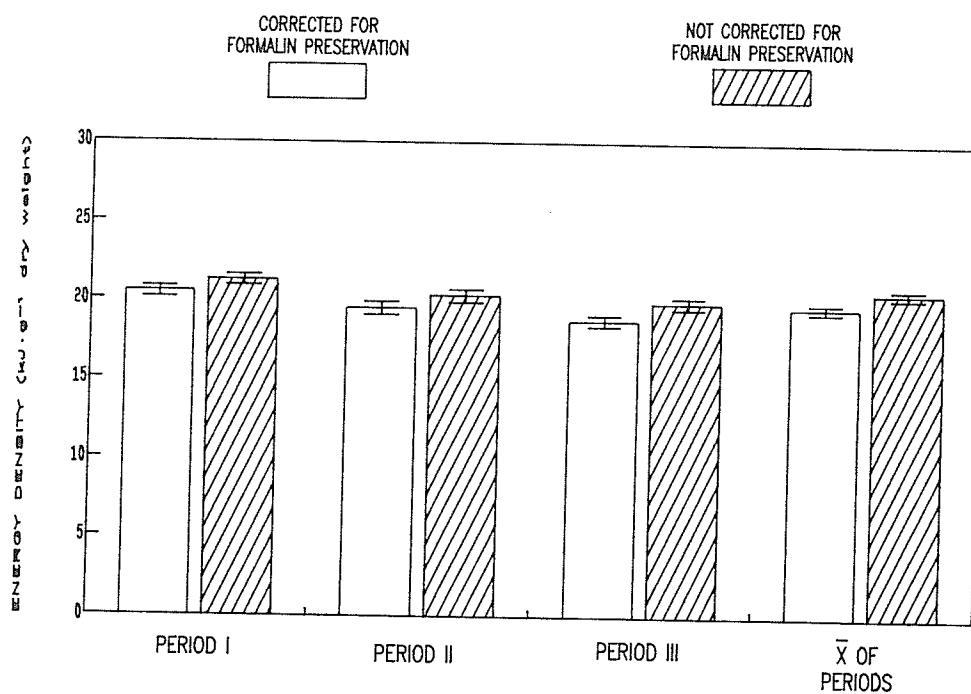
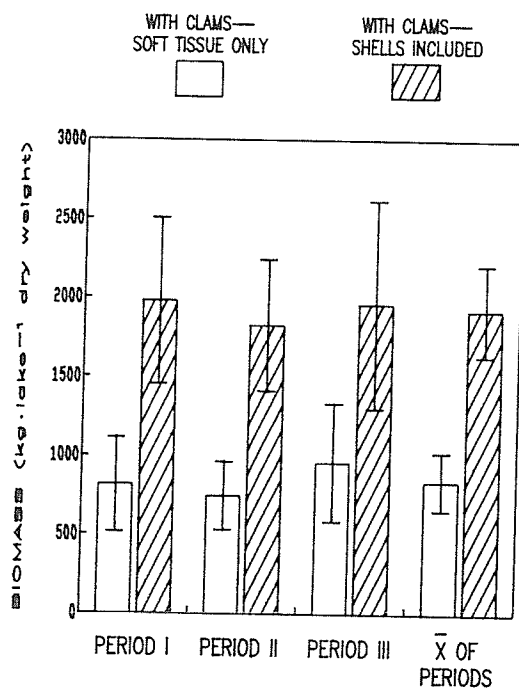


Figure I4. Benthic invertebrates (1985); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

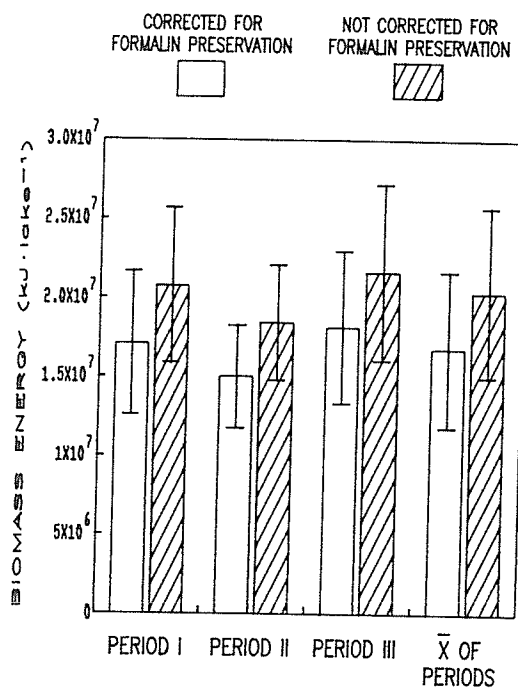
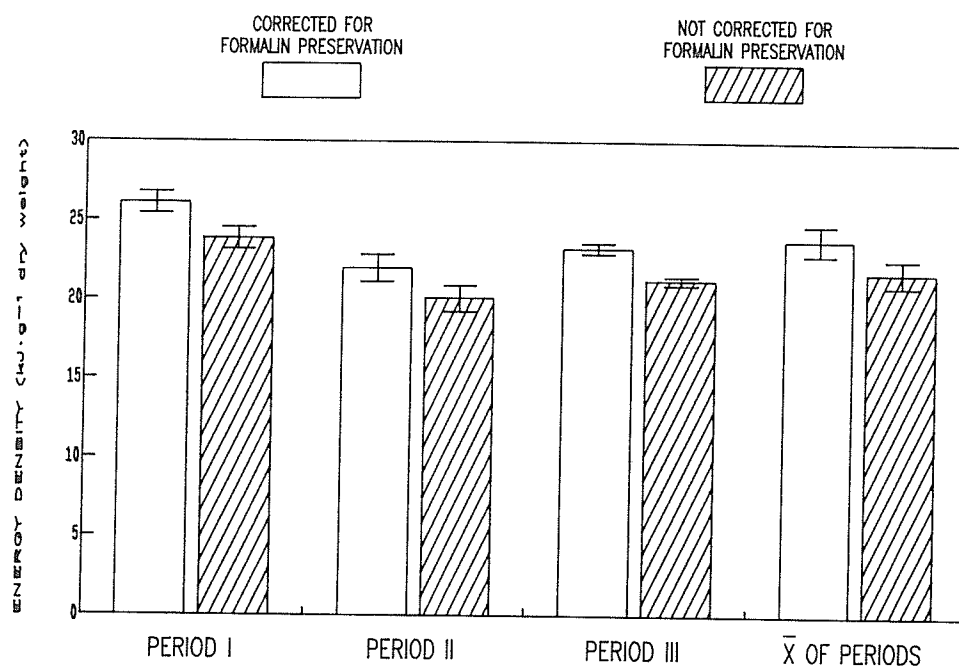
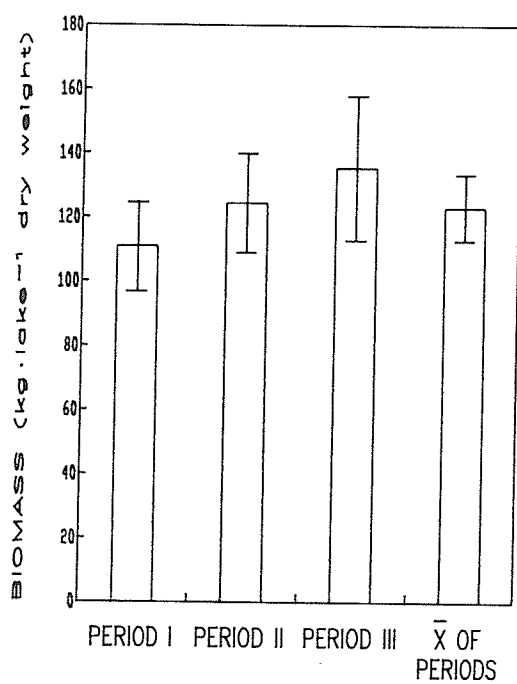


Figure I5. Zooplankton (1985); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

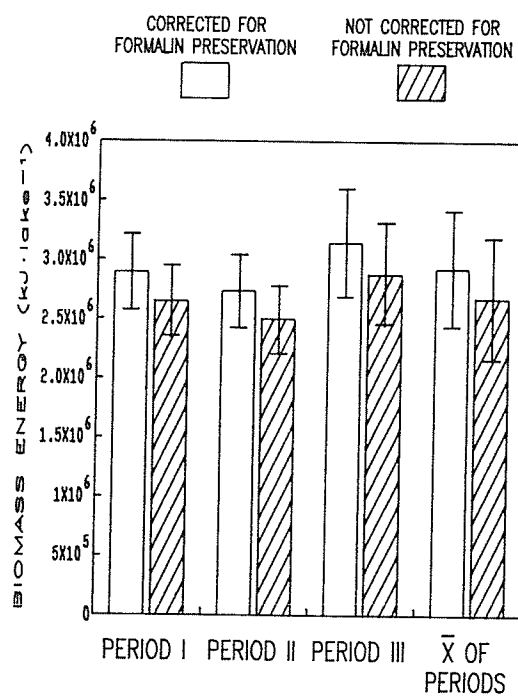
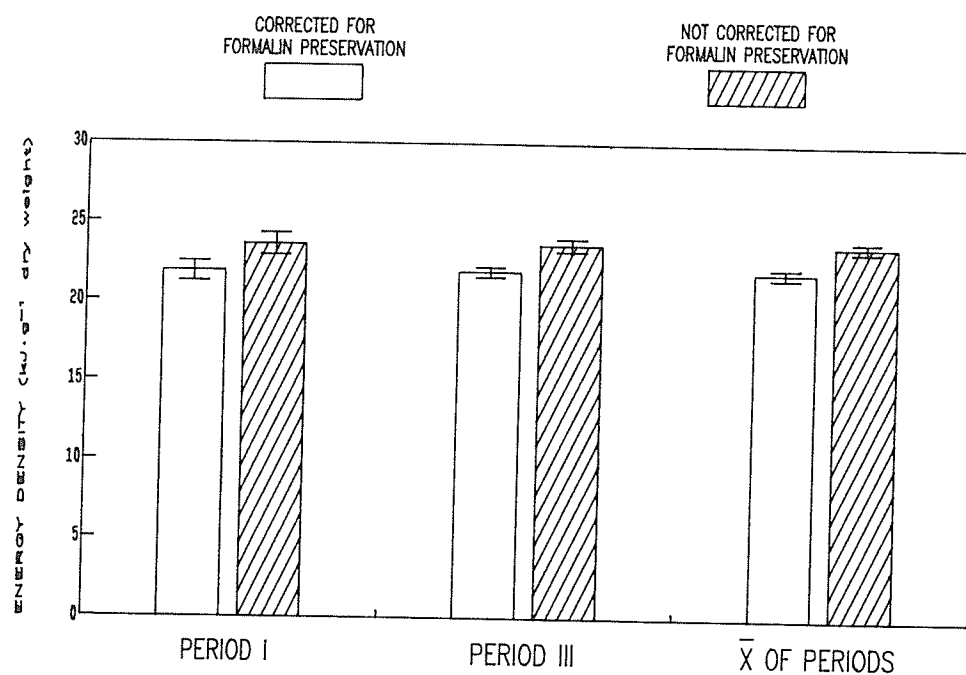
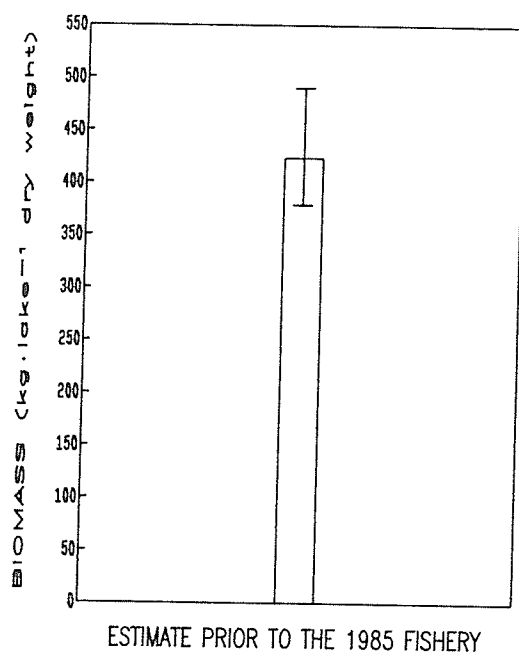


Figure I6. Arctic charr (1985); (A) energy density; (B) biomass; (C) biomass energy. All confidence intervals at the 95% level.

A



B



C

