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Distribution, Ecology, and Postglacial Dispersal of Certain
Crustaceans and Fishes in Eastern North America

by

Michael J. Dadswell, B.Sc.

A thesis

submitted to the Faculty of Graduate Studies
in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

Department of Biology

Carleton University

Ottawa, Ontario.

April, 1973.

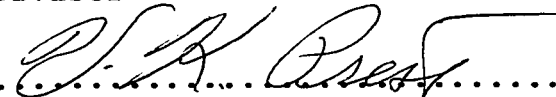
The undersigned hereby recommend to the Faculty of Graduate Studies acceptance of this thesis, submitted by Michael J. Dadswell, B.Sc., in partial fulfilment of the requirements for the degree of Doctor of Philosophy.


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Chairman, Department of Biology


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Supervisor


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External Examiner

Date *April 16/73.*

DEDICATION

I wish to dedicate this work to the late Mr. W. Van Vliet. Bill was a close friend and colleague as well as an exceptional field biologist.

He introduced me to the use of otter trawls from small boats and constructed the trawl that I used throughout my study. Bill died in October, 1968 while scuba diving in Heney Lake, Quebec, during the course of his studies on deepwater sculpins for his doctorate.



N.I.D.

Mysis relicta

X6



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ABSTRACT

One or more of the crustaceans Mysis relicta, Pontoporeia affinis, Gammaracanthus loricatus, Limnocalanus macrurus, Seneccella calanoides, and/or the fish Myoxocephalus quadricornis were found in 245 new localities in eastern North America. One or more of these species are now known from 326 localities east of the 82nd parallel of longitude. Their distributions are restricted to basins in areas formerly occupied by brackish seas or by glacial lakes and their spillways during the retreat of the last ice sheet. Since dispersal of these species seems to have been largely limited to passage through standing bodies of water or to downstream transport, the major factor determining their occurrence in a present-day lake was the elevation of the lake with respect to the upper levels of glacial waters.

Limnocalanus macrurus has the most easterly known range of any of the species in fresh waters of North America. Gammaracanthus loricatus was found only in areas of former marine submergence.

Physicochemical parameters of lakes inside and outside the glacial lake boundaries were similar and cannot be regarded as a reason for the absence of the crustaceans from lakes outside the glacial lake boundaries. However, in lakes containing the crustaceans, maximum depth, temperature, oxygen, total hardness, pH, light penetration, and dissolved organics interact to influence the species composition of the crustacean community. Mysis relicta is the most tolerant to a wide range of factors; Pontoporeia affinis, the least.

Mysis relicta was experimentally determined to tolerate

higher temperatures and greater salinities than Senecella calanoides.

These animals probably originated in brackish arctic seas and have invaded North American fresh waters either by marine inundations or were transported inland by proglacial waters ponded in front of the advancing Labrador Ice Sheet. Postglacial redispersal of the group (except G. loricatus) probably began about 14,500 B.P. from a number of refugia south of the Great Lakes and the animals followed the retreating ice northward in the glacial lake systems. High salinities in the early Champlain Sea acted as a dispersal barrier to some of the crustaceans, limiting their eastward movement in the Ottawa - St. Lawrence Valleys. Gammaracanthus loricatus apparently dispersed from the east via the Atlantic into the St. Lawrence Valley. Except for some minor downstream movement, caused by isostatic readjustment of drainage systems, dispersal in eastern North America ceased about 6,000 B.P. with the termination of the last glacial-lake systems in north central Quebec. The distribution of the group seems to have remained static since then.

Whether these animals, which are often referred to as "glaciomarine relicts," are true relicts in either the Darlingtonian or Ekmanian sense, is discussed. It is proposed that the present distribution of this group can be regarded as positive indication of former glacial lakes; thus the highest glacial lake levels can be mapped with a precision not before possible.

ACKNOWLEDGMENTS

It gives me pleasure to acknowledge the following for their contributions to this study. Messrs. Chris Morry, Don Moxley, Don Rivard, Jim Kelly, and Garry Laver assisted in the field and provided comradeship during the long trips. The late Bill Van Vliet built the otter trawl used throughout this study. Mr. R. J. Mott of the Geological Survey of Canada provided out-board motors and the inflatable rubber boat used when conducting surveys by aircraft. Pilots of Fecteau Aerien, Laurentian Air Services, Brochu Air, Kipawa Air Services, and Lakeland Air Services flew in fair weather and foul. Biologists of the Québec Service de la Faune, Ontario Ministry of Natural Resources, New York Conservation Department, Vermont Department of Fish and Game, and the Maine Department of Inland Fisheries and Game, readily provided information on their respective districts. Mr. W. Traversy of the Inland Waters Branch, Environment Canada, provided for the complete chemical analysis of my water samples. Dr. E. L. Bousfield and Mr. C. H. Douglas of the National Museum of Natural Sciences provided the illustrations of Mysis relicta and Pontoporeia affinis in Fig. 1. Many persons identified or confirmed identifications of captured animals: Dr. A. H. Clarke, Jr. and Rev. H. B. Herrington (molluscs), Dr. E. L. Bousfield (peracaridan crustaceans), Dr. D. E. McAllister and Dr. W. B. Scott (fishes), Dr. D. J. Faber (planktonic crustaceans), and Dr. R. W. Davies (leeches).

I especially thank my thesis supervisors Dr. H. F. Howden and Dr. E. L. Bousfield for their encouragement during this

study and for the stimulating discussions which have influenced many of my ideas. Dr. E. L. Bousfield suggested the topic of this research. Dr. V. K. Prest helped immeasurably in my understanding of the recession of the last ice sheet and the history of the glacial Great Lakes.

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Field equipment was provided by the National Museums of Canada and the Biology Department of Carleton University. Financial support for field work was received from the National Museums of Canada, the Ontario Federation of Anglers and Hunters, The Canadian National Sportsmen's Show, The Canadian Sports Fishing Institute, the Canadian Wildlife Service, the Geological Survey of Canada, and grants-in-aid of [~]Research to Dr. E. L. Bousfield from the National Research Council of Canada. Additional financial support and research facilities were provided by the Biogeographic Unit of Dr. H. F. Howden of Carleton University.

Drs. E. L. Bousfield, H. F. Howden, V. K. Prest, and D. A. Smith critically read the manuscript.

I particularly appreciate the help and understanding of my wife Marilyn, who endured my extended absences and many problems with few complaints.

All mistakes and omissions in this work are mine alone.

TABLE OF CONTENTS

	<u>Page</u>
ABSTRACT	v
ACKNOWLEDGMENTS	vii
GENERAL INTRODUCTION	1
Description of Organisms Studied	3
Biology of Dispersal	9
Taxonomic Positions of North American Populations	11
DISTRIBUTION IN EASTERN NORTH AMERICA	
Introduction	15
Collecting Methods	16
Collecting Results	20
Gatineau Valley Problem	31
<u>Limnocalanus</u> Problem	38
ECOLOGICAL LIMITING FACTORS	
Introduction	42
Methods	43
Comparison Between "Inside" and "Outside" Lakes	45
Major Ecological Limiting Factors	50
Multiplication Effect of Limiting Factors	58
Factors Affecting <u>Mysis relicta</u>	58
Factors Affecting <u>Pontoporeia affinis</u>	62
Factors Affecting <u>Limnocalanus</u> and <u>Senecella</u>	68

	<u>Page</u>
TEMPERATURE AND SALINITY TOLERANCE OF <u>MYSIS RELICTA</u>	
AND <u>SENECELLA CALANOIDES</u>	
Introduction	71
Methods	72
Results and Discussion	74
ORIGIN AND EARLY DISPERSAL	83
POSTGLACIAL DISPERSAL IN EASTERN NORTH AMERICA	94
Refugia	94
Finger Lakes Region	97
Lake Champlain Region	97
Lake Huron - Lake Ontario Region	101
Events in the St. Lawrence Lowland	103
The Champlain Sea Episode	106
Late Glacial Lake Algonquin and Glacial Lake Barlow- Ojibway Events	113
CONCLUSIONS	120
REFERENCES	125
APPENDIX	138

GENERAL INTRODUCTION

The crustaceans Mysis relicta Lovén, Pontoporeia affinis Lindstrom, Gammaracanthus loricatus Sabine, Limnocalanus macrurus Sars, Saduria entomon (L.), and the fish Myoxocephalus quadricornis (L.) are the North American representatives of a group often referred to as "glaciomarine relicts" (Ricker 1959; Johnson 1964). On the basis of their present taxonomic concept these species (Holmquist 1959, 1970) or perhaps species complexes (i.e. Pontoporeia), have a holarctic distribution in brackish portions of arctic seas and in lakes, mainly in the glaciated regions of Eurasia and North America. Senecella calanoides Juday is apparently confined to fresh waters of North America but is often included in this group because it has a similar habitat and distribution (Martin and Chapman 1965).

In view of the wide distribution of this group of animals and their apparent success in fresh water it seems inappropriate to call them "relicts." Mysis, Pontoporeia, Limnocalanus, Senecella, and Myoxocephalus form a distinctive deep-water community (Henson 1966) in lakes throughout most of the North American mainland formerly covered by the Laurentide section of the Wisconsin Ice Sheet. They are the main grouping dealt with in this thesis and for my purposes will be known as the "deepwater community" or simply the "community."

The presence of these animals in lakes of North America was noted as early as 1870 (Smith 1871), but zoogeographical research on them proceeded so slowly that when Ricker (1959)

summarized their North American distribution he could find only 43 localities mentioned in the literature. Recently, knowledge of their distributions has been increased in the Arctic (Johnson 1964; Holmquist 1966) and in Ontario (Martin and Chapman 1965; Hamilton 1971). Martin and Chapman (1965), working in Algonquin Park, Ontario, were the first to determine the precise distributions of these species and relate them to the former extent of glacial lakes.

In North America, the ecology of these species has received greater attention than their zoogeography, but most studies have been confined to animals living in deep, oligotrophic lakes (Larkin 1948; Green 1965; Carter 1969; Brownell 1970) and emphasize only low temperatures and high dissolved oxygen levels as necessary for their survival. On the other hand, it has been shown that these animals can tolerate both high temperatures and low oxygen levels (Juday and Birge 1927; Lasenby 1972) and it is suspected that other factors may influence their survival in a lake (Holmquist 1959).

The present distribution of any organism depends on a number of factors. These include its dispersal mechanisms, dispersal routes open to it in the past, and the present availability of its required habitat. In this study I have attempted to outline the distributions of these species in eastern North America, to determine which ecological factors limit the occurrence of the individual species, and to demonstrate further the relationship between their distribution patterns and the extent of postglacial waters. These exact biological and

zoogeographical data should provide a firm base on which inferences about the past dispersal history of these organisms can be made.

In recent years, fisheries biologists have come to realize the importance of the crustaceans (especially M. relicta) in the food chains of deepwater communities and their usefulness in fisheries management (Cuerrier and Schultz 1951; Dryer et al. 1965; Van Vliet and Qadri 1971; Rawson 1961). For this reason M. relicta has been widely introduced into North American lakes, from which it was originally absent (Sparrow et al. 1964; Linn and Frantz 1965; Schumacher 1969). Consequently, an exact determination of the natural distribution of this deepwater community would be invaluable to future zoogeographic studies. Also, identification of the ecological limiting factors of these organisms should provide fisheries biologists with criteria for selecting lakes into which these animals could be successfully introduced.

Description of Organisms Studied

The animals studied can be divided into two groups; those whose postglacial dispersal in eastern North America was restricted mainly to glacial lakes, and those that apparently dispersed into lakes of eastern North America via postglacial marine inundations. The first group, the "deepwater community", includes the mysid Mysis relicta, the deepwater amphipod Pontoporeia 'affinis', the large, deepwater copepods Limnocalanus macrurus and Senecella calanoides, and the sculpin Myoxocephalus

quadricornis (Figs. 1 and 2). The second group consists of the amphipod Gammaracanthus loricatus, which is known from only one freshwater locality within the study area, and the isopod Saduria entomon, which is unknown in the study area (Fig. 3).

Mysis relicta, L. macrurus, and Myoxocephalus quadricornis have the widest ranges and are found in brackish and fresh waters mostly in the glaciated portions of Eurasia and North America (Fig. 4). The Pontoporeia 'affinis' complex, which may be represented by different species in fresh waters of Eurasia and North America, has nearly as extensive a distribution (Fig. 4). Gammaracanthus loricatus and Saduria entomon are largely confined to arctic, brackish water localities (Lomakina 1952; Segerstråle 1962) and are found in fresh water only in areas of previous marine inundation (Fig. 4). Senecella calanoides is apparently confined to fresh waters of North America (Fig. 4). Although Wilson (1959) stated that Senecella is known from Siberia she did not cite records and I have been unable to locate any primary references to substantiate his claim.

The three deepwater fishes, Cottus ricei, Pungitius pungitius, and Percopsis omiscomaycus (Fig. 2), are included in later discussions on postglacial dispersal because their dispersal seems to have been mainly restricted to glacial lakes (App. II) (Dadswell 1972) and they can be used as subsidiary indicators of ecological conditions of former dispersal routes. They perhaps occupy a comparable zoogeographic position with respect to the "glaciomarine relicts" as the amphipod Pallasea

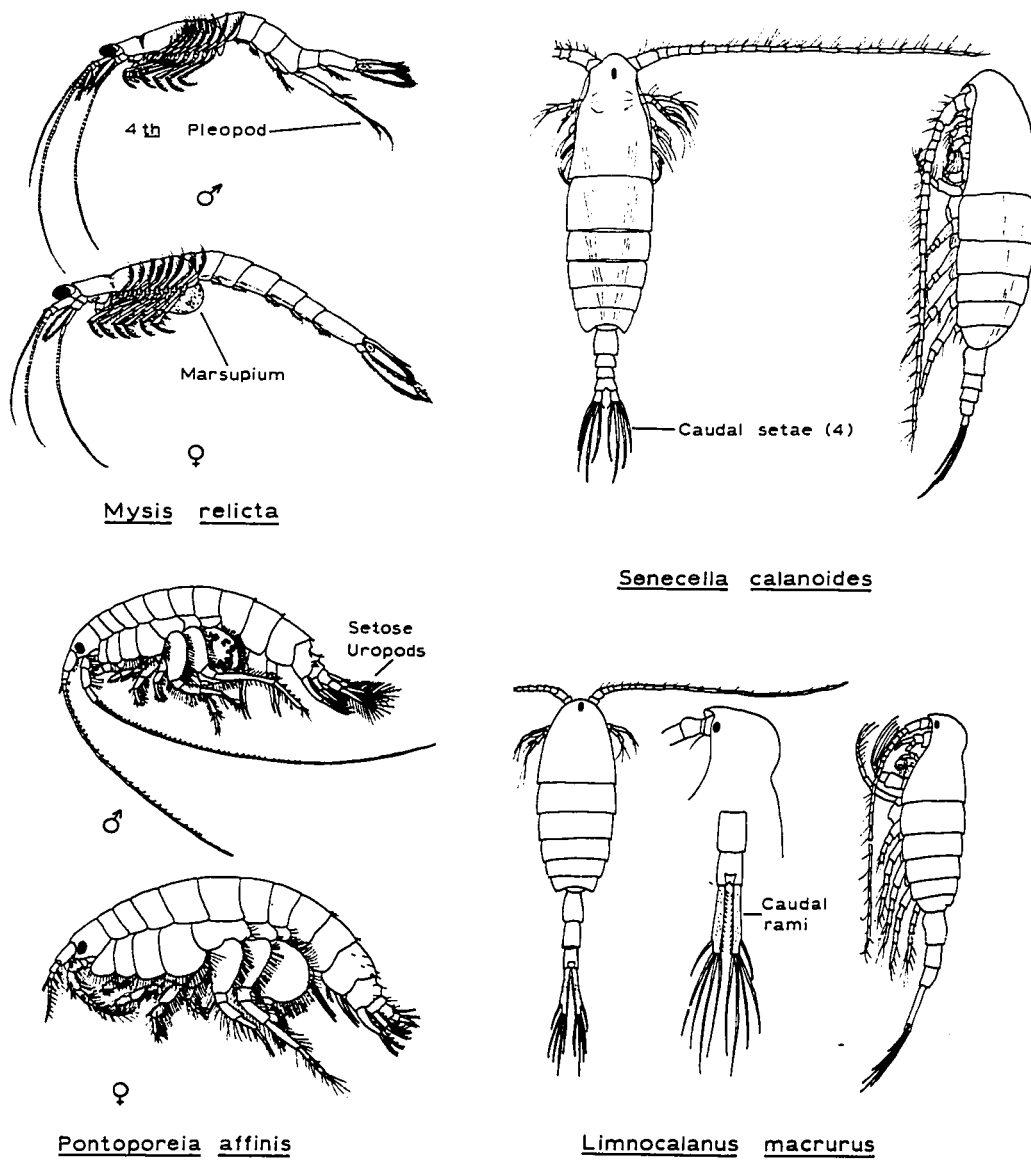
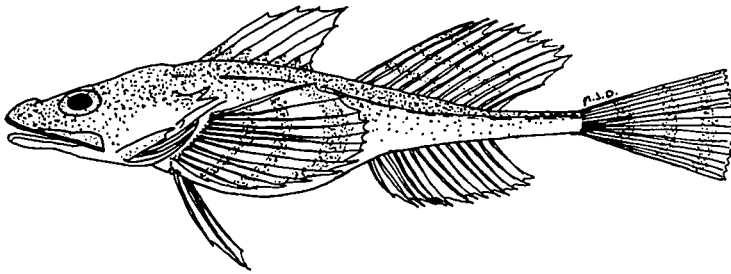
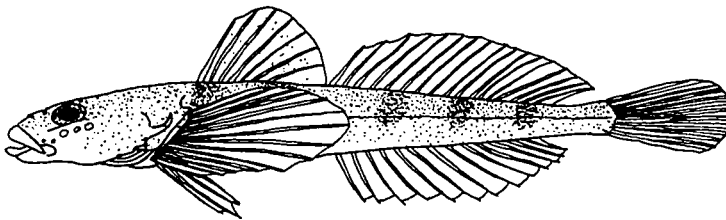


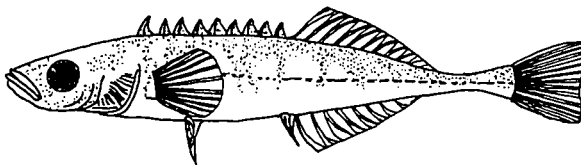
Fig. L. Deepwater crustaceans dispersed mainly by glacial lakes in eastern North America. A. Mysis relicta X3; B. Pontoporeia affinis X5; C. Senecella calanoides X20; D. Limnocalanus macrurus (after Gurney 1923) X20.



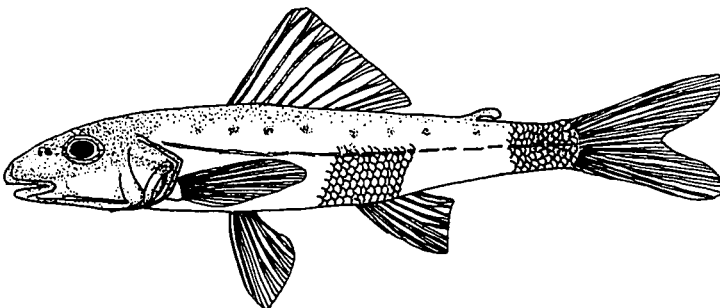
Myoxocephalus quadricornis



Cottus ricei

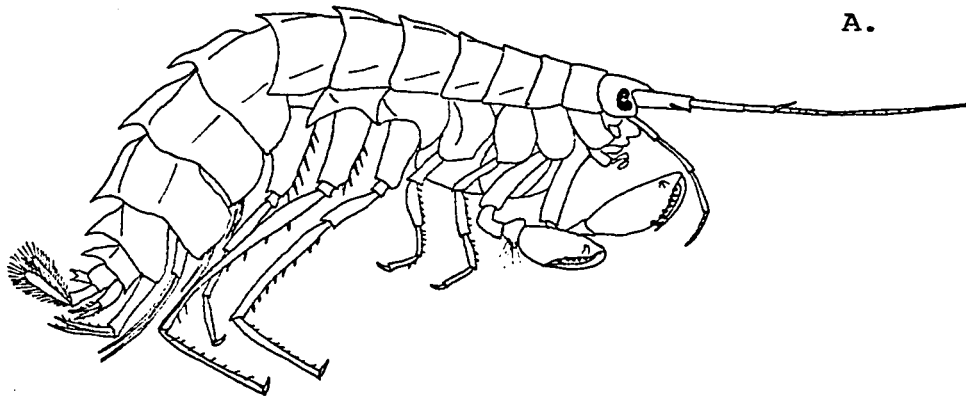


Pungitius pungitius

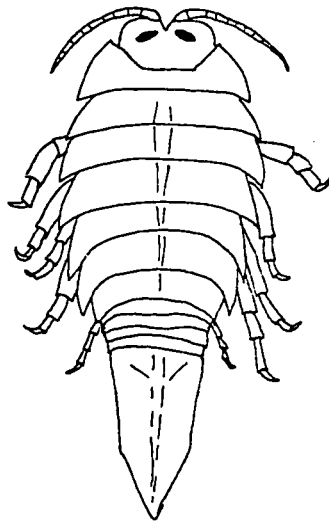


Percopsis omiscomaycus

Fig. 2. The deepwater fishes of eastern North America that were dispersed mainly by glacial lakes. All natural size (after McPhail and Lindsey 1970).



Gammaracanthus loricatus



Saduria entomon

Fig. 3. Crustaceans occurring only in former marine-inundated areas. A. Gammaracanthus loricatus X3; B. Saduria entomon, natural size (both after Segerstråle 1962).

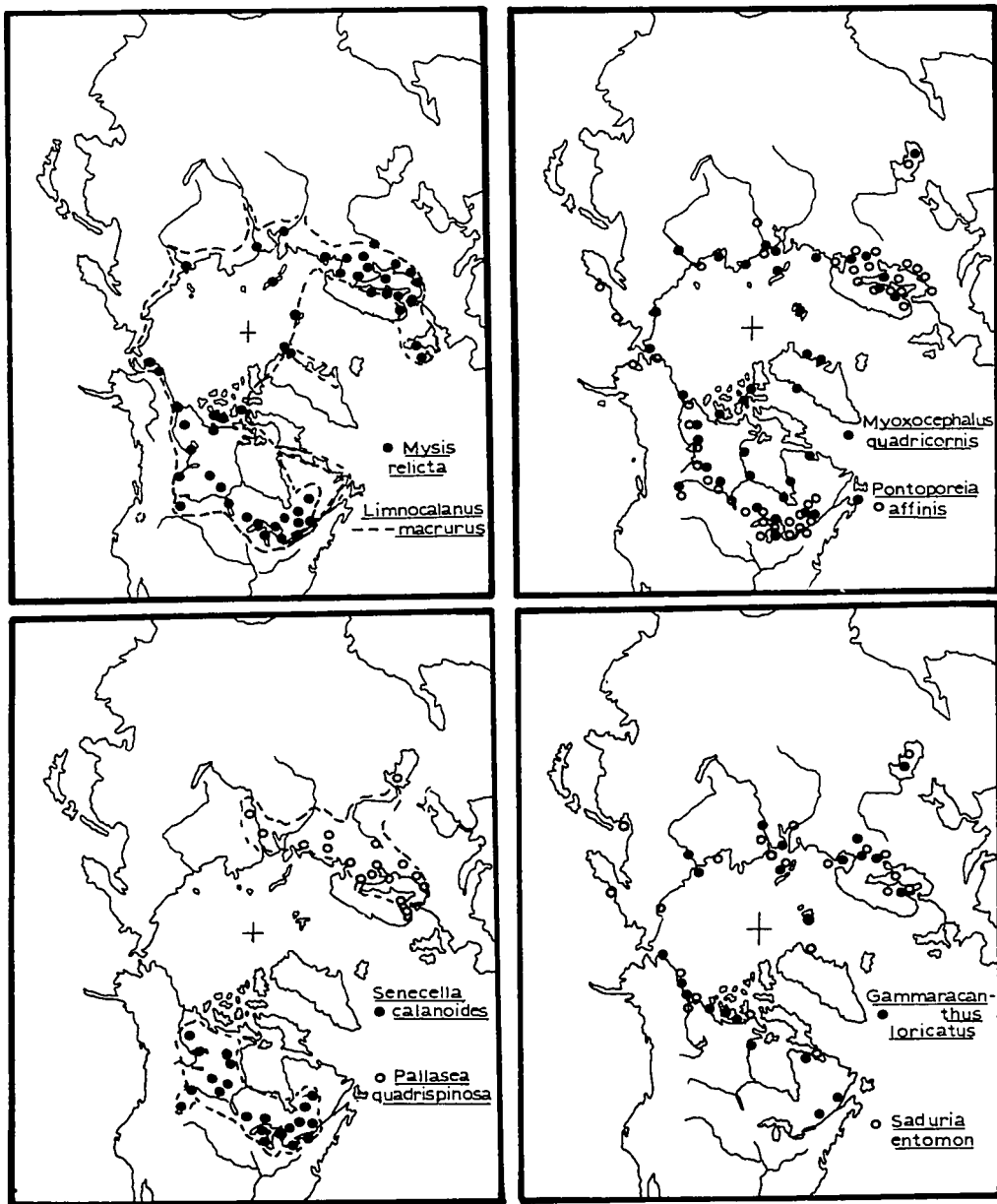


Fig. 4. Distribution of the "glaciomarine relicts" in Eurasia and North America (after Segerstråle 1957; Ricker 1959; Zenkevitch 1963; Johnson 1964; Holmquist 1966). Pallasea quadrispinosa is restricted to fresh waters of Eurasia.

quadrispinosa does in Eurasia (Ekman 1920).

Biology of Dispersal

The biological characteristics of an organism, which govern its possible means of dispersal, are an important consideration when discussing the organism's zoogeography. Certain characteristics of these animals apparently limit them to dispersal primarily through bodies of standing water.

None of the crustaceans have a diapause period during their life cycle. In both Mysis and Pontoporeia, the eggs undergo direct development in a marsupium and are not subject to passive dispersal. Limnocalanus and Senecella shed their eggs in deep water, usually under the ice during winter, and the eggs develop immediately (Roff 1972). It is unlikely that any of the adult crustaceans are resistant enough to desiccation to undergo long-distance, passive aerial dispersal; however, very short-distance wind dispersal may be possible, especially in arctic coastal situations. Strong winds, such as tornadoes, usually occur during the day at these latitudes when these animals are occupying deep water (see below), but this may be the explanation for the slightly different dispersal pattern in Limnocalanus. If passive dispersal has actually occurred to any great extent with these animals one would expect their distribution patterns to show it. They do not.

Usually these animals are light-avoiding and occupy deep water during daylight. Mysis relicta, by vertical migrations, maintains itself at light levels of 10^{-1} lux (Beeton 1960).

This results in a spatial separation of Mysis from most agencies of passive dispersal (i.e. waterfowl, wind), even when surface waters are cold. Pontoporeia is completely benthic and only adult males commonly leave the bottom for more than short periods (McNaught and Hasler 1966). In freshwater, Limnocalanus and Senecella usually remain in the hypolimnion during daylight (Wells 1960; Carter 1969). This light-avoidance tendency, which may be less prevalent in Limnocalanus (MacKay 1924; Grainger 1965), would likely eliminate most possibilities of these animals' coming in contact with agents of passive dispersal, at least in the southern parts of their ranges.

In general these animals swim poorly against currents, especially in fresh water. Mysis is positively rheotactic and can maintain its position against tidal currents in estuaries (Holmquist 1963). However, Summerhayes and Elton (1923) state that M. relicta was unable to swim up the smallest rapids in streams between beach ponds on Spitsbergen Island. More critical evidence was obtained by Dormaar (1970), who showed that M. relicta cannot swim against currents greater than 10 cm/s (1/5 mi/h), and that swimming for even short periods of time in fresh water caused severe osmotic stress to develop in this mysid. Since Limnocalanus and Senecella are planktonic, they probably possess little or no ability to swim against currents (Hutchinson 1967). The marine form of Myoxocephalus quadricornis is known to ascend streams in the Arctic (Johnson 1964) but the lake form has never been

captured in streams. Possibly the deepwater lake form is physiologically different from its marine relative and does not venture from its deepwater habitat. The other deepwater fishes (C. ricei, etc.), which also occur in cool streams, have distribution patterns that clearly indicate upstream dispersal has occurred (Dadswell 1972). Regardless, the now well known distribution pattern of these animals in eastern North America suggests that active upstream movements have not played a major role in their dispersal.

Taxonomic Positions of North American Populations

Research on "glaciomarine relicts" began in 1860 when Lovén described some animals from the deep waters of Swedish lakes and noted that they were the same as, or closely related to, species living in the nearby Baltic Sea. Since then, the nomenclature and the concept of the individual species involved has varied with the views of each author.

Mysis relicta was described by Lovén as separate from the marine M. oculata, but for many years most authors considered it to be only a subspecies of oculata (Ekman 1920; Pennak 1953). Holmquist (1959) revised the genus Mysis and upheld relicta. She also compared North American and Eurasian freshwater populations and concluded they were all the same species, M. relicta (in agreement with Tattersal 1951). In fact, Holmquist remarks, and she is supported by Fürst and Nyman (1969), that relicta is quite phenotypically conservative for an animal with so many widely- and long-isolated populations.

The freshwater Pontoporeia of North America was originally described as P. hoyi. Segerstråle (1937) revised the genus and concluded that one species, P. affinis, occurred in brackish and freshwater localities of Eurasia and North America. Bousfield (personal communication) now believes the North American freshwater populations to be a different species from at least the Baltic affinis. At this time, however, the species concepts are not yet clear, and until they become so, it is better to maintain, with reservation, P. 'affinis' for the eastern North American freshwater populations.

Gammaracanthus has alternately been considered as two species (lacustris in fresh water, loricatus in salt water) or as just one species, loricatus in both salt- and fresh-water. At present the two-species concept is accepted by most authors even though an apparently continuous character cline links the fresh- and salt-water populations (Lomakina 1952; Johnson 1964). The single specimen that I captured from fresh water in eastern North America (e.g. Heart Lake, No. 287) conforms to Lomakina's (1952) description of the estuarine form G. loricatus aestuariorum (Gnathopod I/II ratio of 0.92). The Heart Lake specimen differed somewhat from the typical saltwater G. loricatus from the Saguenay estuary, but since its characters were within the range of loricatus as given by Lomakina, and since it was an immature animal, I have referred it to G. loricatus.

Ekman (1920) and Gurney (1933) considered Limnocalanus in freshwater to be a subspecies of the marine L. grimaldii.

Lindquist (1961) thought the freshwater populations of Eurasia and North America were L. macrurus, a distinct species, although there was a continuous character cline linking the freshwater macrurus and the marine grimaldii. Recently, Holmquist (1970) revised the genus and concluded that only one species, L. macrurus, occurs in salt- and fresh-waters of Eurasia and North America. Whichever situation is in fact true, macrurus is the senior name (Holmquist 1970).

Senecella calanoides is very distinct and has had a stable taxonomic history.

Myoxocephalus quadricornis is considered by most authors to be the same species in salt and fresh waters of Eurasia and North America (Segerstråle 1962; McPhail and Lindsey 1970). McAllister (1959) distinguished the North American freshwater animals as thompsonii on the basis of the loss of tubercles and body plates, and smaller adult size of the freshwater forms. Intermediate forms, however, exist in arctic lakes with a short history of separation from the sea (McPhail and Lindsey 1970), and subfossils in Scandinavia indicate that populations alternately lost and regained bony structures in response to changing salinities in the postglacial Baltic Sea (Segerstråle 1957). It seems reasonable, therefore, to maintain Myoxocephalus quadricornis for the North American freshwater populations until this problem has been resolved.

Comparison among the freshwater populations of M. relictus, L. macrurus, S. calanoides, and Myoxocephalus quadricornis from eastern North America revealed little morphological

variation among themselves or from their accepted descriptions. Pontoporeia 'affinis,' however, was morphologically quite variable. Populations of both Mysis and Pontoporeia differed in adult size depending on the ecological favorableness of the lake in which they were living. In general the adults were smaller in less favorable localities. It is well known that physicochemical characteristics can affect the growth of freshwater organisms (Jewell 1935; Hutchinson 1967).

Zoogeographical and ecological studies demand good systematics since closely related species may differ markedly in various aspects of their biology, and confusion of one species with another can lead to erroneous conclusions. In this case, though, what may prove to be a series of species complexes, zoogeographically appears to behave quite similarly since they are restricted in their dispersal in the same way throughout the Holarctic. Therefore, in view of the prevailing taxonomic confusion surrounding these animals, and because there is little knowledge concerning their environmentally induced morphological changes, it seems best at this time to maintain the current nomenclatorial usage (with reservation in the case of P. 'affinis') when referring to the populations of eastern North America.

DISTRIBUTION IN EASTERN NORTH AMERICA

Introduction

The importance of former glacial lakes and marine inundations to the dispersal of aquatic organisms during the retreat of the last ice sheet has been stressed by numerous authors. Dymond (1939) related the presence of landlocked smelt and arctic char in lakes of the Ottawa Valley to the intrusion of the Champlain Sea into that area. Many authors have attributed the presence of the goldeye (Hiodon alosoides) in northern Ontario and Quebec to the connection that existed between glacial Lakes Agassiz and Barlow-Ojibway (Radforth 1944; McPhail and Lindsey 1970). Turvey (1968) related the distribution of Diaptomus reighardi (Copepoda) in Ontario to the known extent of glacial lakes. He found D. reighardi in 23 of the 119 lakes he examined that were inside the glacial lake boundaries, but only in two of 107 localities outside the boundaries. Dadswell (1972) showed that the distribution of four species of deepwater fishes in eastern North America was closely associated with the occurrence of glacial lakes. Ricker (1959) suggested that the occurrence of Mysis relicta and Pontoporeia affinis in North America was related to former glacial lake coverage. Martin and Chapman (1965) demonstrated the exact relationship between the former extent of glacial Lake Algonquin and the present distribution pattern of the "glaciomarine relicts." Ekman (1920) and Segerstråle (1957) have demonstrated a similar relationship between the distribution of the "relicts" and the extent of former glacial

waters in Scandinavia.

Collecting Methods

The wide study area (82°W - 57°W , 53°N - 41°N) (Fig. 5) was chosen to provide maximum knowledge of the "glaciomarine relict" distribution in relation to a number of glacial lakes and marine inundations. Figure 5 shows the maximum extent of all glacial waters formed during retreat of the last ice sheet, and with some modifications are basically those of Prest et al. (1968).

Field work was carried out between May and December over a 4-year period (1969-1972). Each region was surveyed beforehand using 1:125,000 or 1:250,000 topographic maps, and study lakes were selected according to their geographic situations and elevations with respect to former glacial lakes and marine shorelines, depth (if known), and accessibility. In areas where glacial-lake and marine shorelines were poorly known large numbers of lakes were surveyed to delimit the precise upper elevational limit of the deepwater community.

The main sampling gear was a small otter trawl, 2.5 m across the footrope and 5.5 m long (Fig. 6). Mesh size was 38 mm throughout, with an inner 2-m bag of 3-mm mesh in the cod-end. The trawl was towed along the bottom with a ratio of tow rope to depth of 3:1, at speeds from $\frac{1}{2}$ -3 kph. This trawl was especially effective in collecting the larger benthic organisms (i.e. Mysis, Pontoporeia, fish). Trawling was done from a small boat (14 ft) propelled by a 9.5 HP outboard motor. In lakes accessible only by airplane a 12-ft

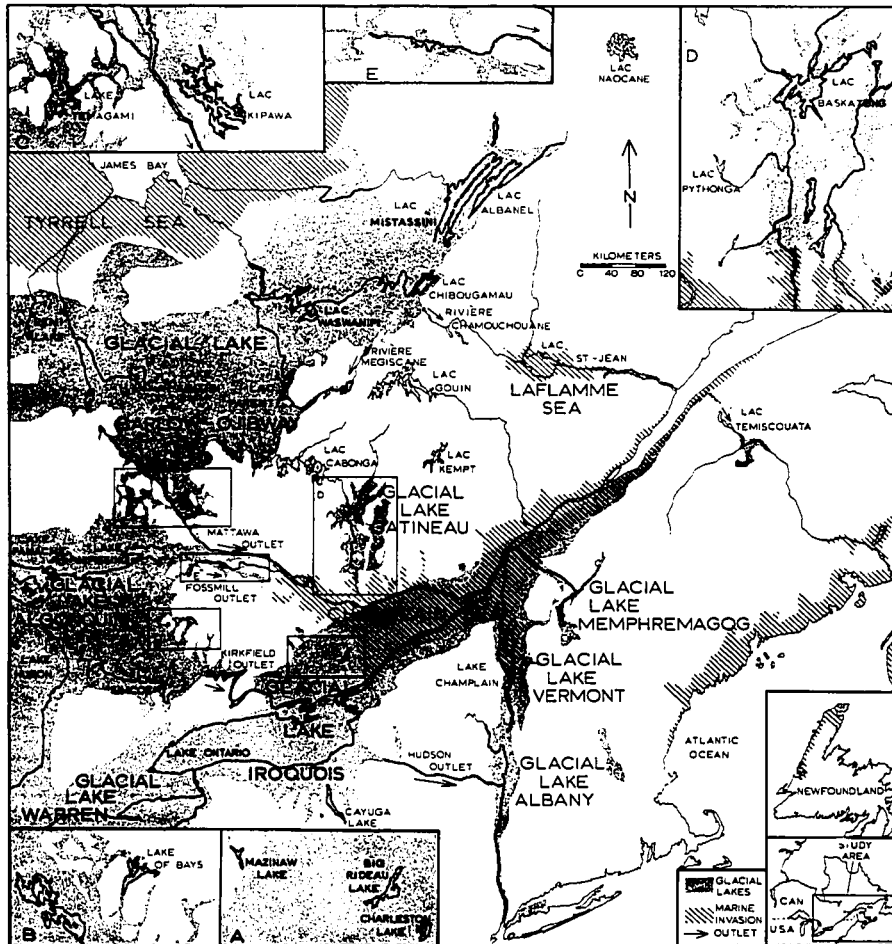


Fig. 5. The study area in eastern North America showing maximum extents of late Wisconsin and Recent glacial lakes and marine inundations (adapted from Prest *et al.* 1968). Glacial Lakes Vermont and Iroquois joined to occupy the St. Lawrence Lowland just prior to the Champlain Sea invasion. The outline of glacial Lake Gatineau was estimated from hypothetical rebound curves (see Figs. 14 and 15). Latitudes of study area: 53°N - 41°N ; Longitudes 82°W - 57°W .

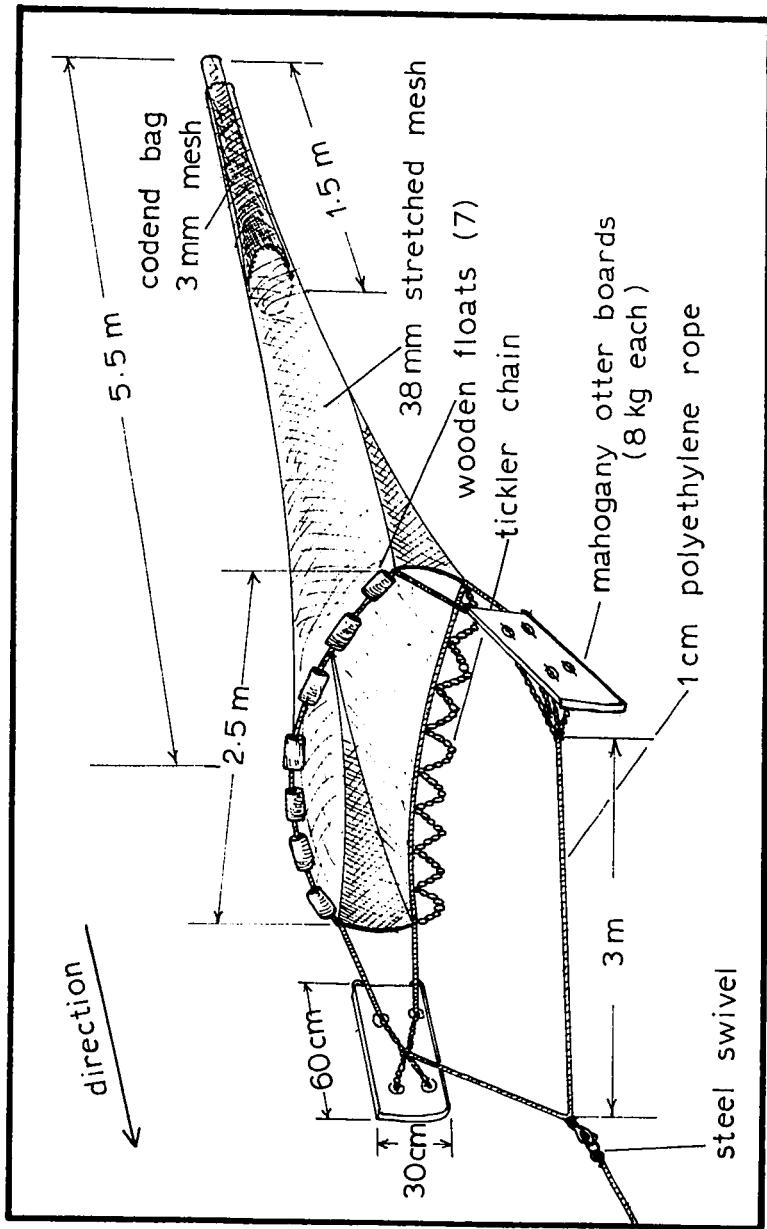


Fig. 6. Small otter trawl used to collect *Mysis*, *Pontoporeia*, and the fishes. Netting is made of nylon. Trawl was towed with a ratio of tow rope to depth of 3:1.

inflatable rubber boat capable of handling the 9.5 HP outboard motor was used.

The sampling procedure in each lake was standardized as follows. Vertical temperature and oxygen profiles were taken from the deepest part of the lake, and from these the best trawling depth for the capture of the crustaceans was selected. Two slow-speed tows of 5-7 min duration were then made at the selected depth, usually 20-50 m. If the crustaceans were present in the lake they were usually captured in the first tow. All trawling was done during daylight.

Limnocalanus and Senecella were collected with a simple plankton net (No. 6 mesh, mouth diam 32 cm), using moderately fast (1 m/s) vertical hauls. At least two hauls were taken in the deepest part of each lake, one from just above the bottom, the second after the net was allowed to settle into the mud for a few seconds. The latter haul often captured Pontoporeia and sometimes was the only way to take Senecella.

If no Pontoporeia were collected with the plankton net or the trawl, two grabs were made with an ekman dredge (23 x 23 x 23) in depths of 15-20 m.

Six hundred and twenty-nine lakes were sampled, 614 of these with the otter trawl. The additional 15 lakes were sampled with the plankton net only, after initial work had indicated that Limnocalanus alone occurred in the area. Usually a lake could be sampled in 2-3 h and normally two lakes were sampled per day, or as many as seven on days when aircraft were used.

Benthic crustaceans were preserved immediately after

capture in 10% formalin and transferred to 70% ethanol within 24 h. Fish were preserved in 10% formalin, and plankton samples in 5% formalin. Sorting and identification of material were usually done the evening of collection. Organisms other than the crustaceans were referred to specialists for identification.

Collecting Results

One or more of the "glaciomarine relicts" were found in 245 new localities. They are now known from 326 localities east of the 82nd parallel of longitude in North America (Fig. 7, Table 1).

The distribution of these animals is closely related to the extent of known postglacial waters (Fig. 7). They are found in 324 (91%) of the 355 lakes considered to be within the glacial lake or marine boundaries. They were found in only two localities that may prove to be outside the boundaries (Fig. 7: Weslemkoon, No. 161; Temiscouata, No. 302). Both of these lakes contain only Limnocalanus.

Mysis relicta was captured most often and is now known from 263 localities within the study area (Fig. 8A). L. macrurus is known from 142 localities (Fig. 8B), P. affinis from 151 localities and G. loricatus from one freshwater and one saltwater locality (Fig. 9A), S. calanoides from 143 localities and Myoxocephalus quadricornis from one saltwater and 10 freshwater localities (Fig. 9B). The record of Gammaracanthus from Heart Lake, Quebec (Fig. 7: No. 287) is the first

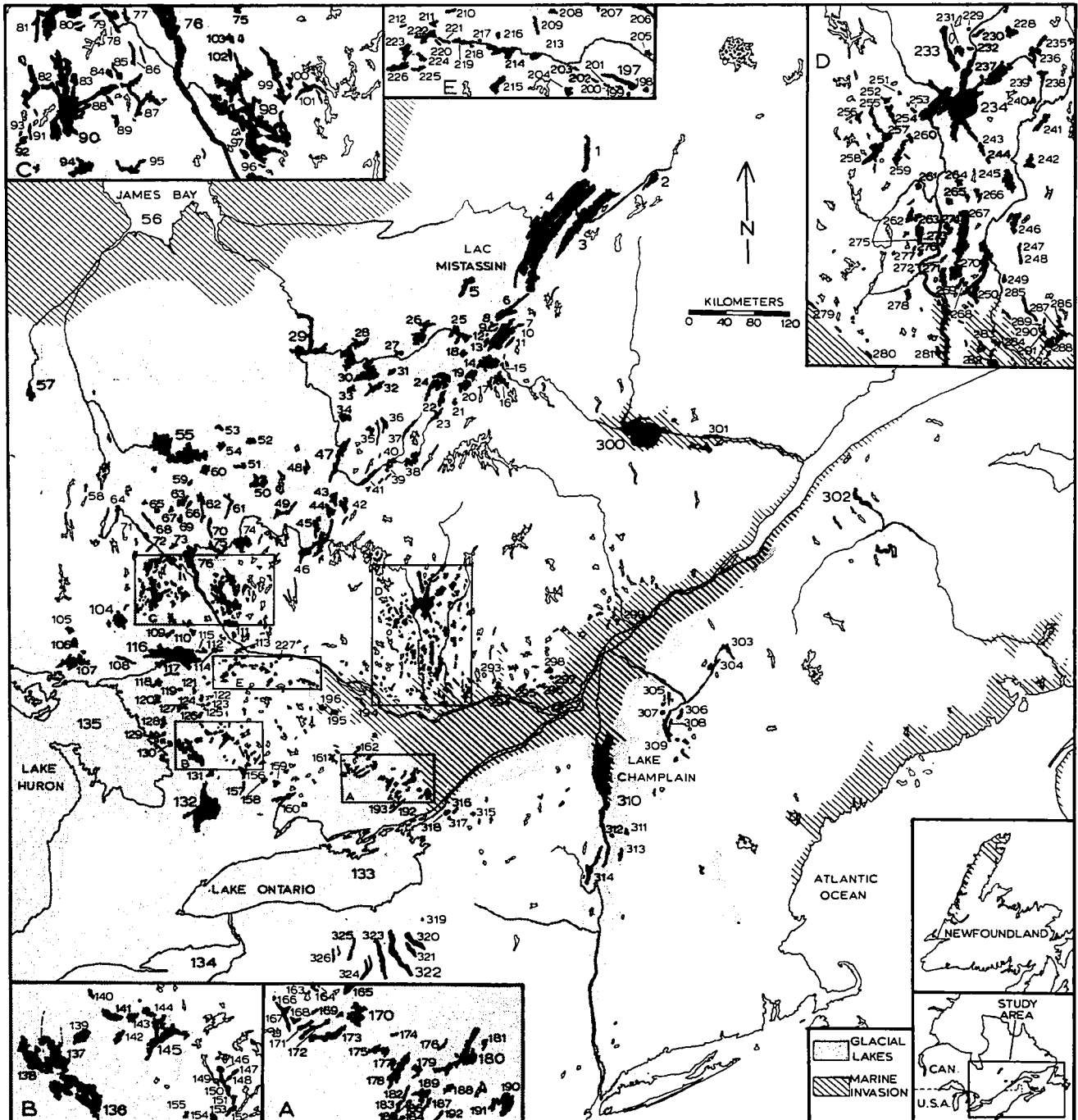


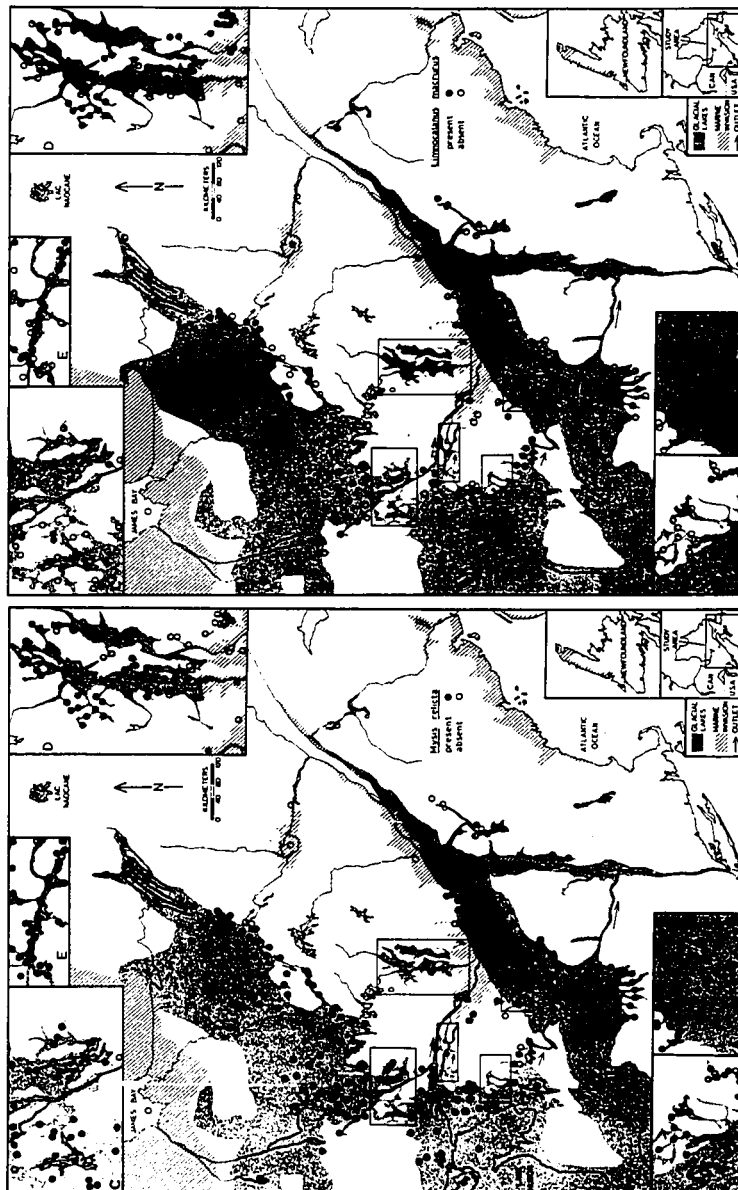
Fig. 7. Localities (solid lakes and numbers) in which one or more species of the deepwater community have been found. Numbers refer to localities listed in Table 1. Open lakes are ecologically acceptable lakes that lack the community.

Table 1. (cont.)

Localities in which one or more of the six glacial-marine relicts were found. Number of locality indicates position of record in Fig. 7. Plus sign (+) indicates presence of species. Abbreviations: z_m , maximum depth (meters); TH, total hardness (ppm); SDV, secchi disk visibility (meters). Previously published records for the Algonquin Park area are from Martin and Chapman (1965); for Stony Lake from Lasenby (1972); for the Finger Lakes from Birse and Juday (1921); for the Great Lakes from Ricker (1959) and Davis (1966) and for Lake Nipissing, Langford (1938). Unless otherwise specified all localities are lakes.

No.	Locality	z_m	TH	SDV	<u>Mysis</u> <u>relicta</u>	<u>Pontoporeia</u> <u>affinis</u>	<u>Limnocalanus</u> <u>macrurus</u>	<u>Senecella</u> <u>calanoides</u>	No.	Locality	z_m	TH	SDV	<u>Mysis</u> <u>relicta</u>	<u>Pontoporeia</u> <u>affinis</u>	<u>Limnocalanus</u> <u>macrurus</u>	<u>Senecella</u> <u>calanoides</u>
171.	Mississaugon	26	106	6.6	+	+	-	-	249.	O'Neil	37	40	5.7	-	-	+	-
172.	Kasvakamak	24	55	6.3	+	+	-	+	250.	Poisson Blanc	75	30	7.8	-	-	+	-
173.	Clarendon	21	35	4.1	+	+	+	-	251.	Leamy	28	16	2.1	+	-	-	+
174.	Silver	25	154	4.2	-	-	+	-	252.	Serpant	24	17	3.3	+	-	+	-
175.	Sharbot	34	125	4.1	+	+	-	-	253.	Quinn	28	15	3.8	+	-	-	-
176.	Pike	42	75	4.1	+	+	-	-	254.	de la Voille	28	18	4.2	+	-	+	+
177.	Croze	33	70	4.5	+	+	-	-	255.	Tomasine	28	10	4.0	+	-	+	+
178.	Bohs	25	110	5.1	+	+	-	-	256.	Savary	55	8	5.1	+	-	+	-
179.	Wolfe	28	130	3.9	-	+	+	+	257.	Rond	29	18	4.1	+	-	-	-
180.	Big Rideau	108	100	4.5	+	+	+	+	258.	Désert	42	20	5.4	+	-	+	+
181.	Otter	34	110	3.3	-	+	-	-	259.	Bras Coupé	49	30	5.7	+	-	+	+
182.	Canoe	42	90	6.0	+	+	+	-	260.	Lytton	30	25	6.5	+	-	+	-
183.	Desert	68	110	5.1	+	+	+	-	261.	Pocknock	36	35	5.7	+	+	-	+
184.	Knowlton	33	130	4.3	+	+	+	-	262.	Grand Cédres	37	70	6.0	+	+	-	+
185.	Birch	36	85	5.5	+	+	+	-	263.	Petit Cédres	37	75	6.3	+	+	-	+
186.	Clear	57	35	8.4	+	+	-	-	264.	Murray	24	45	2.8	+	+	-	+
187.	Buck	39	90	5.1	+	+	+	-	265.	à l'Achigan	25	62	6.0	+	+	-	-
188.	Indian	29	110	4.3	+	+	+	-	266.	Kensington	39	68	6.3	+	+	-	-
189.	Devil	40	103	5.4	+	+	+	-	267.	Thirty-one Mile	33	72	6.7	+	+	-	+
190.	Charleston (BW)	44	130	3.0	+	+	+	-	268.	Vert	96	95	12.2	-	-	-	+
	(RB)	92	130	5.7	+	+	+	+	269.	Bangall	43	78	7.8	-	-	-	+
191.	Red Horse	39	135	4.2	+	+	-	-	270.	Pemichangan (S)	35	85	6.4	+	+	-	+
192.	Loughborough	34	155	4.8	+	+	-	-		(D)	54	85	7.9	+	+	-	+
193.	Sydenham	33	140	3.1	-	+	-	-	271.	Honey *	32	75	4.9	+	+	-	+
194.	Muskat	56	100	1.5	+	+	-	-	272.	Bitobi	29	35	3.9	+	+	-	+
195.	Golden	25	45	4.2	+	+	-	+	273.	Cameron	24	45	3.8	+	+	-	+
196.	Round	44	34	4.5	+	+	-	-	274.	Roddick *	45	80	7.3	+	+	-	+
197.	Grand	38	34	4.5	+	-	-	+	275.	Blue Sea	59	90	6.0	+	+	-	+
198.	St. Andrews #	24	26	4.0	+	+	+	+	276.	Paquin	48	95	10.0	+	+	-	-
199.	Guthrie #	33	33	3.3	+	+	+	+	277.	Profond	33	55	7.8	-	-	-	-
200.	Little Carcajou	48	30	3.8	-	+	+	+	278.	Danford	34	86	6.3	+	+	-	-
201.	Carcajou #	43	43	3.3	+	-	-	-	279.	Gruice	37	55	5.6	+	+	-	-
202.	Greenleaf #	72	72	7.2	+	-	-	+	280.	Thorne	29	60	6.0	-	-	-	-
203.	Eustache #	100	100	10.0	+	+	-	-	281.	Johnston	34	70	3.3	-	+	-	-
204.	White Partridge	45	25	4.5	+	+	-	-	282.	MacGregor	43	62	5.1	-	+	-	-
205.	Cartier #	21	34	3.0	-	+	-	-	283.	McFee	48	35	8.7	-	+	-	-
206.	Ottawa River	150	35	4.3	+	-	+	+	284.	Dodds	42	26	8.1	-	+	-	-
207.	McSourley #	33	33	3.3	+	-	-	-	285.	Echo	60	35	9.6	-	-	-	-
208.	Waterloo #	28	20	3.9	+	-	-	-	286.	St. Sixte	45	35	6.0	-	-	-	-
209.	Wendigo #	28	20	4.2	+	-	-	-	287.	Heart (GL) ^c	41	45	5.7	-	-	-	-
210.	Papineau #	24	24	2.4	+	-	-	-	288.	Britannique	60	35	6.6	-	-	-	-
211.	Lauder #	35	35	3.5	+	-	-	+	289.	Lady	45	35	9.3	-	-	-	-
212.	Guilmette #	33	33	3.3	+	-	-	+	290.	Hawk	39	35	8.7	-	-	-	-
213.	Radiant #	36	34	3.5	+	-	-	+	291.	Gull	39	51	9.6	-	-	-	-
214.	Cedar #	58	34	4.0	+	-	-	+	292.	la Blanche	14	35	2.7	-	-	-	-
215.	Hogan #	29	29	2.9	+	-	-	+	293.	Papineau	81	25	10.7	-	-	-	-
216.	Gilmour #	25	25	2.5	+	-	-	-	294.	Whitfish	16	34	3.6	-	-	-	-
217.	Laurie #	28	28	2.8	+	-	-	-	295.	Louisa	33	20	6.0	+	+	-	-
218.	Gouinlock #	46	46	4.6	+	-	-	-	296.	Barron	31	16	3.0	+	+	-	-
219.	Cauchon #	43	43	4.3	+	-	-	-	297.	Connelly	19	24	3.9	+	+	-	-
220.	Whitebirch #	28	28	2.8	+	-	-	-	298.	l'Achigan	21	25	4.8	+	+	-	-
221.	Mink #	43	43	4.3	+	+	-	+	299.	des Piles	66	14	10.2	-	-	-	-
222.	Kiohkokwi #	39	39	3.9	+	+	-	+	300.	St. Jean	68	15	2.7	-	-	-	-
223.	Wilkes #	32	32	3.2	+	+	-	+	301.	Sagueny Estuary	60	-	3.0	-	-	-	-
224.	Threemile #	37	37	3.7	+	+	-	+		(GL)	66	55	2.9	-	-	-	-
225.	Biggar #	31	31	3.1	+	+	-	+	302.	Temiscouata	66	55	2.9	-	-	-	-
226.	Waskigonog #	32	32	3.2	+	-	-	-	303.	St. François	37	43	2.1	-	-	-	-
227.	Big Gibson #	38	38	3.8	+	-	-	-	304.	Aylmer	30	36	2.0	-	-	-	-
228.	Hottawissi	36	20	4.2	+	+	-	+	305.	Grand Brompton	44	30	3.9	+	+	-	-
229.	Kettle	57	10	6.9	+	+	-	+	306.	Massiwiippi	82	102	4.5	+	+	-	-
230.	Crevier	30	35	4.5	+	+	-	-	307.	Orford	47	55	8.1	-	-	-	-
231.	Maguerite	48	15	7.5	+	+	-	+	308.	Loversing	25	38	3.6	-	-	-	-
232.	Cobble	21	15	3.5	-	+	-	+	309.	Memphremagog	117	70	5.7	+	+	-	-
233.	Petawaga	44	10	5.1	+	+	-	+	310.	Champlain	120	45	3.9	+	+	-	-
234.	Haukatong	82	10	3.6	+	+	-	+	311.	Dunmore	30	40	3.9	+	-	-	-
235.	Chopin	30	11	2.9	+	+	-	+	312.	Sunset	36	35	9.0	-	-	-	-
236.	Polonais	40	15	3.6	+	-	-	+	313.	St. Catherine	21	55	5.4	+	+	-	-
237.	Piscatosine	50	20	4.2	+	+	-	+	314.	George	56	42	9.0	+	+	-	-
238.	Tapani	24	23	6.7	-	-	-	-	315.	Sylvia	42	130	8.4	+	+	-	-
239.	Chinard	57	16	6.9	-	-	-	-	316.	of the Woods	25	45	4.2	+	+	-	-
240.	Gravel	36	25	3.9	-	-	-	-	317.	Sixberry	27	40	2.8	+	+	-	-
241.	Moreau	33	40	4.6	-	-	-	-	318.	Millsite	22	40	5.7	+	+	-	-
242.	des Ecorces	35	35	3.5	-	-	-	-	319.	Green #	59	150	9.0	+	+	-	-
243.	Pope	30	30	4.6	-	-	-	-	320.	Skaneateles #	90	110	8.4	+	+	-	-
244.	Gatineau	30	38	6.9	-	-	-	-	321.	Owasco #	48	110	4.3	+	+	-	-
245.	des Iles *	39	45	3.9	-	-	-	-	322.	Cayuga #	130	104	6.3	+	+	-	-
246.	du Cerf	72	35	5.4	-	-	-	-	323.	Seneca #	180	110	9.3	+	+	-	-
247.	Corbeau	57	35	4.2	-	-	-	-	324.	Kouka	48	110	4.5	+	+	-	-
248.	Serpant	60	45	4.7	-	-	-	-	325.	Canadaigua	75	120	4.5	+	+	-	-
									326.	Hemlock	27	95	3.0	+	-	-	-

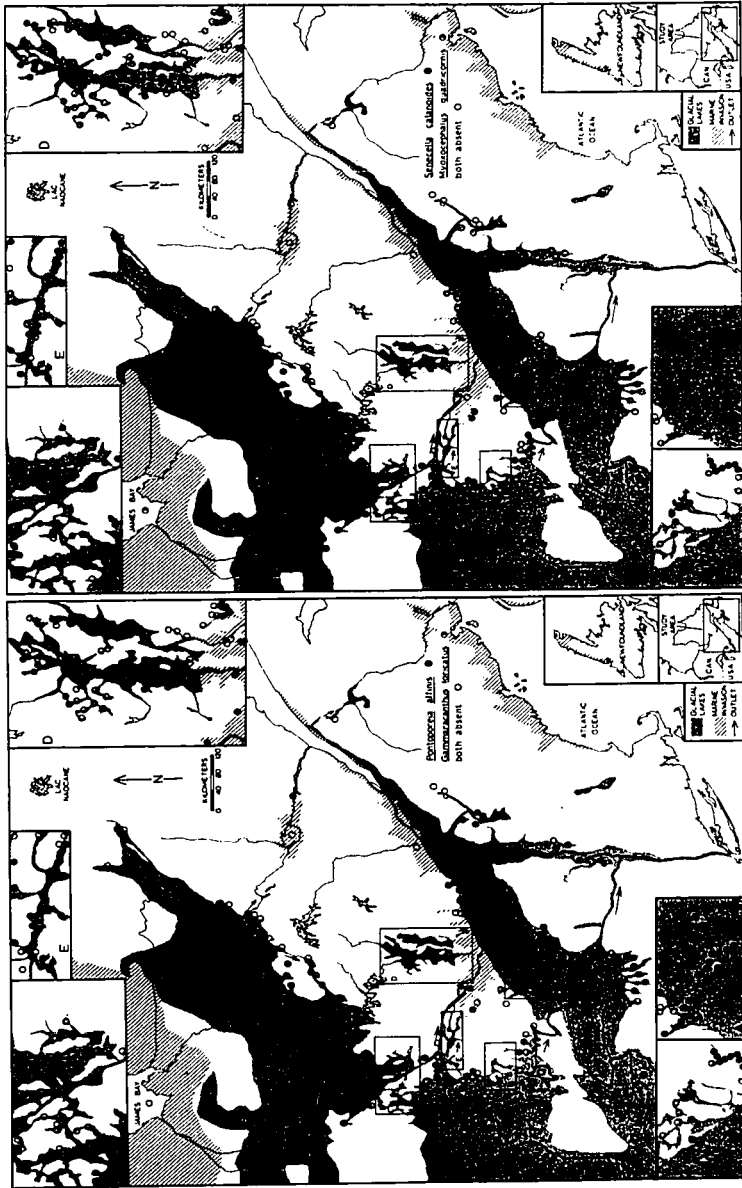
a * indicates *Myoxocephalus quadricornis* found in locality.
 b # indicates locality not sampled by the author, records from literature.
 c (GL) indicates *Gammaracanthus loricatus* found in locality.



A.

B.

Fig. 8. A. Distribution of *Mysis relicta* in eastern North America.
B. Distribution of *Limnocalanus macrurus* in eastern North America.



A.

B.

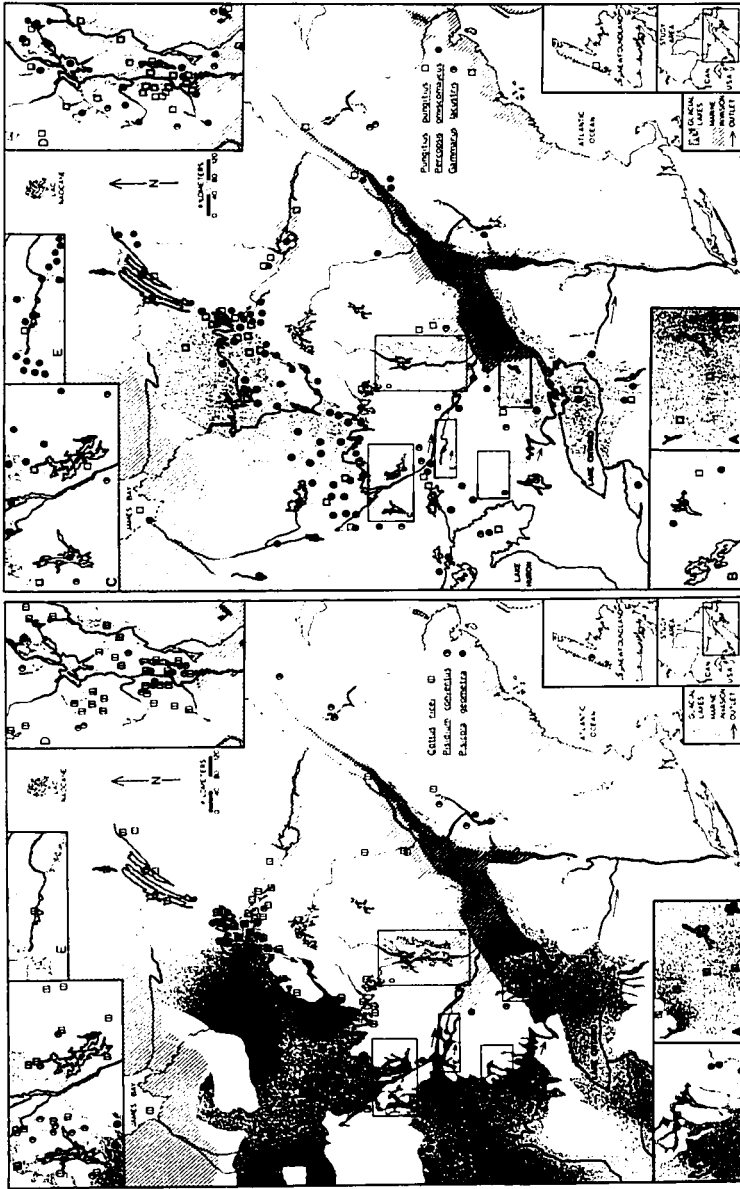
Fig. 9. A. Distribution of *Pontoporeia affinis* and *Gammaracanthus loricatus* in eastern North America. B. Distribution of *Senecella calanoides* and *Myoxocephalus quadricornis* in eastern North America.

from fresh water south of the Arctic in North America.

The dispersal ability of other deepwater animals that use but do not depend solely on glacial lakes for dispersal (i.e. that are capable of active upstream movement or passive dispersal) is clearly shown in their present distribution patterns (Fig. 10). Approximately 30% of the localities where these animals are known to occur lies outside the glacial lake boundaries (Table 2) (Dadswell 1972). Pisidium conventus, which is commonly found in association with the deepwater community and has been considered part of this group by some authors (Henson 1966), is particularly capable of dispersal beyond glacial lake boundaries (Fig. 10A). So far it is the only member of the Great Lakes profundal community (sensu Henson 1966) that is known from Newfoundland.

Certain locality records which have persisted in the literature for some time must be discarded. The record of Pontoporeia (Norton 1909) from Chamberlain Lake, Maine (Fig. 42: No. 667) is apparently wrong. Intensive sampling by myself and biologists of the Maine Department of Inland Fisheries and Game failed to find any of the deepwater community in this lake. It is possible that the specimen of Pontoporeia supposedly from this lake was actually taken by Kendall (the collector of the specimen) from Lake Champlain, where Pontoporeia is known to occur (Henson et al. 1966), and was mislabeled or labels were confused (Note: Cham-p-lain to Cham-ber-lain).

The record of Mysis from Upper Saranac Lake, New York



B.

A.

Fig. 10. Distributions of fishes and invertebrates whose dispersal was influenced, but not wholly controlled, by glacial lakes.

Table 2. Localities for invertebrates captured during this study whose distributions are influenced, but not wholly controlled, by glacial lakes. Number of locality is as in Base Map (Fig. 42). Distribution patterns are shown in Figure 10.

No.	Locality	<u>Pisidium</u>		No.	Locality	<u>Pisicola</u>		<u>Gammarus</u>
		<u>conventus</u>	<u>geometra</u>			<u>conventus</u>	<u>geometra</u>	
3.	Albanel	+	-	102.	St. Amand	-	-	-
4.	Mistassini	+	-	105.	Windy	-	-	-
8.	Bourbeau	+	+	106.	Fairbank	-	-	-
9.	Gilman	-	+	111.	Marin	-	-	-
10.	Chibougamau	+	-	115.	Trout	+	+	-
12.	Antoinette	+	-	117.	Restoule	+	-	-
20.	de la Surprise	+	-	132.	Simcoe	-	-	+
25.	Opemisa	+	-	133.	Ontario	+	-	-
31.	Bachelor	+	-	135.	Huron	+	-	+
42.	Matchi-Manitou	+	-	137.	Rousseau	+	-	-
66.	Raven	+	+	139.	Skeleton	+	-	-
68.	Kinogami	+	-	146.	Halls	+	-	-
69.	Wendigo	+	-	149.	Boshkung	+	-	-
78.	Bay	+	-	154.	Bob	+	-	-
83.	Kokoko	+	-	156.	Gull	+	-	-
84.	Kanichee	+	-	161.	Weslemkoon	+	-	-
85.	Net	+	-	167.	Mazinaw	+	-	-
86.	Rib	+	-	180.	Big Rideau	+	+	-
88.	Herridge	+	-	190.	Charleston	+	-	-
89.	Jumping Caribou	+	-	196.	Round	-	+	-
90.	Temagami	+	-	228.	Nottawissi	+	-	-
91.	Manitou	+	-	262.	Grand Cedres	+	-	-
94.	Red Cedar	+	-	266.	Kensington	+	-	-
95.	Marten	+	-	270.	Pemichangan	+	+	-
100.	Cooks	+	-	271.	Heney	+	-	-

Table 2. (cont.)

No.	Locality	<u>Pisidium</u> <u>conventus</u>	<u>Pisicola</u> <u>geometra</u>	<u>Gammarus</u> <u>lacustris</u>	No.	Locality	<u>Pisidium</u> <u>conventus</u>	<u>Pisicola</u> <u>geometra</u>	<u>Gammarus</u> <u>lacustris</u>
272.	Bitobi	-	+	-	519.	aux Vers	-	-	+
274.	Roddick	-	+	-	530.	Corbeau	+	-	-
275.	Blue Sea	+	+	-	531.	Gilmore	+	-	-
278.	Danford	-	-	+	536.	Caroline	-	-	+
286.	St. Sixte	-	-	+	554.	Dumont	-	-	+
288.	Britannique	-	-	+	565.	Harrington	-	-	+
302.	Temiscouata	+	-	-	574.	Normandeau	-	-	+
306.	Massawippi	+	-	-	594.	Bondy	+	-	-
309.	Memphremagog	+	-	-	603.	Désormeaux	-	-	+
310.	ChAMPLAIN	+	-	-	650.	Matapedia	+	-	-
322.	Cayuga	+	-	-	654.	Squatec	+	-	-
378.	Poutrincourt	+	-	-	662.	Pushineer	-	-	+
382.	Gouin	+	-	-	672.	Nicolet	+	-	-
421.	Yorstan	-	-	+	675.	Stukely	+	-	-
422.	Emerald	-	-	+	714.	Western Brock	+	-	-
427.	Anima-Nipissing	+	-	-					
431.	Spring	-	-	+					
452.	Sand	-	-	+					
454.	Caugnawana	-	-	+					
459.	McCracken	-	-	+					

(Fig. 42: No. 694) (Greene 1930) is apparently also wrong. Intensive collecting in this lake failed to discover any of the deepwater community. This lake, however, contains a massive population of Chaoborus and they may have been mistaken for Mysis. When these midges are found in fish stomachs (source of the original record) their transparent bodies with the large, black hydrostatic organs look superficially like chewed-up mysids.

The population of Pontoporeia (referred to as P. affinis by Ricker (1959)) known from one locality in the St. Lawrence estuary (Bousfield 1955), is now considered to be distinct from the North American freshwater form (Bousfield, personal communication). This form is apparently adapted to conditions of high salinity (20-30^o/oo) (Bousfield and Laubitz 1972) and so far as is known, it has been unable to establish populations in fresh water in eastern North America.

The validity of the Senecella record from Lake Ontario (Davis 1966) is in doubt. The original and only record of it from this lake came from a fish stomach. Intensive sampling by Patalas (1969) and some collections examined by Juday (1923) failed to reveal Senecella. It should be considered as absent from this lake until clearly shown to be present.

Thirty-seven of the lakes sampled by Martin and Chapman (1965) were rechecked and our results were in close agreement with theirs. We did not find the animals in any lake in which they did not find them and our more intensive sampling added only one new crustacean species in each of three lakes.

No discrepancies occurred between my findings and the published records from other lakes that were rechecked (i.e. Simcoe, Champlain, Keuka, George, etc.).

To check the efficiency of my collecting methods 55 of the study lakes were visited two or more times. In only eight lakes (21%) were species of the deepwater community captured that were not obtained during the first visit, and no additional species were taken in any lake after the second visit (Table 3). The only three study lakes where the community is known, and in which at least one species was not found during the first visit, were ultraeutrophic and contained very small populations of the crustaceans. The only reason I was able to capture any of them from this type of lake was because of the efficiency of the otter trawl. Most of the lakes inside the glacial lake - marine boundaries, in which I was unable to find any of the crustaceans, were ultraeutrophic (App. 1, lake Nos. 327-357). This type of lake was avoided when sampling outside the glacial lake - marine boundaries.

Three of the lakes in which only Limnocalanus was found (St. Jean, Temiscouata, Aylmer) were trawled extensively (5-10 times) at all depths to make certain the other crustaceans did not occur there.

The Gatineau Valley Problem

The discovery of the deepwater community in the Gatineau Valley, western Quebec (Delisle and Van Vliet 1968) presented a special problem because the extent of glacial lakes in this

Table 3. Efficiency of collecting methods. Species in the deepwater community found during the first and subsequent samplings of certain lakes. Numbers following the lake name are total species found in that lake on each visit. Numbers in brackets are previously unrecorded species found during the second or subsequent visit. Abbreviation: No., Base Map Lake number (Fig. 42).

No.	Locality	Visit					No.	Locality	Visit				
		1	2	3	4	5			1	2	3	4	5
3.	Albanel	2	2(0)	2(0)			242.	des Ecorces	1	1(0)			
4.	Mistassini	4	4(0)				259.	Bras Coupé	2	2(0)	2(0)	2(0)	
14.	Obatogamau	2	2(0)				263.	Petit Cèdres	3	3(0)	3(0)		
15.	Malo	1	1(0)				270.	Pemichangan	4	4(0)			
41.	Faillon	2	2(0)				271.	Henev	4	4(0)	4(0)		
63.	Larder	1	1(0)				274.	Roddick	5	5(0)			
82.	Obabika	1	3(2)				275.	Blue Sea	4	4(0)			
90.	Temagami	3	3(0)				276.	Paquin	2	3(1)	3(0)	3(0)	
98.	Kipawa	4	4(0)				278.	Danford	1	2(1)			
122.	Bernard	2	2(0)				282.	MacGregor	1	1(0)	1(0)		
143.	Fairy	2	2(0)	2(0)	2(0)	2(0)	300.	St. Jean	1	1(0)			
167.	Mazinaw	4	4(0)				302.	Temiscouata	1	1(0)			
176.	Pike	0	2(2)				304.	Aylmer	1	1(0)			
179.	Wolfe	0	1(1)				205.	Grand Brompton	2	2(0)			
180.	Big Rideau	3	4(1)	4(0)			306.	Massawippi	3	3(0)	3(0)		
182.	Canoe	3	3(0)				308.	Lovering	0	1(1)			
189.	Devil	3	3(0)				309.	Memphremagog	3	4(1)			
190.	Charleston	4	4(0)	4(0)	4(0)	4(0)	373.	Nicabeau	0	0(0)			
195.	Golden	2	2(0)				376.	Argenson	0	0(0)			
196.	Round	3	3(0)	3(0)	3(0)		416.	Gowganda	0	0(0)			

Table 3. (cont.)

No.	Locality	Visit					No.	Locality	Visit				
		1	2	3	4	5			1	2	3	4	5
430.	Upper Twin	0	0(0)				645.	Kenogami	0	0(0)			
454.	Caughnawana	0	0(0)				667.	Chamberlain	0	0(0)			
515.	Stevens	0	0(0)				669.	Megantic	0	0(0)			
519.	aux Vers	0	0(0)				674.	Bowker	0	0(0)			
536.	Caroline	0	0(0)				675.	Stukely	0	0(0)			
570.	Meach	0	0(0)				676.	Lyster	0	0(0)			
577.	Grand	0	0(0)				714.	Western Brook	0	0(0)			
621.	la Pêche	0	0(0)										

Number of lakes in which additional species of the deepwater community were found during the second or subsequent sampling trip 8/37 = 21%

Efficiency of sampling methods, i.e. trips without additional species/ total trips 82/90 = 91%

region has not been mapped by geologists. Antevs (1928) reported glacial lake sediments around Maniwaki, and various authors have mentioned that the Champlain Sea had penetrated into the Valley (Mauffette 1948; Bickel 1970; Gadd 1971), but this is the extent of geological knowledge.

The distribution pattern of the community in lakes of the Gatineau Valley is consistent with dispersal through a glacially controlled, standing water body (Fig. 11). Isostatic depression of the region to form this water body is indicated by the south-to-north rise in the maximum elevation of their occurrence in lakes, but graphical analysis of the overall depression shows that the Gatineau curve does not fit the normal isostatic rebound curve form (Fig. 12) (Andrews 1968; Broeker 1966). This means that the apparent maximum extent of the Gatineau water body was actually a combination of stages formed at different levels and times during ice retreat.

The maximum shoreline of the Champlain Sea, formed about 11,800 B.P.*, is quite well known (Prest et al. 1968; Scott 1971) (Fig. 13A) and can be used to estimate a rebound curve for the central portion of the study area. When the south-to-north change in distance between successive 100-ft isobases of sea level at that time is graphed, a normal isostatic rebound curve is obtained (Fig. 13B). Good evidence that this

*B.P. "Before Present." Present refers to 1950 A.D. and this format is to be understood with all datings that follow.

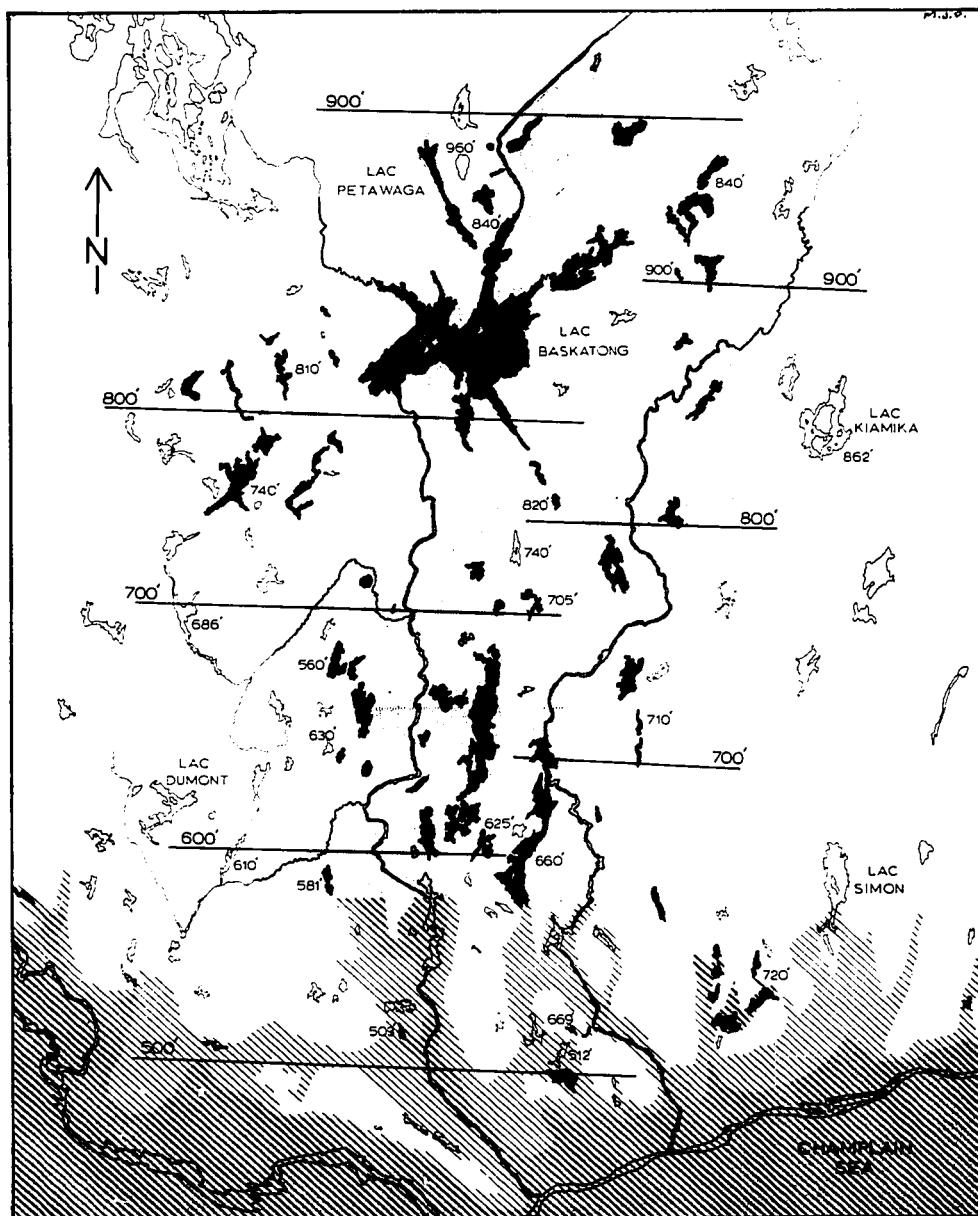


Fig. 11. Distribution of the community in the Gatineau (left basin) and Lièvre (right basin) Valleys. Solid lakes contain one or more of the species, open lakes are ecologically suitable lakes that contain none. Lines are isobases of maximum occurrence of the community. Numbers are elevations of lakes and isobases, in ft. Probable maximum extents of the Champlain Sea (cross-hatching); and glacial Lake Gatineau (shading).

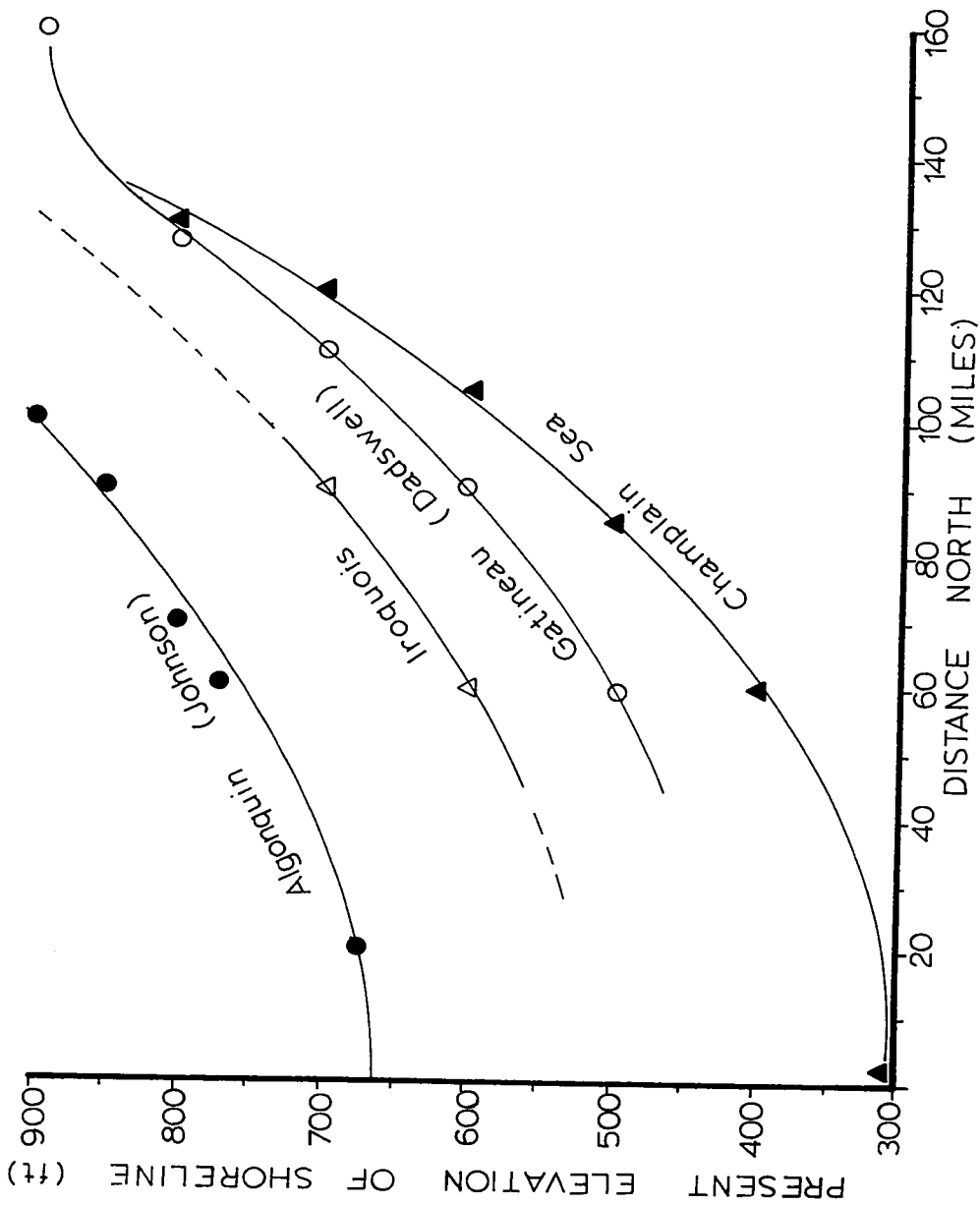


Fig. 12. Warped shorelines of various glacial waters. Champlain Sea is after Prest et al. (1968). The Iroquois shoreline is extrapolated parallel to the Algonquin shoreline (after Johnson 1916). The Gatineau isobases of maximum elevation of the community occurrence do not conform.

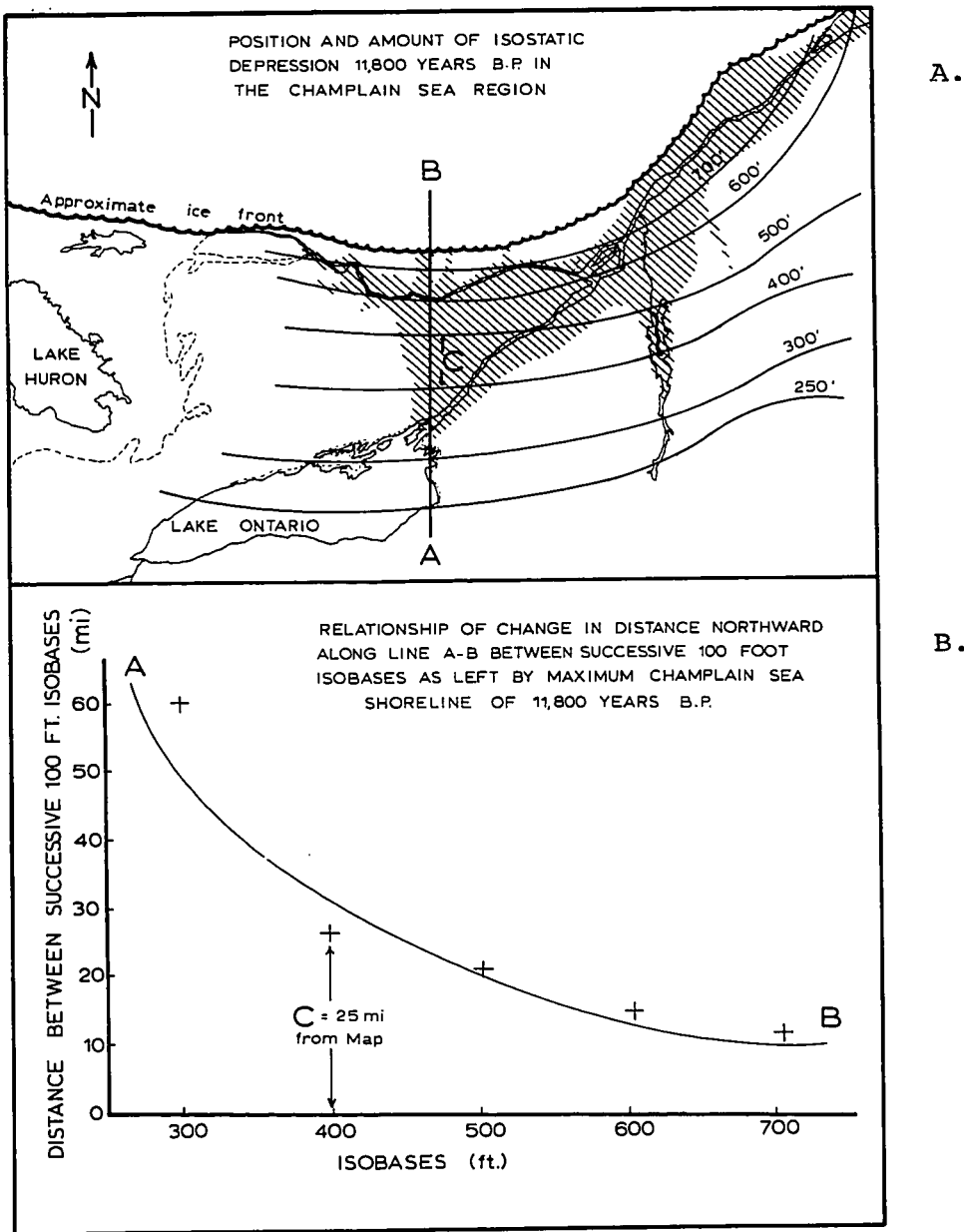


Fig. 13. A. Isobases of the Champlain Sea shoreline, 11,800 B.P. (after Prest et al. (1968)). B. Isobase-distance relationship (in miles) northward in the maximum Champlain Sea.

rebound curve is real for that moment in time is indicated by an inverse transformation of the values, resulting in a straight line $Y = 0.02X - 4.19$ ($r = 0.99$) (Fig. 14A), much like that obtained by Lewis (1970) for uplift of Manitoulin Island. Then the radiocarbon dates of Lowden and Blake (1968, 1970); Mott (1968), and Romanelli (1972) were used to construct a time-rebound curve for Kingsmere, Quebec (Fig. 14B). This curve agrees closely with the Champlain Sea isobase curve. Therefore it is probable that the isobase-distance relationship (i.e. Fig. 13B) for this area holds through time.

Assuming a continuous retreat of the ice sheet at an even rate and an equally smooth isostatic uplift of the region, we can predict the isobase positions at any one time, provided we have one dated shoreline in the area (Andrews 1970). When the Kingsmere dated-shoreline levels are used in conjunction with the isobase-distance relationship in Figure 12B, a series of hypothetical water planes for various times can be projected up the Gatineau Valley (Fig. 15). These hypothetical water planes show very good correlation to the distribution pattern of the deepwater community in the Valley.

The Limnocalanus Problem

The eastern North American freshwater distribution pattern of Limnocalanus macrurus is slightly different from that of the other glacial lake-dispersed deepwater crustaceans (Fig. 8B). It was consistently found in lakes at slightly higher elevations and further eastward than the others. Limnocalanus macrurus appears to enter shallower waters habitually and seems

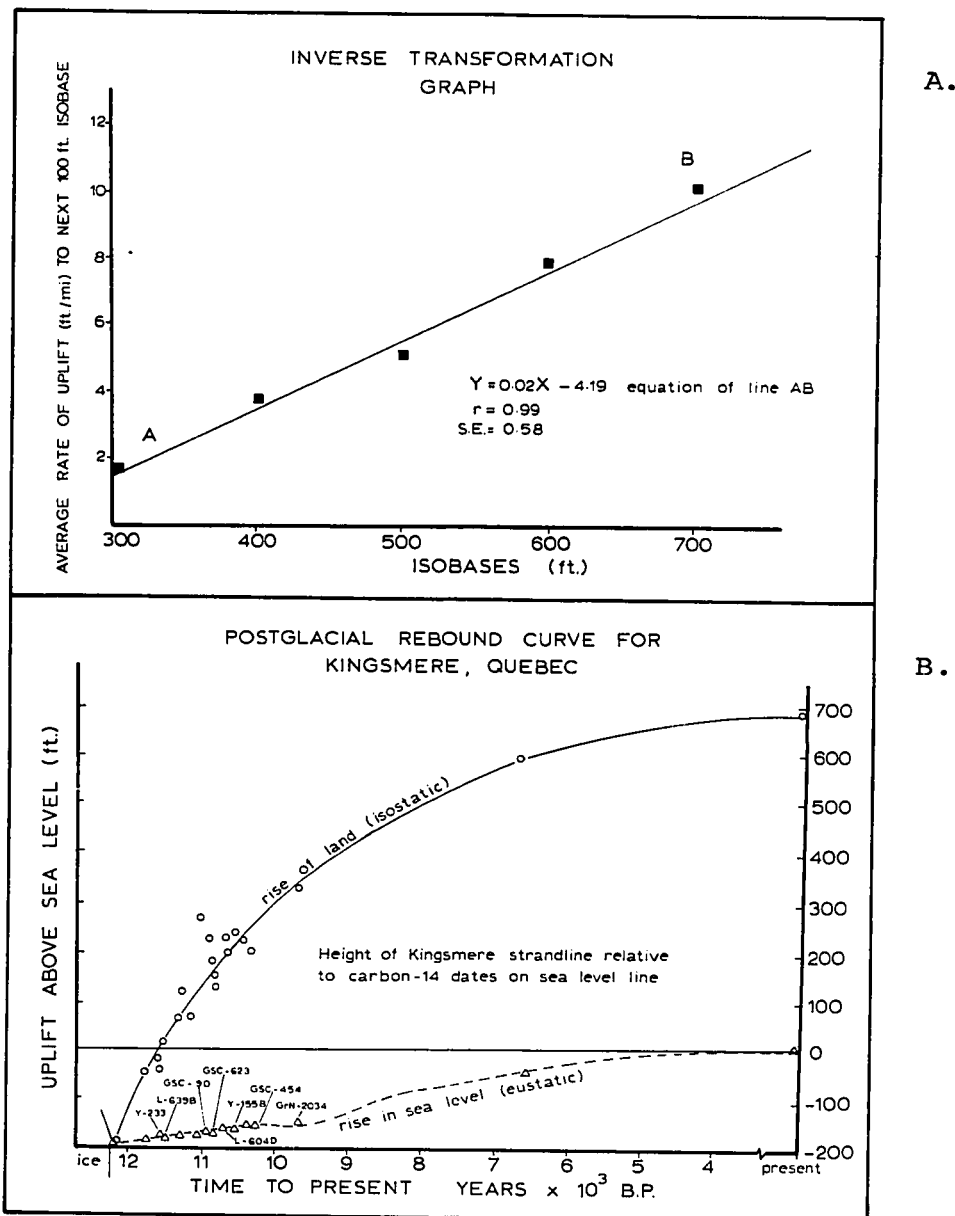


Fig. 14. A. Inverse transformation of the isobase-distance relationship in Fig. 12B. B. Time-rebound curve for Kingsmere, Quebec (see Fig. 15). Eustatic rise in sea level is after Godwin et al. (1958) and Kenny (1964).

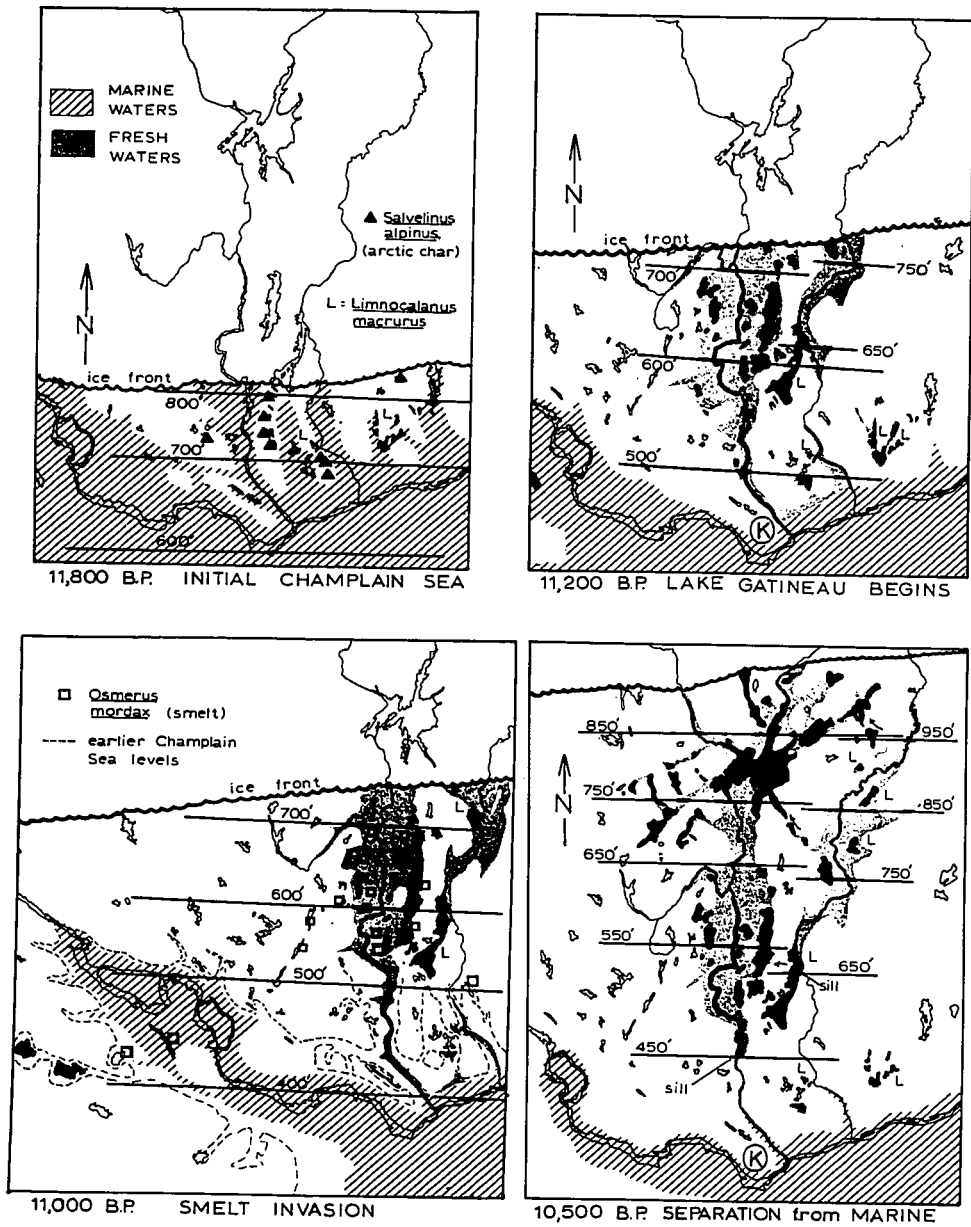


Fig. 15. Hypothetical stages of the Champlain Sea and glacial Lake Gatineau based on the known shoreline level times at Kingsmere, and the distance-isobase relationship from Fig. 12B. Solid lakes contain the community. Ⓚ indicates geographic location of Kingsmere, Quebec.

to be more light-tolerant than the other crustaceans (MacKay 1924; Wilson 1929). This behavior may have enabled it to gain access to lake basins formerly connected to the glacial lakes by only shallow, transient straits.

Perhaps Limnocalanus can disperse short distances by passive means. If this were the case, however, one would expect the distribution pattern to be somewhat random and Limnocalanus should be found in numerous lakes outside of, and at higher elevations than, the main distribution of the rest of the community. In fact, it is usually found only close to, or just slightly higher than, the known glacial lake shoreline. Westemkoon Lake (No. 161) and Lac Temiscouata (No. 302) are the two known exceptions. Both occurrences could be the result of human transport. Temiscouata, however, is the lowest lake in elevation in its region and the most likely route through which any glacial waters would have passed. Why, if human and/or other means of passive dispersal are possible, does it alone of all the suitable lakes in its region contain Limnocalanus.

Limnocalanus macrurus is known to survive in and disperse through, brackish surface layers of arctic seas (Grainger 1962, 1965; Holmquist 1970) and to have dispersed widely in the Arctic Ocean (Bowman and Long 1968). This salinity tolerance as well as its tolerance for light apparently enabled it to disperse in the early stages of the Champlain Sea and may explain its presence, by itself, in a number of lakes inundated only by the early, highest levels of the sea (e.g. Fig. 7: Lac des Piles, No. 299).

ECOLOGICAL LIMITING FACTORS

Introduction

There are two main reasons why an organism may not occur in a specific locality: either it has never dispersed into the area, or it cannot survive in the particular ecosystem found there. Survival is dictated by the organism's tolerance to its physical and biological environment. Accordingly, the distribution of the deepwater community depends not only on events in the past, but also on conditions of the present-day habitat.

Aquatic biologists generally associate "glaciomarine relicts" with oligotrophic lakes, emphasizing low temperatures and high levels of dissolved oxygen as necessary for their survival (Samter and Wettner 1904; Theinemann 1928; Larkin 1948). Holmquist (1959, 1966) points out that high temperatures and low dissolved oxygen are not especially limiting to these organisms and that other unknown factors seem to limit their distribution, at least within lakes. Rawson (1960) observed that P. affinis and L. macrurus were absent from Cree Lake, Saskatchewan for no apparent reason. Koshinsky (1965) could not explain why P. affinis was absent from depths greater than 10 m in one lake when it was abundant in less oxygenated, greater depths in nearby lakes.

It is apparent from numerous studies that other limnological factors can limit the occurrence of aquatic organisms. Tucker (1957) implicated calcium levels in combination with dissolved organic matter as a reason for the absence of leeches,

crustaceans, and molluscs from certain lakes. Delorme (1964) found that pH limits the distribution of ostracods, and Carter (1971) obtained similar results from planktonic crustaceans. Green (1971) used a combination of physical and chemical factors to explain the difference among molluscan communities in some Manitoban lakes.

Physicochemical parameters of study lakes were determined for two reasons: (1) to ascertain whether lakes without glacial lake inundation differed significantly from lakes that were inundated, and whether this difference has influenced the community's distribution; and (2) to determine the limiting factors of the individual crustacean species.

Holmquist (1966) seems to attribute the different distribution patterns of the individual "relict" species to their dispersal history. In eastern North America it is more likely that dispersal of the deepwater community as a whole was similar (except for the slight variation for Limnocalanus), but that present-day limnological conditions have caused one or more species to disappear from certain lakes.

Methods

Physicochemical parameters were measured for each study lake. To check the accuracy of field determinations and obtain values for oxygen consumption and color, 1-liter samples of surface water were collected from 150 selected lakes and a complete chemical analysis of them was made by the Inland Waters Branch of Environment Canada. Physicochemical data on

lakes not sampled were obtained from the literature (15 lakes), or from the records of regional fisheries biologists (22 lakes). Pertinent physicochemical parameters for all lakes are listed in Appendix I.

Vertical temperature profiles were taken with an Applied Research FT-3 hydrographic thermometer, accurate to 0.5°C . Dissolved oxygen was determined by the azide modified Winkler method. Hydrogen ion concentration (pH) was determined at the surface and just above the bottom using a Hach comparator (5.5-8.5 Brom thymol blue or 4-10 wide range indicator). Total hardness (TH) was measured at the surface using the EDTA titration method (Hach kit). Light penetration was measured with a secchi disk 20 cm in diam. Oxygen consumption was determined by the potassium permanganate oxidation method for the 150 lakes analyzed by the Inland Waters Branch. Oxygen consumption and color of these lakes were then plotted against the log of their secchi visibilities in centimeters and the oxygen consumption and color of the remaining study lakes were estimated from these graphs using the lakes' secchi visibility (Fig. 43).

Field determinations were in good agreement with laboratory determinations, but averaged 10% higher. This difference may have been due to the storage period of the water samples (up to 6 months) and for this reason field determinations (except for oxygen consumption) were used in the following discussions. Throughout the study an effort was made to sample lakes suspected to have low dissolved oxygen, in the fall when,

oxygen levels were lowest.

Nine lakes were selected, on the basis of depth, total hardness, and oxygen consumption, for sampling positive occurrence, population density, and depth distribution of Pontoporeia. In each lake two or three ekman grabs were taken at each of 10% increments of hypolimnion depth (i.e. 9-10 stations/lake or 20-30 samples/lake). Temperature and pH were determined at each depth. Pontoporeia were separated from the mud by sieving in a wash bucket (11 meshes /cm). Counts from each depth were averaged.

Comparison between "Inside" and "Outside" Lakes

The lakes sampled during this study can be divided into three groups: lakes inside the glacial lake or marine boundaries which are positive for the community; lakes inside the boundaries which are negative for the community because of unsuitable ecological conditions; and lakes outside the glacial lake or marine boundaries which are negative for zoogeographical reasons. For the purpose of discussing physicochemical (ecological) limiting factors, the first two groups will be lumped and called "inside" lakes, the third group will be known as "outside" lakes. Physicochemical data were obtained for 328 inside lakes of which 313 were examined personally. The outside group includes 337 lakes of which 317 were personally sampled.

Means and ranges of physicochemical conditions for inside and outside lakes were similar (Fig. 16). Outside lakes were

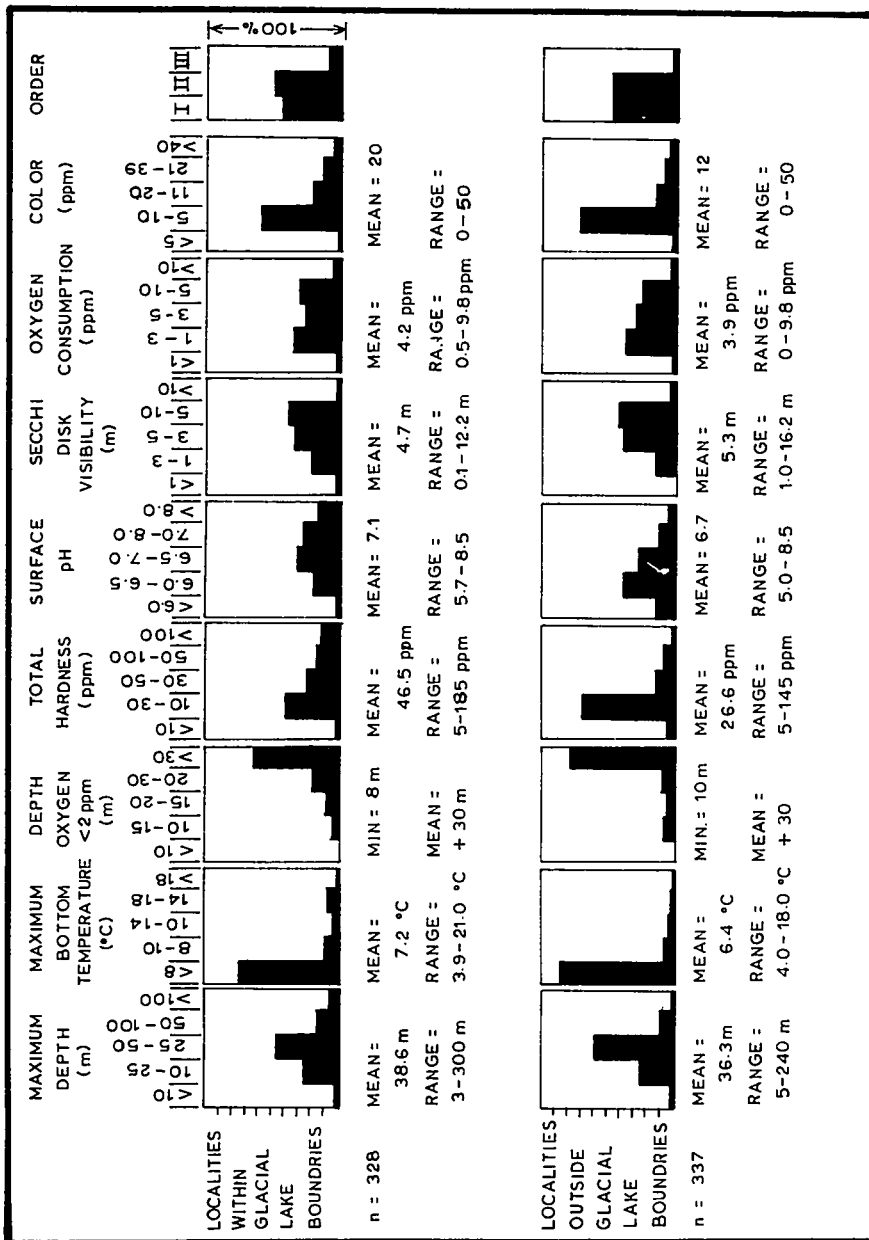


Fig. 16. Frequency distribution of physicochemical parameters in the two groups of study lakes. Height of the graphs (i.e. boxes) corresponds to 100% of the lakes in a particular category. The height of the solid bars indicate the percentage of lakes in each category.

characterized by lower mean total hardness, lower pH, and clearer water than inside lakes. Inside lakes had slightly higher amounts of dissolved organic matter (oxygen consumption 4.2 ppm vs 3.9 ppm) which probably caused the lower than expected mean pH for this group. Average surface pH of inside lakes was only slightly higher than that of outside lakes (7.1 vs 6.7) although average total hardness of inside lakes was significantly higher than for outside lakes ($t_{0.01} = 5.38^{**}$; d.f. = 663). Christman and Ghassemi (1966) found that high organic levels reduced the pH of water.

The higher elevation of the outside lakes is probably the main reason for these differences. Headwater lakes receive less influx of dissolved solids and organics because of smaller drainage basins (Schindler and Nighswander 1970), and they lack former glacial lake coverage, the presence of which has been shown to contribute dissolved solids to a lake basin (Ryder 1964). Interestingly enough, outside lakes would probably be categorized as more oligotrophic (Hutchinson 1957) and therefore, as better habitat for the deepwater community.

The community, as a whole, was found to tolerate nearly the complete range of physicochemical conditions presently existing in the inside lakes (Fig. 17, Table 4). Although the means of physicochemical factors of inside and outside lakes differed (sometimes significantly), the ranges of outside lake conditions were within the ranges tolerated by the community in the inside lakes (Table 4). Consequently, physicochemical factors cannot be regarded as contributing to the absence of

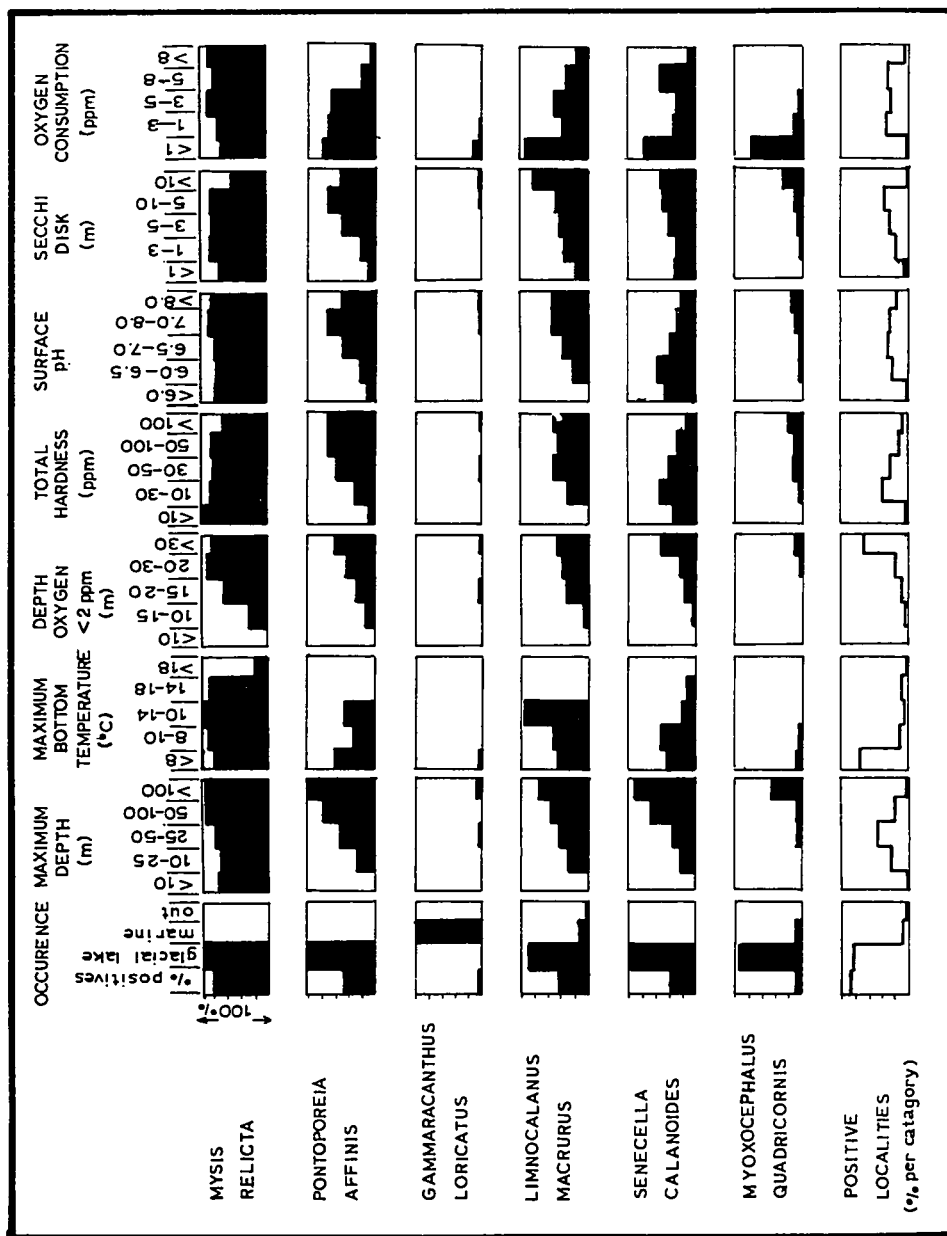


Fig. 17. Frequency distribution of the occurrence of the "glaciomarine relicts" in the study lakes in relation to the major physicochemical parameters. Height of the graphs (i.e. boxes) corresponds to 100% of the lakes in a particular category. The height of the solid bars indicate the percentage of lakes in each category in which the species were found.

Table 4. Total range of physicochemical parameters in the study lakes and ranges tolerated by the crustaceans. Additional parameters are from the complete chemical analysis of 150 study lakes. Abbreviations: TH, total hardness; SDV, secchi disk visibility; O₂c, Oxygen consumption; HCO₃, bicarbonate; CO₂, dissolved carbon dioxide.

Parameter	Outside		Inside		Mysis		Pontoporeia		Limnocalanus		Senecella	
	lakes		lakes		relicta		affinis		macrurus		calanoides	
Depth (m)	5-240		3-300		5-300		18-300		14-300		14-240	
Temperature (°C)	4.0-18.0		3.9-21.0		3.9-18.0		3.9-14.0		3.9-14.0		3.9-15.0	
Oxygen (ppm)	12-0		12-0		12-2		12-1		12-0.6		12-0.6	
TH (ppm)	5-145		6-185		5-185		8-185		10-185		8-130	
Surface pH	5.0-8.5		5.7-8.5		5.7-8.5		6.1-8.5		6.1-8.5		5.7-8.5	
SDV (m)	1.0-16.2		0.1-12.2		0.1-10		1.1-10		0.8-12.2		0.8-12.2	
O ₂ c (ppm)	0.0-9.8		0.5-9.8		1.0-9.8		1.0-6.7		0.5-8.8		0.5-9.5	
Alkalinity (ppm)	0.0-95.9		0.0-118		0.0-118		0.0-118		1.3-96		0.0-96	
Calcium (ppm)	1.3-39.7		1.4-38.2		1.4-38.2		2.0-38.2		3.6-32.9		1.4-32.9	
Magnesium (ppm)	0.01-2.8		0.08-9.6		0.08-9.6		0.08-9.6		0.1-7.5		0.08-7.5	
Potassium (ppm)	0.1-0.9		0.1-2.0		0.1-1.5		0.1-1.3		0.1-2.0		0.1-1.5	
Sodium (ppm)	0.2-2.9		0.2-3.2		0.2-3.2		0.4-3.2		0.3-2.9		0.2-3.2	
HCO ₃ (ppm)	0.0-117		0.0-144		0.0-144		0.0-144		1.6-118		0.0-118	
Chlorine (ppm)	0.0-14		0.0-7.2		0.0-7.2		0.0-7.2		0.0-6.7		0.0-7.2	
Sulphate (ppm)	2.6-20.6		3.1-24.3		3.1-24.3		3.6-18.5		3.1-18.5		3.4-16.6	
CO ₂ (ppm)	0.1-30.4		0.8-9.2		0.8-9.2		0.8-6.7		0.8-6.4		0.8-8.4	

the community from the outside lakes.

Major Ecological Limiting Factors

My findings, however, indicate that ecological conditions can affect the species composition of the crustacean community in a given lake. In this section I will be referring only to the four glacial lake-dispersed crustaceans (i.e. those shown in Fig. 1). Myoxocephalus and Gammaracanthus are not included because they were captured so few times. Also, only lakes with the potential possibility to contain all four crustaceans have been considered. Positive lakes in areas reached only by Limnocalanus (i.e. Lièvre River Valley) have not been included.

It is probable that when each present-day lake basin separated from the glacial lake, conditions in the new lake were oligotrophic, and it contained populations of all four crustaceans. But lakes change through time from the oligotrophic state to either eutrophic or dystrophic and this causes a corresponding change in their profundal community (Brundin 1958). Consequently, depending on the original depth of the basin and on whatever chemical changes have occurred in the intervening years, one or more of the crustaceans may have become extinct there. Obviously this is the case, since only 33 of 291 possible lakes were found to contain all four crustaceans (Table 1).

A species' niche is theoretically defined as an "N-dimensional hypervolume" in which fitness of individuals is positive (Green 1971). This definition makes it impossible to delimit a species' hypervolume, and in practice N is reduced to a reasonable number of measurable parameters. In this study, seven

parameters were chosen, based on the criteria set out by Green (1971). (1) Parameters should describe the environment in direct contact with the organism; (2) parameters must be easy to determine in the field, or later in the laboratory without error induced by storage; (3) parameters should have the theoretical possibility of affecting, or have been described as having an effect on, aquatic organisms.

Maximum depth (z_m) has been emphasized by various authors as important to survival of these crustaceans (Ricker 1959; Segerstråle 1957). Martin and Chapman (1965) give 24 m as the minimum depth of lake in which these crustaceans were found in Algonquin Park, Ontario.

Maximum depth is not an independent parameter within a lake, but rather its effect is to influence maximum bottom temperatures and levels of incipient light. It may also represent a spatial separation factor. Depth, however, is an easily measurable, independent parameter for each lake and can be used in comparison between lakes.

The occurrence of Pontoporeia, Limnocalanus, and Senecella was positively correlated with deep lakes (Fig. 17). Pontoporeia was found in 100% of lakes deeper than 100 m and in none of the lakes shallower than 10 m. Mysis was found as often in shallow lakes (78%) as it was in deeper ones (80-96%).

Maximum depth was the main factor determining the total number of crustacean species in a lake (Fig. 18). Shallow lakes or shallow basins of one lake usually contain fewer species of the community than deeper lakes or basins. For

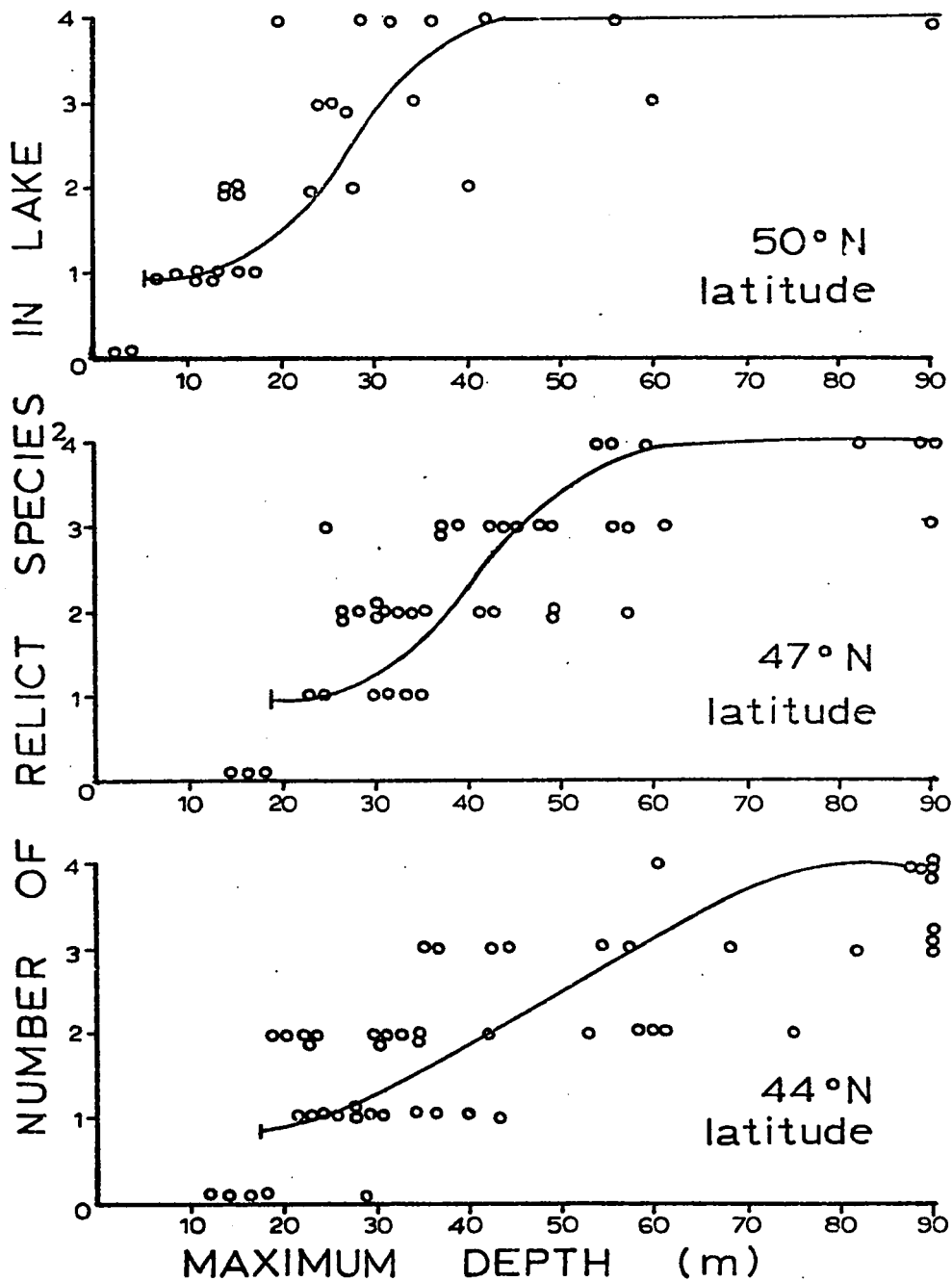


Fig. 18. Relationship between maximum depth, latitude, and the number of crustacean species of the community occurring in a lake.

example, the deepest basin of Charleston Lake (No. 190) contains four members of the community, the shallow basins only three (Table 1). The minimum depth necessary for the survival of the total crustacean community and/or the individual species decreases with an increase in latitude. Johnson (1962) found these crustaceans in lakes as shallow as 2 m on Victoria Island (70°N). In the study area, lakes at the latitude of Chibougamau (50°N) usually contain all four species if they are deeper than 20 m and Mysis survives in lakes as shallow as 5 m. In southern Ontario (44°N), only lakes over 60 m deep contained all four species and the shallowest lake found to contain any of the community was 18 m in depth.

Maximum bottom temperature (T_m), above 14°C , has been considered one of the most important factors limiting the occurrence of the deepwater community (Theinemann 1928; Ricker 1959), but my findings indicate this is not wholly true. Mysis was found as often in lakes with T_m 's between 14 and 18°C as it was in colder lakes (Fig. 17). But bottom temperatures are limiting once they exceed the upper lethal limit of the individual species.

The warmest bottom temperature at which a Mysis population was found surviving was 18°C (Lac Grand Victoria, No. 46). This temperature is considerably higher than values quoted in the literature (Theinemann 1928; Ricker 1959), although Holmquist (1966) gave 16°C as the upper limit known for Mysis in Swedish lakes. In my study area, lakes with T_m 's up to 16°C contained large, healthy populations of Mysis (2000 animals/

trawl). Pontoporeia and Limnocalanus were never found in lakes with bottom temperatures above 14°C (Fig. 17). Senecella was found a number of times in lakes with a T_m of 15°C.

Depth at which dissolved oxygen was less than 2 ppm (z_{O_2}) was chosen as a parameter because the depth at which minimum tolerable oxygen levels occur is critical depending on the transparency of the lake water. Many authors stress low oxygen levels as a factor limiting the occurrence of these crustaceans (Theinmann 1928; Samter and Wettner 1904).

Low hypolimnion oxygen is the only condition that severely limits the occurrence of Mysis (Fig. 17). Limnocalanus and Senecella were absent from lakes with sharp oxygen stratification (i.e. no trace at bottom). Pontoporeia is very tolerant of low oxygen and was often the only species found in ultraeutrophic lakes (i.e. Wolfe Lake, No. 179).

Minimum oxygen values at which these species were found to occur in the study lakes are as follows: Mysis, 2 ppm (Redhorse Lake, Oct. 12, 1970); Pontoporeia, 1 ppm (Devil Lake, Oct. 7, 1969, 30 m); Limnocalanus and Senecella, 0.6 ppm (Murray Lake, Oct. 5, 1970, 20-23 m). Except for Senecella, whose oxygen tolerance is unreported, these values agree closely with those given by other authors (Juday and Birge 1927; Strøm 1946; Lasenby 1971).

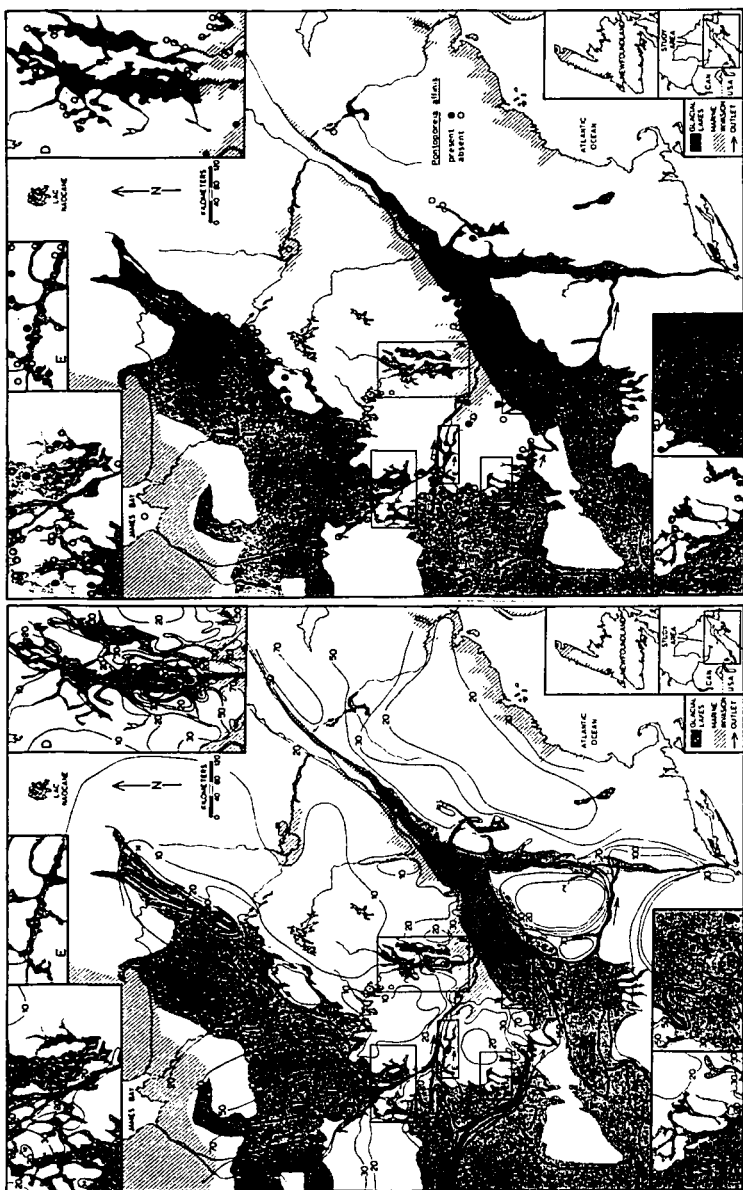
Total hardness (TH) is the measure of total content of calcium and magnesium in the water (Hutchinson 1957). Calcium is necessary to crustaceans for building exoskeletons. Green (1971) and Tucker (1958) found that low calcium limited the

occurrence of aquatic organisms.

Mysis was present less often in lakes with high TH (Fig. 17). This, however, may be an artifact since lakes with high TH commonly had low hypolimnion oxygen. Occurrence of Pontoporeia and Limnocalanus was correlated with high TH (Fig. 17). Pontoporeia was found in only 27% of lakes with TH less than 30 ppm (43% of the study lakes). In eastern North America the distribution pattern of Pontoporeia is closely associated with the distribution of lakes having high TH within the boundaries of the former glacial lakes (Fig. 19). Senecella occurred most often in lakes with low TH (Fig. 17).

Surface pH. Hydrogen ion concentration is a dominant factor in fresh water, as it affects the deposition of calcium and the availability of the bicarbonate ion (Hutchinson 1957). Delorme (1964) gave 6.1 as the lower limit of pH tolerance for ostracods. Beamish (1970) showed that low pH could inhibit fish reproduction. Surface pH, rather than hypolimnion pH, was used as a parameter because it varies less during the open-water season. This means that lakes sampled at different times of the year can be compared.

The occurrence of Mysis was not restricted by pH (Fig. 17). The occurrence of Pontoporeia and Limnocalanus was related to high pH. Neither of these species was found in lakes with surface pH less than 6.0 (Table 4). Senecella, on the other hand, was most common in lakes with low pH (found in 60% of lakes between 6.0 and 6.5) (Fig. 17).



A.

B.

Fig. 19. Distribution of *Pontoporeia affinis* in eastern North America in relation to total hardness of the lakes. A. Distribution of total hardness (TH), isobars are in ppm. B. Distribution of *Pontoporeia*. Note that the frequency of occurrence increases sharply in regions with lakes of high TH.

Secchi disk visibility (SDV) approximates the 15% level of percentage transmission of surface light intensity (Beeton 1958). Secchi visibility indicates the amount of transmitted light reaching the deepwater organisms. Light is known to affect the behavior of these crustaceans (Beeton 1960; Brownell 1970) but it has not been suggested as an absolute limiting factor to occurrence. My findings indicate that strong light penetration, especially in combination with other factors, is very detrimental to these species.

Mysis was found least often in very clear lakes, particularly if there was an oxygen deficiency in the hypolimnion. Senecella and Limnocalanus were absent from a number of quite deep, well oxygenated lakes with high SDV's (Table 1: Clear Lake, No. 186; Skeleton Lake, No. 139).

Oxygen consumption (O_2c) is a measure of the dissolved organic matter in water. This organic matter or "humic acid" consists of acidic, phenolic macromolecules originating from the decay of plant material (Christman and Ghassemi 1966). What effect high macromolecule concentrations have on aquatic organisms is unknown (Shapiro 1957), but it may be possible that they increase osmotic stress. Tucker (1957) found that lakes with high O_2c contained fewer aquatic species and that high levels of dissolved organic matter were lethal to flatworms.

Occurrence of Mysis shows no significant relation to O_2c (Fig. 17). Pontoporeia and Limnocalanus occurrence was related to lakes with low O_2c . Pontoporeia was seldom

captured in lakes with O_2c greater than 5 ppm. Senecella occurrence was slightly correlated with lakes having heavily stained water (O_2c greater than 5 ppm) (Fig. 17).

Multiplication Effect of Limiting Factors

In reality no ecological limiting factor ever functions completely independently. Each of the preceding factors may place a certain amount of environmental stress on the crustaceans but the effect can be alleviated or intensified by levels of one or more of the other six factors. In this study it was found that three major factors account for most of the differences in the distributions of each of the crustaceans.

Factors Affecting *Mysis relicta*

Mysis is the most eurytopic of the crustaceans. It occurred in the most localities (263) and was found in nearly every type of lake sampled (Fig. 17). Mysis was only commonly absent from or rare in small, clear-water lakes with sharp thermal stratification and low hypolimnion dissolved oxygen (e.g. App. 1: Thorne Lake, No. 280; Orford Lake, No. 307).

Charleton (1972) found that depth distribution of M. relicta was related to temperature and incipient light. I found that in a given lake mysid populations usually selected an optimum depth balancing minimum incipient light, minimum temperature, and maximum dissolved oxygen. Substantial mysid populations still exist in many lakes with low hypolimnion oxygen because the low light transparency of their water allows the mysids to occupy shallower depths during the critical low

oxygen periods of the year. For example, in Murray Lake (No. 264, SDV 2.8 m) during October the mysids can occupy depths of 8 to 12 m, the only part of the hypolimnion with temperatures below 18°C and oxygen above 2 ppm. On the other hand, in Danford Lake (No. 278, SDV 6.3 m) during the fall, even though temperatures below 18°C were found as shallow as 8 m, no mysids were found in depths less than 18 m (presumably because of high incipient light) nor deeper than 20 m (because of low oxygen) so that the mysid population in this lake has been reduced almost to extinction.

Mysis relicta reaches its greatest abundance in three lake types: shallow, unstratified lakes with T_m 's under 16°C and low SDV's (e.g. Lac Gueguen, No. 43); moderately deep, stratified lakes with low SDV's (e.g. Lac Bitobi, No. 272); and very deep lakes (e.g. Trout Lake, No. 115). These lakes all have in common very low levels of transmitted light occurring at some depth in conjunction with optimum temperatures and oxygen.

The type of lake inhabited also affects the growth and reproductive timing of Mysis. Normally these crustacean species reproduce during winter (Carter 1969; Segerstråle 1970). I found the deeper the lake the less distinct was reproductive timing, resulting in all sizes and reproductive stages in the population at any one time (e.g. Charleston Lake, z_m 90 m (Fig. 20); Cayuga Lake, z_m 120 m (Brownell 1970)). Populations in shallow lakes have very distinct size classes, indicating precise reproductive timing (Fig. 21). The average

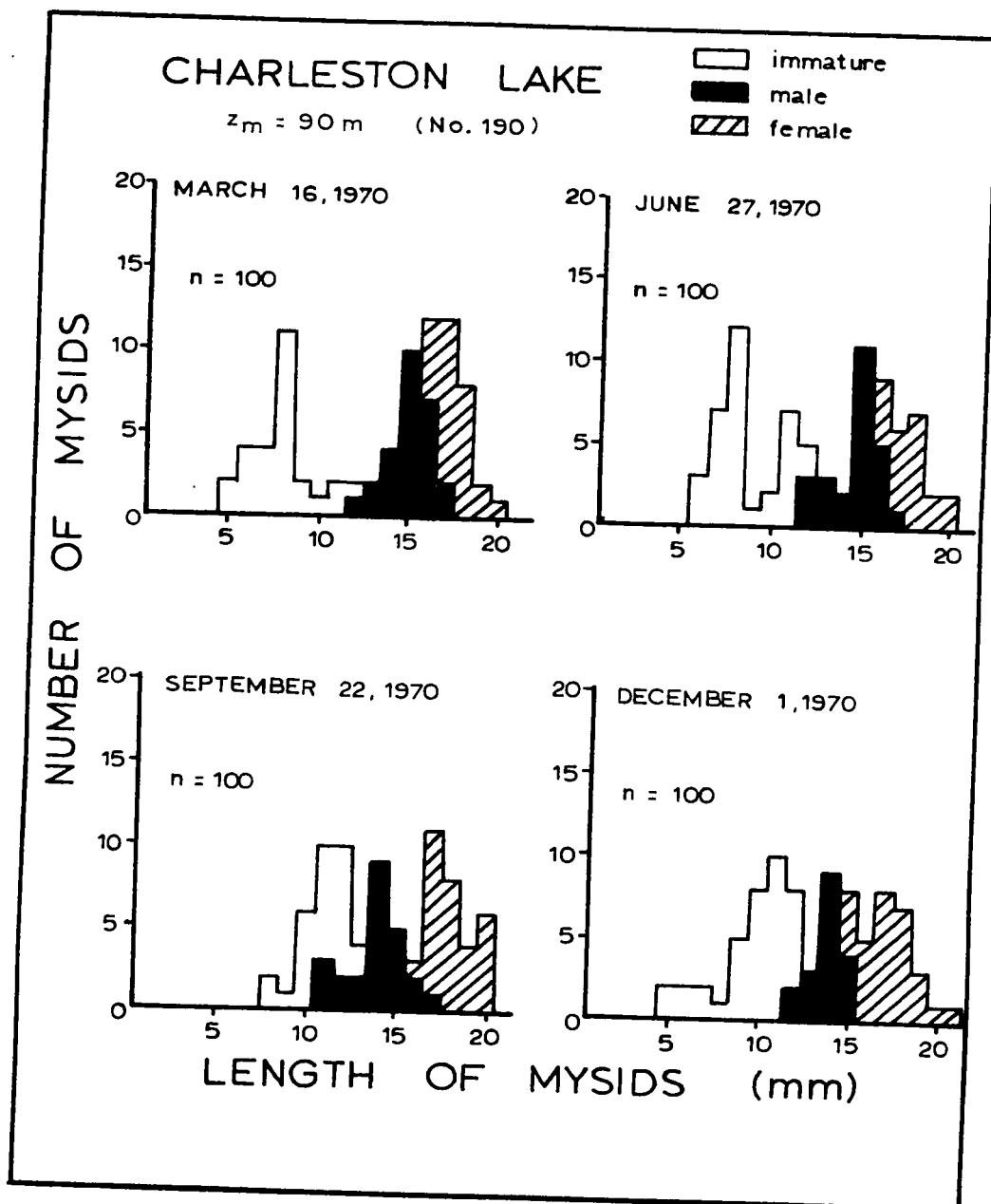


Fig. 20. Length distribution of mysids in population samples from Charleston Lake at different times of the year.

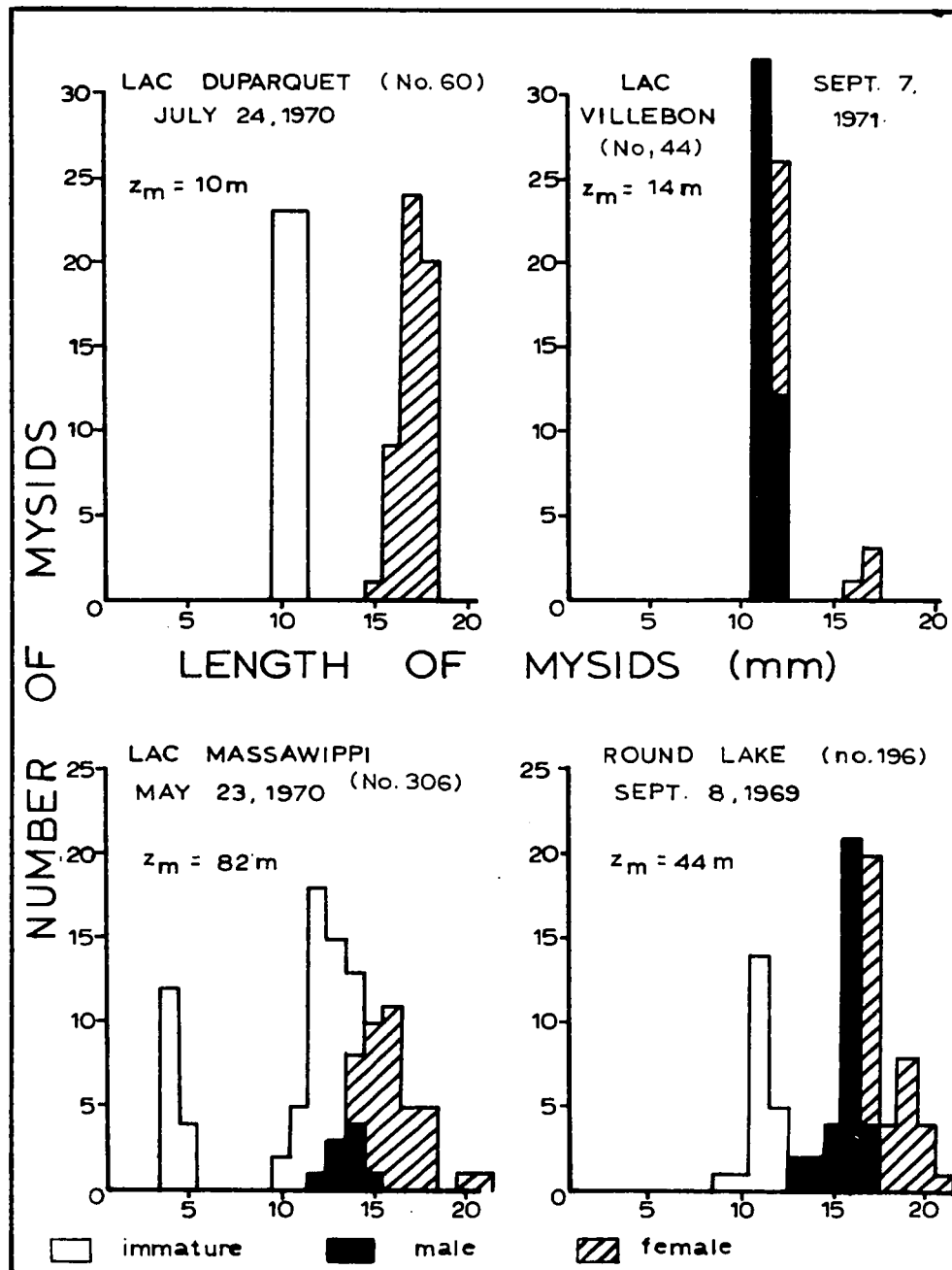


Fig. 21. Length distribution of mysids in population samples from very shallow lakes (top) and medium depth lakes (bottom).

adult size is smaller in shallow lakes (Fig. 21).

Segerstråle (1970) showed that photoperiod was responsible for initiating reproduction of Pontoporeia. Photoperiod may also be responsible for initiating Mysis reproduction. Absence of light penetration in deep water would blur the photoperiod change, whereas in shallow lakes it would be very noticeable. Interestingly, all North American lakes known to have summer breeding populations of Pontoporeia are very deep (Segerstråle 1971).

Factors Affecting Pontoporeia affinis

Early in this study it became evident that factors other than temperature and oxygen were limiting the occurrence of Pontoporeia. Intensive sampling in a few lakes in which these two parameters were not a problem revealed that in fact the amphipod was either absent or very rare (e.g. Fairy Lake, 30 ekman grabs, 6 trawls between 10-70 m, captured no Pontoporeia).

The relationship between maximum depth, TH, O_2c and the occurrence of Pontoporeia is demonstrated in Fig. 22. Shallow lakes with low TH and high O_2c almost always lack Pontoporeia; deep lakes with low O_2c , and high TH always contain it. The absence of Pontoporeia from Cree Lake, Saskatchewan (Rawson 1960) was probably due to the TH- O_2c relationship of that lake. Cree had the lowest TH and hypolimnion pH of all the lakes sampled by Rawson. In general, dystrophic lakes provide poor habitat for Pontoporeia.

It was also noted that there was a relationship between the adult size of Pontoporeia and the favorableness of the lake.

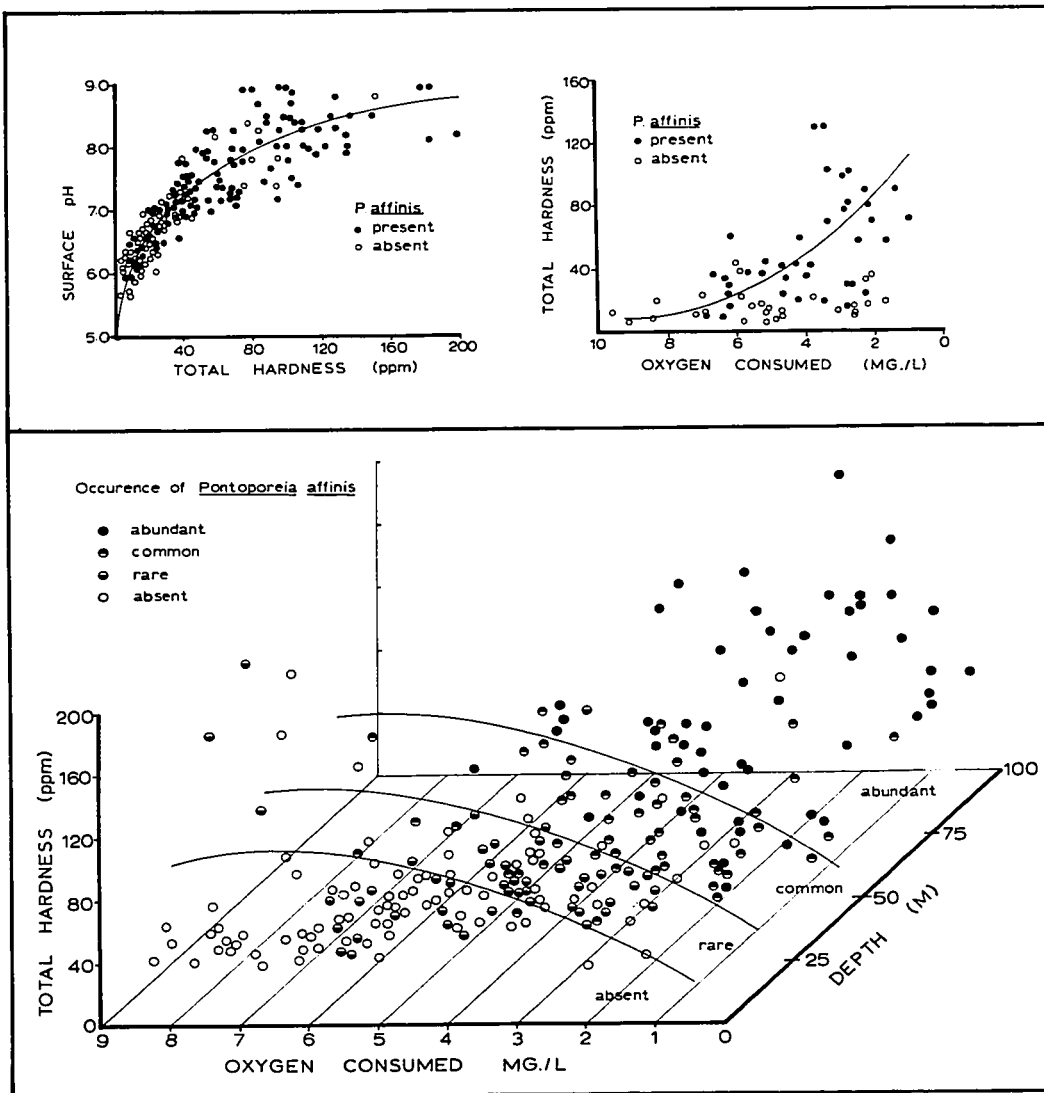


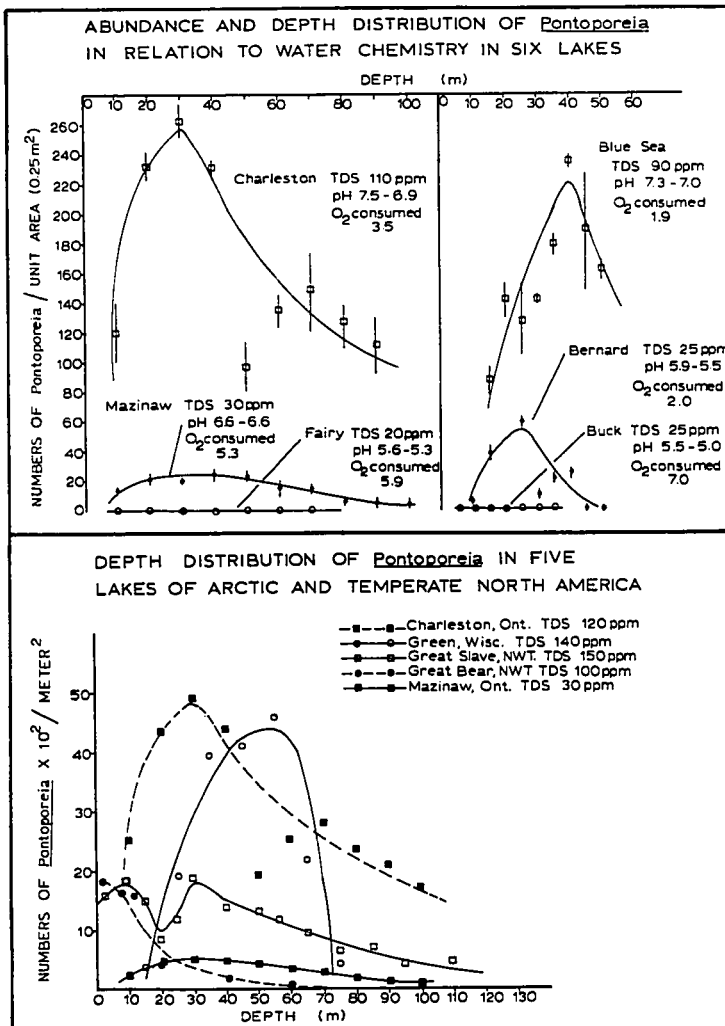
Fig. 22. Relationship between maximum depth, total hardness, oxygen consumption, and the occurrence of *Pontoporeia affinis* in the study lakes.

For example, the average size of penultimate animals in Mazinaw Lake (TH 36 ppm, O₂c 5.3 ppm) was only 6.2 mm, whereas in nearby Canoe Lake (TH 90 ppm, O₂c 1.4 ppm) the average size was 9.5 mm. Intermediate sizes between these extremes occurred in lakes with intermediate chemical conditions.

Results of the ekman sampling indicate that population size of Pontoporeia decreases with decreasing TH and increasing O₂c (Fig. 23A, Table 5). The abundance and depth distribution of Pontoporeia in my study lakes were similar to findings in other lakes (Fig. 23B) (Juday and Birge 1927; Larkin 1948).

Abundance of Pontoporeia first increases and then decreases with depth (Fig. 23A), but this change does not seem to be precisely related to changes in pH (Table 5). Other factors such as increase of CO₂ or decrease of food with depth, may be important in the decline of Pontoporeia abundance at greater depths. Usually Pontoporeia was absent from lakes with hypolimnion pH below 5.5 or from deeper regions of hypolimnions, where pH is below 5.5 (i.e. Lake Bernard, Table 5). The absence of Pontoporeia below 10 m in Little Deer Lake, Saskatchewan (Koshinsky 1965) was probably due to the pH-O₂c situation in that lake. Koshinsky gave a color of 26, which corresponds to 6 ppm O₂c (Fig. 43), and a hypolimnion pH of 6.5 for this lake. Both levels are within the critical range of these factors for survival of Pontoporeia (Fig. 22).

Obviously, low TH-pH and high O₂c restrict the occurrence of Pontoporeia both between and within lakes. It is probable that these factors are linked to osmoregulation and calcium



A.

B.

Fig. 23. A. Results of ekman dredging in six of the study lakes (see Table 5). B. Comparison of the depth distributions of *Pontoporeia* in five North American lakes. (Green Lake, Juday and Birge 1927; Great Slave and Great Bear Lakes, Larkin 1948; Charleston and Mazinaw Lakes, Dadswell, this study).

Table 5. Average number of Pontoporeia affinis per ekman grab in relation to depth and water chemistry in nine selected lakes.

Charleston Lake, Aug.18, 1971

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto-poreia</u>
0	22.0		8.5	0
10	12.0		7.5	120
20	6.5		7.2	232
30	5.5	6	7.2	263
40	5.0		7.2	231
50	5.0		7.2	96
60	5.0		7.2	134
70	4.5		7.2	147
80	4.5		7.1	145
90	4.0	6	7.0	111

Total hardness ... 130 ppm
 O₂ consumed 20 m .. 4.3 ppm
 90 m .. 3.5 ppm
 Nos. ekman/depth .. 2

Mazinaw Lake, Aug.17, 1971

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto-poreia</u>
0	21.5		7.3	0
10	13.0	8	6.6	14
20	6.5		6.6	21
30	5.5		6.6	20
40	5.0		6.6	25
50	5.0		6.6	23
60	4.5		6.6	15
70	4.5		6.6	14
80	4.5		6.6	6
90	4.0		6.6	5
100	4.0	6	6.6	4

Total hardness ... 36 ppm
 O₂ consumed 10 m .. 5.3 ppm
 100 m .. 5.9 ppm
 Nos. ekman/depth .. 2

Round Lake, Aug.16, 1971

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto-poreia</u>
0	21.0		7.4	0
10	13.0		6.4	12
15	7.5	8	6.3	27
20	7.0		6.1	22
25	7.0		6.1	16
30	7.0		6.1	22
35	7.0		6.1	16
40	6.5		6.1	33
45	6.5		6.0	44
50	6.5	6	6.0	45

Total hardness ... 30 ppm
 O₂ consumed 10 m .. 5.8 ppm
 50 m .. 4.0 ppm
 Nos. ekman/depth .. 2

Fairy Lake, July 14, 1972

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto-poreia</u>
0	21.5		6.3	0
10	8.0	11	5.6	0
20	5.5		5.6	0
30	5.0		5.6	0
40	5.0		5.5	0
50	4.5		5.4	0
60	4.5		5.3	0
70	4.5	7	5.3	0

Total hardness ... 20 ppm
 O₂ consumed 0 m .. 5.9 ppm
 Nos. ekman/depth .. 3

Blue Sea Lake, Aug. 20, 1971

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto- poreia</u>
0	21.0		8.5	0
10	18.0		8.5	0
15	8.0	7	7.3	86
20	7.0		7.1	140
25	6.5		7.1	125
30	6.5		7.1	141
35	6.5		7.1	178
40	6.0		7.0	235
45	5.5		7.0	188
50	5.5	6	7.0	161

Total hardness ... 90 ppm

O₂ consumed 15 m .. 1.9 ppm
50 m .. 2.3 ppm

Nos. ekman/depth .. 2

Canoe Lake, Aug. 19, 1971

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto- poreia</u>
0	22.0		8.5	0
10	12.0		8.5	5
15	8.0	6	7.3	32
20	7.0		7.3	10
25	6.5		7.2	13
30	6.5		7.1	33
35	6.5		7.0	11
40	6.0		7.0	16
45	5.5	6	7.0	1

Total hardness ... 90 ppm

O₂ consumed 15 m .. 2.8 ppm
45 m .. 1.4 ppm

Nos. ekman/depth .. 2

Bernard Lake, Aug. 7, 1972

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto- poreia</u>
0	22.0		6.7	0
10	13.5		6.0	2.5
15	10.5	9	5.9	38
20	9.0		5.9	42.5
25	8.0		5.8	58.5
30	7.5		5.8	10.5
35	7.0		5.7	21
40	6.0		5.5	24.5
45	6.0		5.5	0
50	6.0	8	5.5	0

Total hardness ... 25 ppm

O₂ consumed 10 m .. 2.0 ppm

Nos. ekman/depth .. 2

Buck Lake, Aug. 1, 1972

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto- poreia</u>
0	22.0		5.7	0
10	7.5	9	5.5	0
15	6.5		5.3	0
20	6.0		5.2	0
25	6.0		5.0	0
30	6.0		5.0	0
35	6.0	6	5.0	0

Total hardness ... 25 ppm

O₂ consumed 10 m .. 9.2 ppm

Nos. ekman/depth .. 3

Lac Albanel, July 10, 1970

Total hardness ... 17 ppm

O₂ consumed 10 m .. 5.3 ppm

Nos. ekman/depth .. 2

Depth (m)	Temp. (°C)	O ₂ (ppm)	pH	<u>Ponto- poreia</u>
0	16.0		6.6	0
10	12.0		6.5	0
15	9.0	9	6.3	0
20	8.5		6.3	0
25	8.0		6.3	0
30	8.0		6.3	0
40	8.0	9	6.3	0

requirements of this amphipod. Further studies are necessary to answer this question.

Factors Affecting Limnocalanus and Senecella

These two copepods are considered together since it appears that interspecific competitive exclusion between the two is taking place in certain lakes, limiting their individual occurrences. Both species can survive the full range of physicochemical conditions found in the study lakes (Fig. 17, Table 4), but they occur together in only 63 (33%) of the 191 localities containing one or the other.

Figure 24A demonstrates the relationship between surface pH, SDV, z_m , and the occurrence of the copepods. Hypervolumes of the four possible community combinations - that is, both occurring, Limnocalanus only, Senecella only, and neither occurring - are outlined in Fig. 24B. Unlike the results of previous workers (Patalas 1971), lake area was not found to be a limiting factor in the distribution of these copepods. They were often found in very small lakes (e.g. Lac Leamy, No. 251, 18 ha).

Limnocalanus usually dominates in lakes with pH over 7.0; Senecella, in lakes under 7.0. The species composition of other crustacean plankton communities is known to be affected by pH (Carter 1971).

Absence of light penetration, however, was the dominant factor determining coexistence of these two species in a lake. Lakes that were either very deep or had low light penetration often contained both copepods. Perhaps in these situations

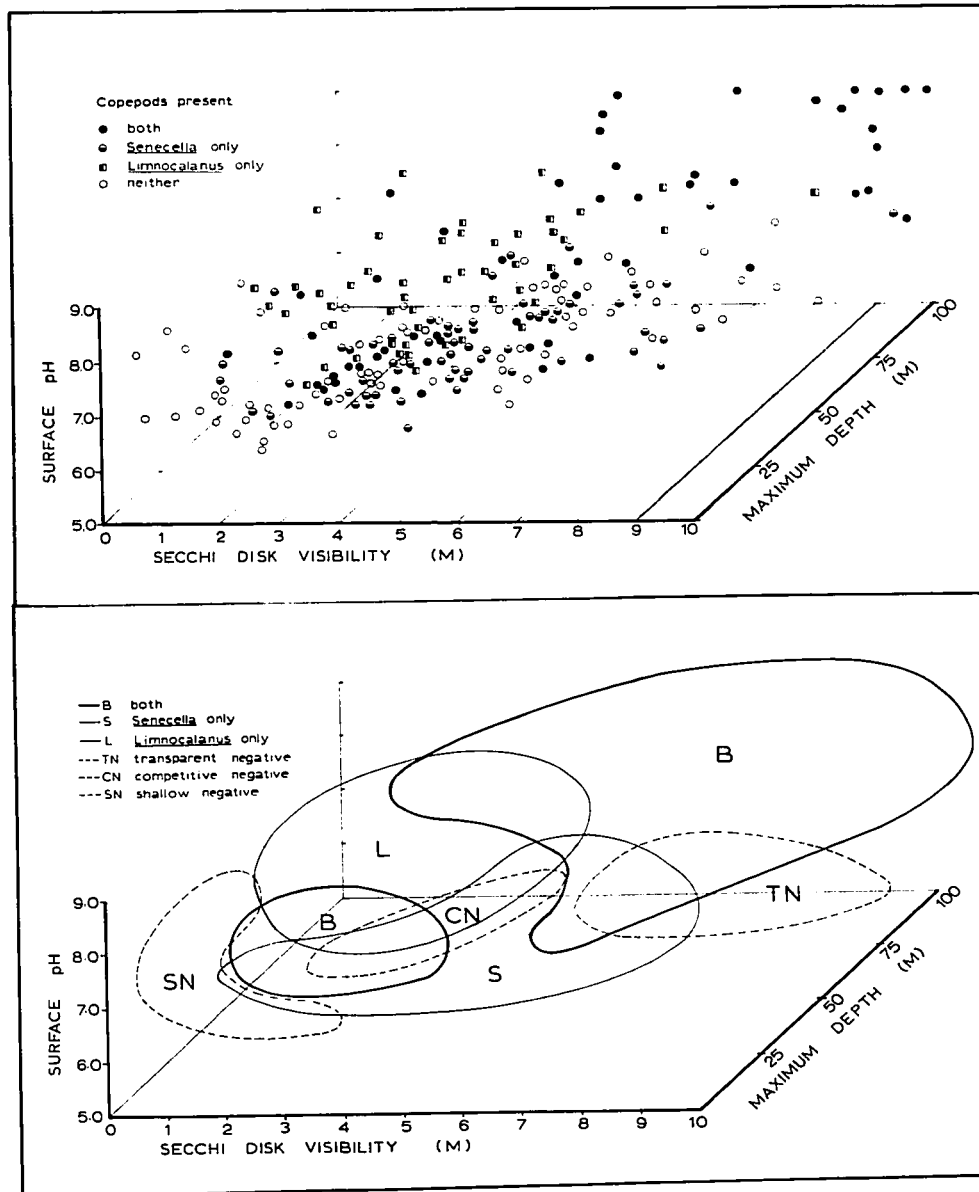


Fig. 24. A. Occurrence of *Limnocalanus* and *Senecella* in the study lakes in relation to maximum depth, surface pH, and secchi visibility. B. Hypervolumes of the deep-water copepod communities.

light tolerance levels of the copepods are not exceeded in most of the hypolimnion, allowing room for populations of the two species to segregate themselves vertically in the water column. Vertical separation of copepod species, usually to avoid interspecific competition for food and space, is a necessary condition in most planktonic communities (Rigler and Langford 1967). Carter (1969) found that Limnocalanus and Senecella vertically segregated themselves in Parry Sound.

Three lake types lack both of the copepods (Fig. 24B). Very shallow lakes were probably unsuitable because of high water temperatures and high levels of incipient light. In moderately deep lakes with extremely transparent water (SDV over 8 m), light tolerance levels of the copepods may be exceeded even in the deepest water, or perhaps fish predation is increased, creating intense selective pressure against these large copepods. Brooks (1968) and Wells (1970) have documented cases in which planktivorous fish have eliminated the larger planktonic forms from certain lakes. Higgins (1966) found that cisco, Coregonus artedii, (the dominant planktivorous fish in the study area) feeds selectively on larger species of zooplankton. The "competitive negative" lakes have physico-chemical conditions that place them in the overlap region of the single species community hypervolumes (Fig. 24B). Possibly, if neither copepod has an adaptive advantage under these conditions, both populations may be reduced to extinction, or to such low numbers as to be virtually unobtainable, in the face of competition with each other.

TEMPERATURE AND SALINITY TOLERANCE OF MYSIS RELICTA
AND SENECELLA CALANOIDES

Introduction

Early in this study it was found that ecologically acceptable lakes east of Ottawa, which had been part of the Champlain Sea, contained few or none of the "glaciomarine relicts." Records from the Arctic Ocean and the Baltic Sea, however, indicate that most of these species are holeuryhaline and that they are found in, or can disperse through, fairly saline water (Holmquist 1959, 1963, 1970; Zenkevitch 1963; Grainger 1965). What factors then prevented widespread dispersal of the community through the Champlain Sea?

Experiments on the thermal and saline tolerances of these species are numerous. Holmquist (1959), Belyeav (1949), Ricker (1959), and Smith (1970) report on M. relictata; Green (1965) and Smith (1972) on P. 'affinis'; Westin (1968) on Myoxocephalus quadricornis; and Lockwood and Groghan (1957) on Saduria. Their results, however, are conflicting, and seem to have been influenced by the physiological adaptations of the test population or the length of acclimation and test periods, that is, if actually no more than one true species is involved in each case. Senecella has never been studied in the laboratory. Nor have previous workers (except Holmquist) considered the combined effects of temperature, salinity, and light, all of which probably acted together to limit dispersal in the Champlain Sea.

Mysis and Senecella were chosen to work with because

they were obtainable in large numbers, were easy to keep, and seemed likely to have the greatest differences in tolerance to the experimental parameters (e.g. M. relictus is known from water of 29°/oo; Senecella has not yet been found in salt water).

Methods

Specimens of Mysis and Senecella were collected from Charleston Lake (Fig. 7, No. 190). Collections were made in 80-90 m of water with a large, conical plankton net (1-m mouth, 11 meshes/cm) hauled vertically by hand. The catch was stored in large plastic bags one-third filled with lake water, inflated with oxygen, and placed in cardboard boxes for transportation. Surface water temperatures during the December-March collecting period ranged from 8° to 0°C. Collecting was done on cool, overcast days and temperatures in the transportation chambers were kept below 6°C. Animals exhibited negligible mortality during collecting and transportation.

Mysis and Senecella were kept separately in 12-liter plastic tanks, 200-300 animals per tank, in a dark constant-temperature room. Laboratory well water and lake water were mixed 50:50 during the first 24 h of captivity to reduce osmotic shock (Fürst 1965) and then replaced by well water. Water in the holding tanks was changed weekly, and dead animals removed daily. The water in the tanks was not aerated, as this has been shown to be detrimental to survival (Smith 1972), but because of its small volume in relation to surface area the water maintained adequate oxygen (8 ppm). Lake-bottom mud was placed in the tanks to provide food, and was

supplemented with a daily feeding of a commercial, dry egg-yolk preparation.

Experimental duration was 10,000 min (7 days), and animals were fed during the test period. Salt tests were done in 6-liter battery jars, thermal tests in 3-liter beakers. Thermal acclimation was at 2, 7, 12, and 17°C for Mysis, and 2, 7, and 12°C for Senecella. Salinity acclimation at each temperature was at 0, 5, 10, 15, and 20‰ for Mysis, and 0, 5, and 10‰ for Senecella. Acclimation was gradual, that is, temperature was raised to the required level by 0.5°C/day and salinity by 5‰ increments/ week. Since earlier workers (Dormaar 1970; Sturgeon 1970) have found that these animals acclimate slowly, they were kept at the acclimation level for at least two weeks, before tests were conducted.

Test temperatures were maintained using a constant-temperature chamber. Solutions for salinity tests were made by dilution of a 32‰ stock solution made from "Instant Ocean Sea Salts" (App. III). Salinity levels were determined by the silver nitrate - potassium chromate low precision titration method (Strickland and Parsons 1970), standardized at 7°C. Saline solutions were made up to 6000 ml and evaporation losses during the test period were replaced by the addition of distilled water. Halfway through each test period, salinity was redetermined and adjusted (if necessary) to within 0.1‰ of the desired level. All tests were done in total darkness.

Depending on the availability of animals, up to 10 but never fewer than six mysids, and up to 50 but never fewer than

10 Senecella, were used at each test level. Testing was by plunging animals directly into the test level from the acclimation level. Test tanks were observed twice daily to record mortality. Mysis was determined as dead when probing with a fine needle produced no response; Senecella, when the animal became opaque (approximately 2 h after death). Percent mortality was recorded after 10,000 min. All tests were duplicated.

Controls containing 10 animals at the original acclimation level were run concurrently with the tests. Invariably, mortality was less than 10%, and was not considered when calculating the LD50's.

Long term survival experiments on Mysis, Pontoporeia and Senecella in 0, 5, 10, 15, and 25^o/oo were run for a period of six months. These were kept at 7^oC, in 6000 ml tanks provided with bottom mud and food. Tanks were examined at weekly intervals and mortality recorded.

Results and Discussion

Upper lethal temperatures of Mysis and Senecella were 20.3^oC and 14.5^oC, respectively. Both values agree more closely with the observed upper thermal limit of these species in nature (Fig. 25) than values obtained by previous workers. Ricker (1959, quoting Larkin's unpublished data) gave the upper thermal limit of M. relictta from Waterton Lake as 22^oC. Smith (1970) disagreed, and obtained a value of only 16.5^oC for animals from Lake Superior. In the first case test times were apparently too short; in the latter acclimation periods (only

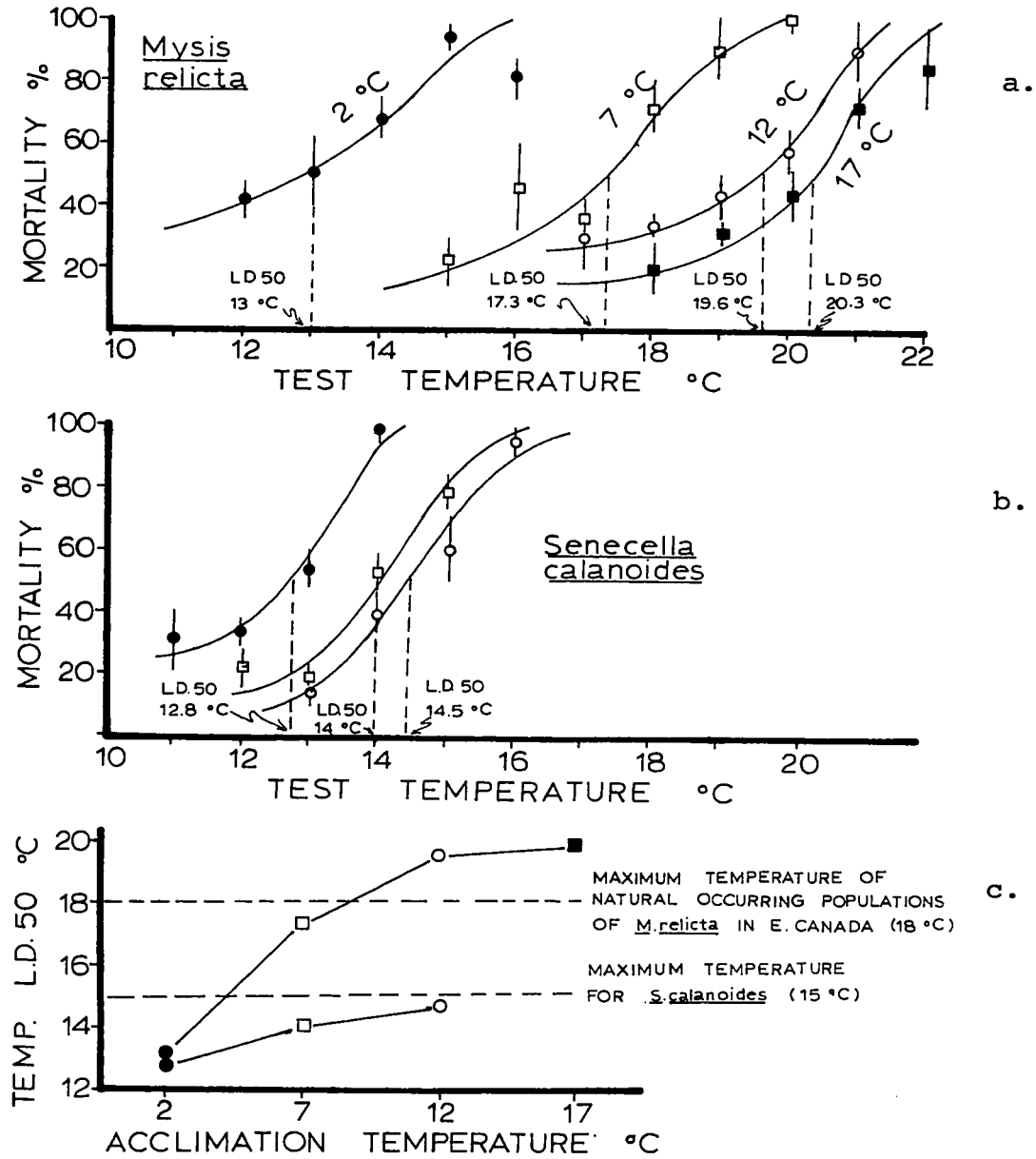


Fig. 25. a. and b. Mortality at various test temperatures after acclimation to 2, 7, 12, and (*Mysis* only) 17°C. c. Change of the thermal LD50 in relation to the level of thermal acclimation.

1 week) were not long enough.

Mysis was able to acclimate and survive over a wide thermal range (2-17°C), and its thermal tolerance rose significantly with acclimation to higher temperatures (Fig. 25). Senecella had only a narrow thermal range. A 10-degree increase in acclimation temperature only raised the upper lethal limit by 2°C (Fig. 25).

Salinity experiments yielded much the same results. Mysis survived up to almost full seawater concentrations (30‰), and its salinity LD50 rose with an elevation of acclimation level (Fig. 26). Holmquist (1959) gave a range of 3-11‰ for occurrence of M. relicta in the Baltic Sea, and reports on a population living at 29‰ in an Alaskan lagoon (Holmquist 1963). Senecella, on the other hand, showed virtually no acclimation to rising salinities, and had an upper lethal limit of only 17.5‰ (Fig. 27). But the salinity tolerance of Senecella is still better than most oligohaline freshwater invertebrates (usually no tolerance above 10‰ (Kinne 1963)) and possibly reflects a moderately recent marine ancestry.

The combined lethal effect of high temperature and salinity is even more striking. Salinity tolerance of Mysis is reduced by high temperatures, particularly at low salinities (Fig. 28a). At higher salinity acclimation levels this effect was negligible. Correspondingly, a rise in salinity at a standard temperature lowers the thermal LD50 (Fig. 28c). With Senecella, rising temperatures lower the salinity resistance,

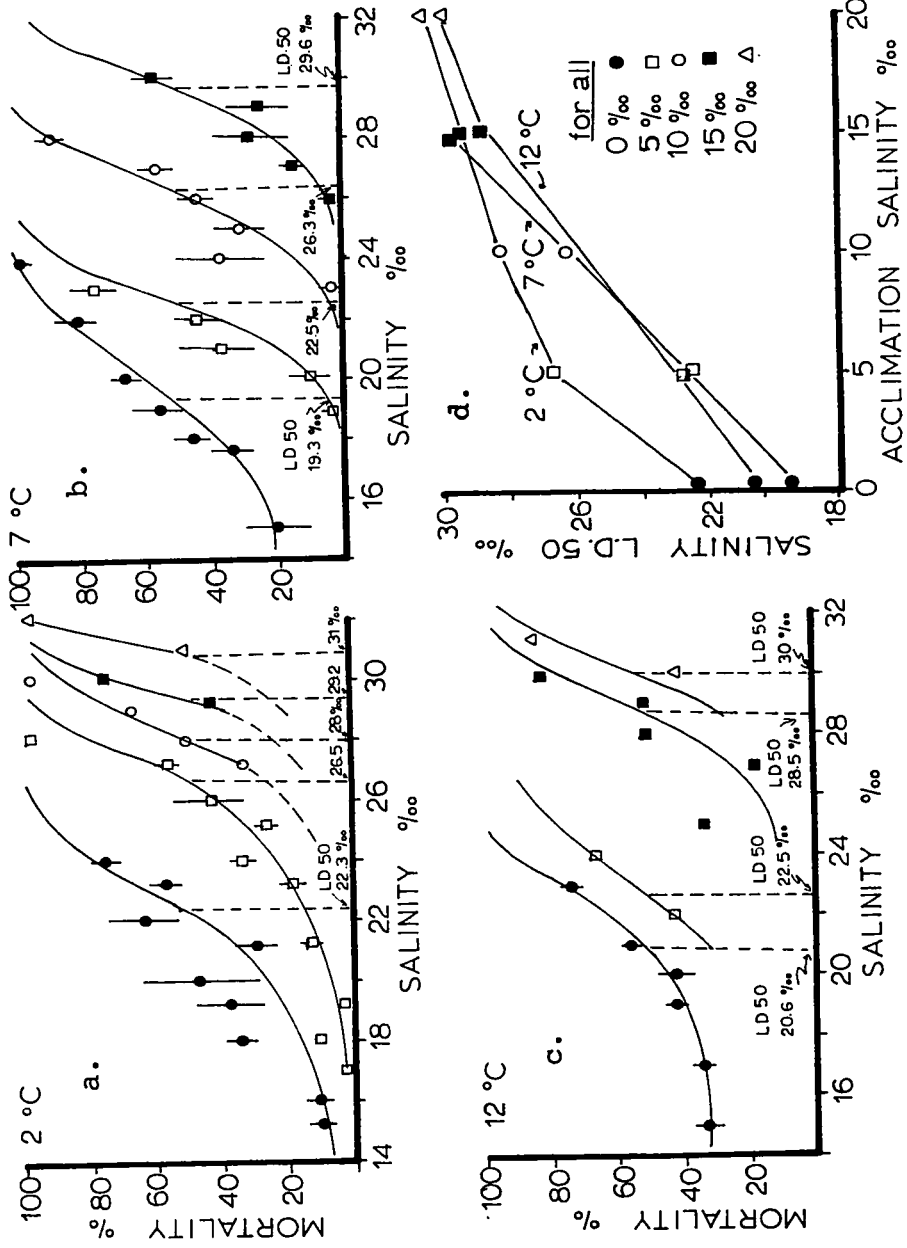


Fig. 26. a,b,c. Mortality of *Mysis relicta* at various test salinities after acclimation at 2, 7, 12°C and 0, 5, 10, 15, and 20‰ salt. d. Effect of acclimation salinity on the salinity LD50 at various temperatures.

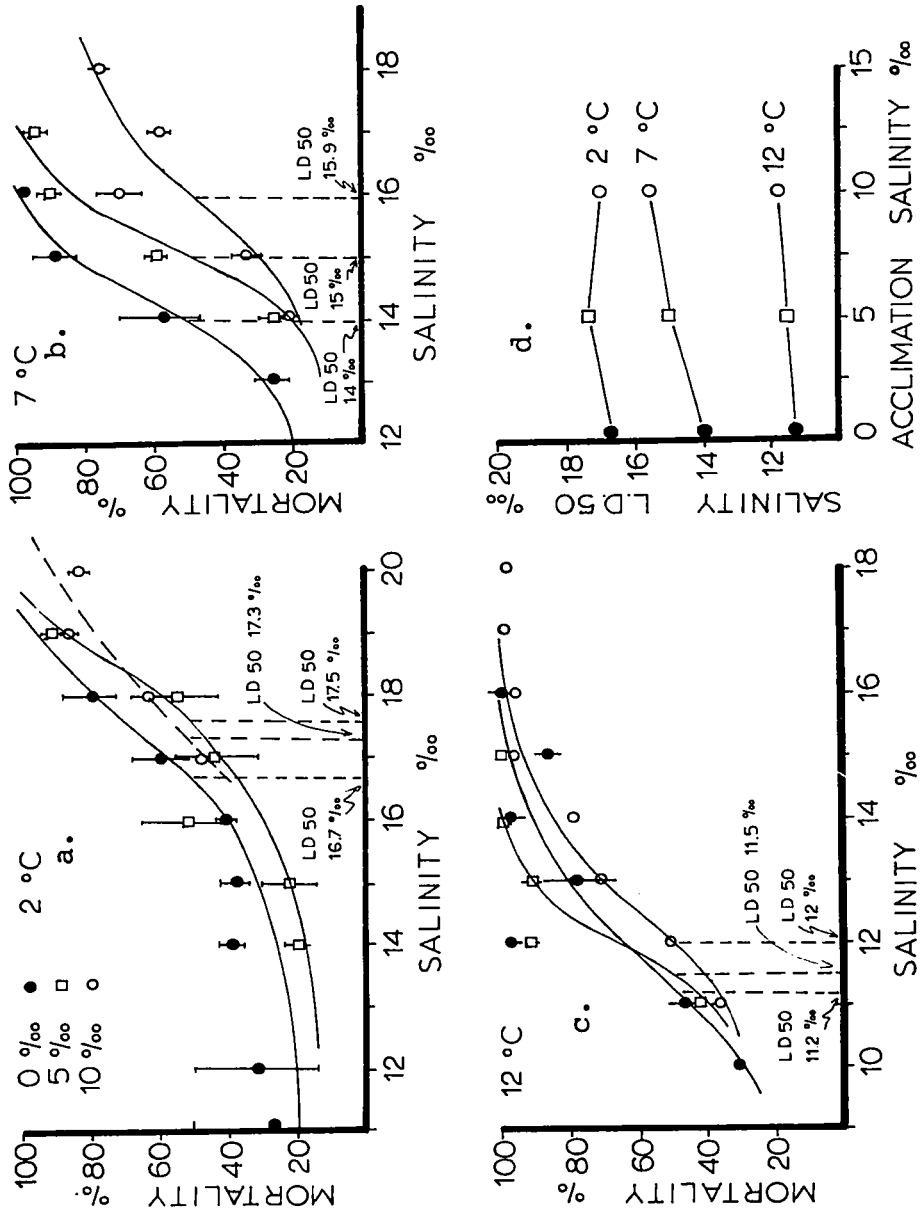


Fig. 27. a,b,c. Mortality of *Senecella calanoides* at various test salinities after acclimation at 2, 7, 12°C and 0, 5, 10‰ salt. d. Effect of acclimation salinity on the salinity LD50 at various temperatures.

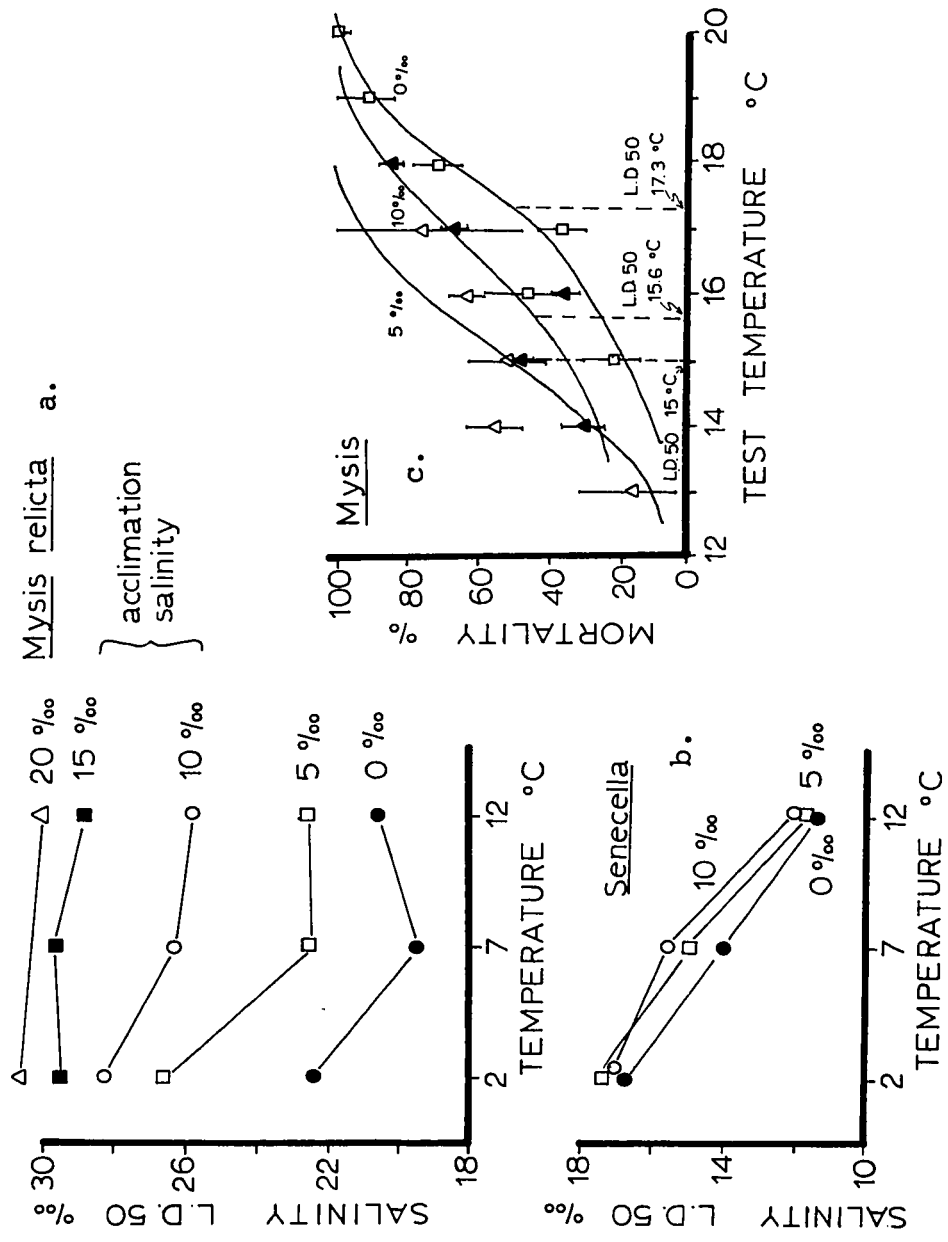


Fig. 28. a and b. Salinity LD50 of *Mysis* and *Senecella* at 2, 7, and 12 °C after acclimation to various salinities. c. Mortality of *Mysis* in relation to thermal acclimation of 7 °C and salinity acclimation of 0, 5, and 10 ‰.

but unlike results with Mysis, prior acclimation to higher salinities does not raise the tolerance level (Fig. 28b).

Long-term experiments (six months) disclosed that freshwater populations of Mysis, Pontoporeia, and Senecella are capable of extended survival in saline water but that survival was best at low salinities (Fig. 29A). Dormaar (1970) stated that M. relicta from Lake Ontario survived more than a month at 30^o/oo. The major loss of animals during the long-term experiments was due to natural die-off of adults; some immatures were kept as long as 16 months. The natural acclimation rate of Mysis to high temperatures in the shallow lakes of the Abitibi district is shown in Fig. 29B. The rate of temperature rise (0.2^oC/day) is quite rapid. The mysids survive up to 2 months at 16-18^oC in these lakes.

Smith (1970) found that a laboratory population of M. relicta underwent continuous die-off when subjected to normal laboratory lighting over extended periods. This confirmed similar reports by Larkin (1948) and Holmquist (1959). I was unable to study light-induced mortality of Mysis, but one observation was made. When an attempt was made to test the salinity resistance of freshwater 2^oC-acclimated Mysis in a lighted room, 100% mortality occurred after only 24 h at salinities as low as 18^o/oo. The LD50 at 2^oC when tested in the dark for a 7-day period was 22.3^o/oo (Fig. 26). Merker (1940) observed that light increased the permeability of crustacean integuments and in some cases caused osmotic failure. Perhaps this is what occurs in M. relicta.

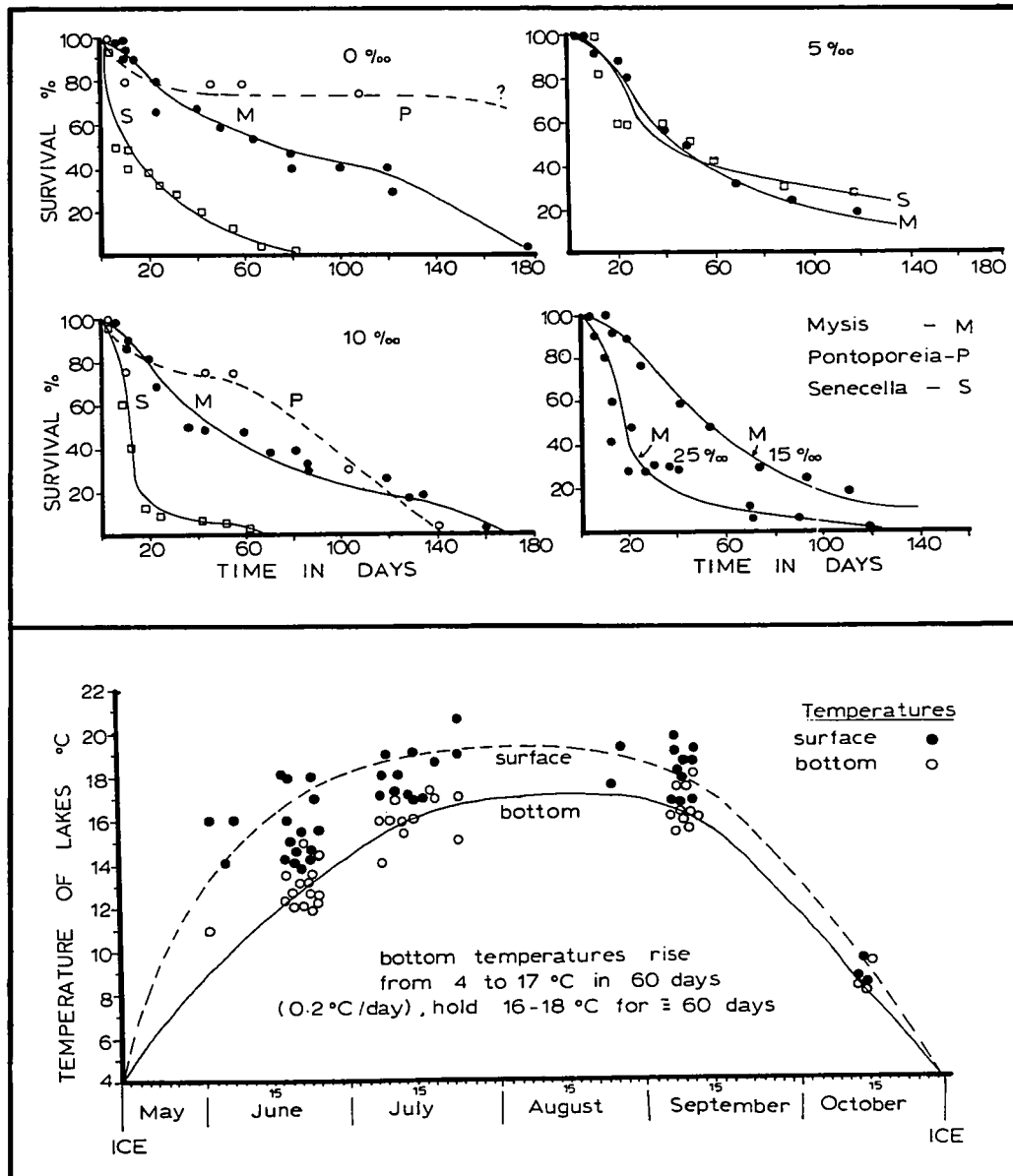


Fig. 29. A. Long-term survival of *Mysis*, *Pontoporeia*, and *Senecella* at various salinity levels. B. Thermograph of the shallow lakes (III Order) in the Abitibi region that contain populations of *Mysis relicta*. Lakes were sampled over a period of three summers.

One source of error that should be mentioned is the differential survival of immature and mature Mysis under environmental stress. Animal shortage made it impossible to consider this factor in my experiments and it has introduced some error in the results. General observations in the field and during experiments indicate that immatures are more tolerant to high temperatures but less tolerant to high salinities than adults.

In conclusion, the experiments indicate that Mysis relicta is a eurythermic, holeuryhaline animal but that Senecella calanoides is only slightly eurythermic and is oligohaline.

. ORIGIN AND EARLY DISPERSAL

During the last 100 years zoogeographers have developed a number of hypotheses to explain the time and place of origin and subsequent holarctic dispersal of the "glaciomarine relicts." Three major views are held: a widespread, multiple independent origin in fresh water after isolation from the sea; a single freshwater origin from salt water and a later dispersal in both fresh and salt water; and a single marine origin and spread to fresh water. Whichever view is true, as Ricker (1959) states:

"The problem of the origin of North American relicts is inseparable from that of the origin of the corresponding relicts in Eurasia."

The multiple origin hypothesis holds that "relict" species evolved independently in each lake from marine ancestors after separation of the lake from a postglacial marine inundation. This was the original argument put forward by Lovén in 1860 to explain the morphological differences between the marine and freshwater "species." Since then, in some of the species, forms identical to the "freshwater" species have been found in marine situations (Holmquist 1959, 1970) and it seems that they, and not their marine relatives, gave rise to the freshwater populations. Moreover, in view of the genetic drift usual in small founding populations, it seems unlikely that independent evolution could lead to such phenotypically similar populations of certain species in Eurasia and North America (Holmquist 1959; Lindquist 1961).

Segerstråle (1962) supports the view of a recent single

origin in fresh water from saltwater forms. He proposed that the "glaciomarine relicts" evolved their form and freshwater tolerance in a large Siberian ice-dammed lake resulting from the trapping of a shallow sea in that area by glaciers during the Riss glaciation, and that they then dispersed east and west mainly by freshwater routes. Segerstråle (1966) later admits there is no good geological evidence in support of this Siberian ice-dammed lake. Holmquist (1959) holds a similar view, but believes the time of origin was earlier, perhaps during the Miocene, when the seas that had covered central Eurasia regressed leaving populations of their ancestors isolated in lakes, and these evolved into the freshwater species.

Lomakina (1952) and a number of other Russian authors (such as Gurjanova and Pirozhnikov, cited in Ricker 1959) believe the "glaciomarine relicts" evolved from marine ancestors in brackish portions of the Arctic Ocean during the Pleistocene and then spread to fresh water. Most new evidence supports this latter view. Some of the "freshwater" species are known to form a major portion of the fauna in arctic, brackish situations (Zenkevitch 1963; Holmquist 1970). Holmquist (1963) found two closely related species of Mysis, the "marine" litoralis and the "freshwater" relicta, living in an Alaskan lagoon without introgression. Other species apparently form morphological clines along salinity gradients (Gammaracanthus, Myoxocephalus, Limnocalanus), what is essentially the "freshwater" form occupying very brackish water, and the "marine" form the open sea. Dormaar (1970) found that "freshwater"

M. relicta still osmoregulates as an estuarine animal, and Lockwood and Groghan (1957) showed that chloride regulation in Saduria entomon living in fresh water was characteristic of a marine organism. All these facts suggest that^{at} the "glaciomarine relicts" evolved recently from marine ancestors, or that they are true marine animals capable of survival in fresh water.

Senecella calanoides may have a different history since it seems to be a primarily freshwater organism. However, it is the only paracalanid in fresh water (Marsh 1933), and all of its relatives are marine. It may have entered the fresh waters of North America earlier than the other species.

It seems plausible to me that the evolution of the "relict" species now occurring in fresh water took place originally in brackish portions of the Arctic Ocean during the late Pliocene - early Pleistocene. During Pleistocene glacial periods, sea levels were lowered by approximately 100 m (Flint 1957) and the Arctic Ocean was cut off from saltwater influx except through the Greenland Strait (Fig. 30). This decrease in area and volume coupled with the tremendous inflow of fresh water by the MacKenzie and the other large rivers, probably created a very brackish Arctic Ocean (Bowman and Long 1968). A stable salinity gradient could have existed in the western part of the ocean for long periods during each glacial maximum, and habitat selection according to salinity could have resulted in speciation (Smith 1966), and in the ultimate development of pre-adapted freshwater animals. I believe a slow recurring situation like this would have been necessary to develop

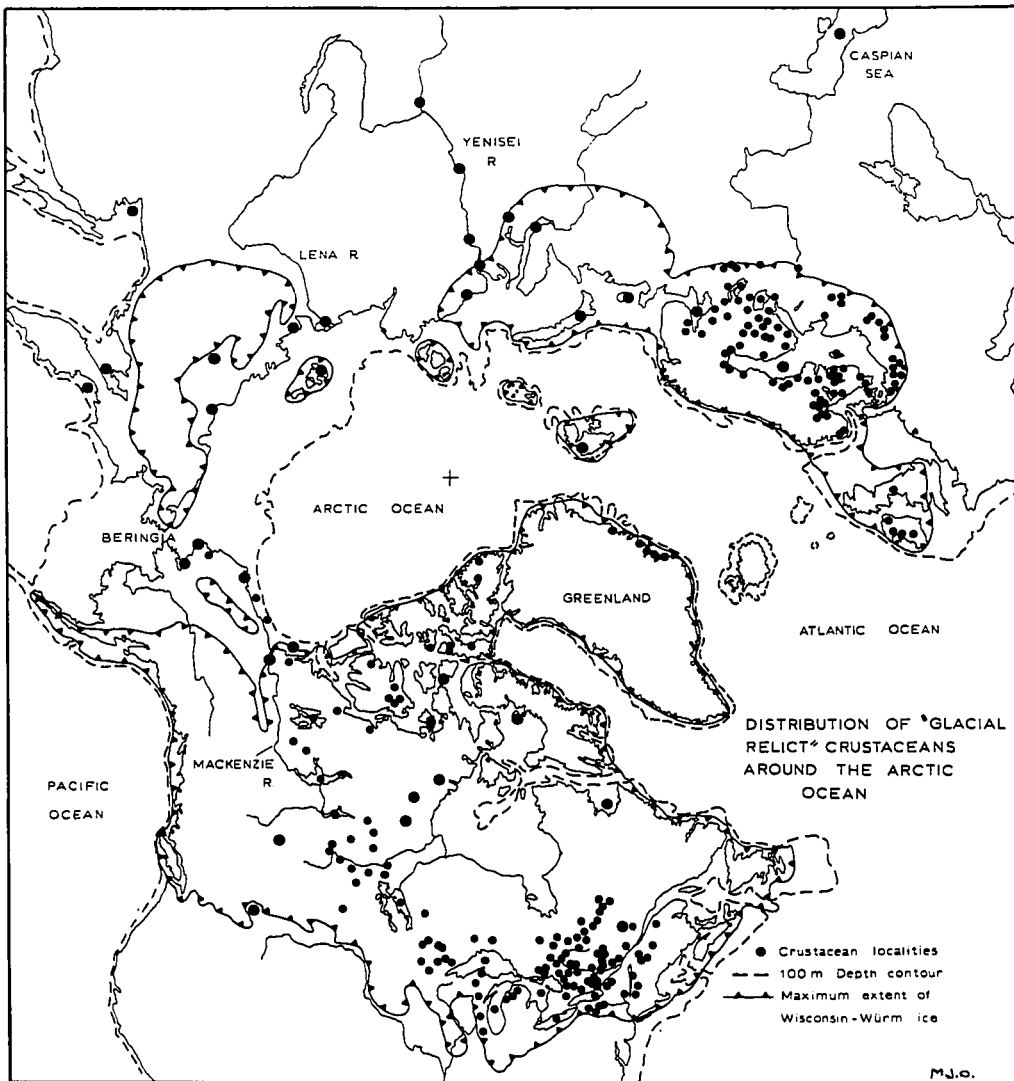


Fig. 30. Maximum extent of Wisconsin - Würm glacial ice and the probable minimum size of the Arctic Ocean during maximum glaciation. Maximum influx of fresh water would have been in the western portion of the Ocean. Distribution of the crustaceans is after Segerstråle 1957; Ricker 1959; Zenkevitch 1963; Johnson 1964; Holmquist 1966 and Dadswell, this study.

freshwater tolerance in these animals. Stable salinity gradients of the type envisaged occur in the Baltic and Kara Seas today, and one or the other of a number of marine-brackish sister species or subspecies dominates, depending on salinity (Lomakina 1952; Segerstråle 1957; Zenkevitch 1963; Van der Land 1970).

Habitat stability usually results in species diversity (Valentine 1971). Organisms adapted to living between 0 and 4°C should respond genetically to stability at this temperature as organisms adapted to, and evolving in, tropical situations do. For example, the stability of the hypolimnion of Lake Baikal over the last 60 million years has resulted in the evolution of over 30 endemic genera of amphipods inhabiting this part of the lake (Hutchinson 1967). It seems reasonable that at least one species pair could have evolved in a cold, moderately stable environment in the last 3-4 million years. Of course these species may be even older and may have been involved in multiple invasions and reinvasions of fresh and salt water. Without a fossil record it is impossible to say.

Although post- and inter-glacial marine inundations have undoubtedly dispersed these animals slightly inland around the Arctic Ocean (Holmquist 1963; Johnson 1964), dispersal to more inland localities not inundated by marine waters during the Tertiary requires another mechanism. Marsh (1893) suggested avian transportation, but this seems unlikely for reasons discussed earlier (see pp. 9-10). Gurney (1923) proposed upstream migration, but this is improbable in view of the planktonic nature of some of the community. Högbom (1917) proposed an

alternate means of dispersal, by proglacial* lakes, a hypothesis that has gained wide support from subsequent authors (Ricker 1959; Segerstråle 1962).

Högbom's "sluicing-up" theory proposed that the "relicts" existed in brackish seas in front of the advancing ice and were trapped and carried inland in the ice-frontal, proglacial waters formed by isostatic depression (Fig. 31). Then from refugia situated at the maximum extents of glaciation, the animals redispersed through the glacial lakes formed during ice retreat. Figures 32 and 33 show that this kind of distribution pattern occurs in both Europe and North America.

I agree with Ricker (1959), in that the likely source of "glaciomarine relicts" for lakes in eastern North America is Hudson and James Bays. Two of the species, Myoxocephalus quadricornis and G. loricatus, are known to occur there (McAllister 1964; Johnson 1964). Early introduction of the organisms into fresh water around the Bay could have occurred during previous postglacial marine maxima, and with the advance of Labrador ice from the east (Flint 1957; Prest 1970) they were "sluiced-up" either from salt or fresh water and carried inland to the south and west in ice-dammed, proglacial lakes.

Senecella may have been in the fresh waters of North America before the Pleistocene. Perhaps it was left behind in arctic, coastal ponds after earlier marine regressions. Species of the marine copepod genus Eurytemora seem to be entering fresh water in this manner at the present time (Holmquist 1970).

* A "glacial" or "proglacial" lake is a lake of which one shore consists of glacial ice.

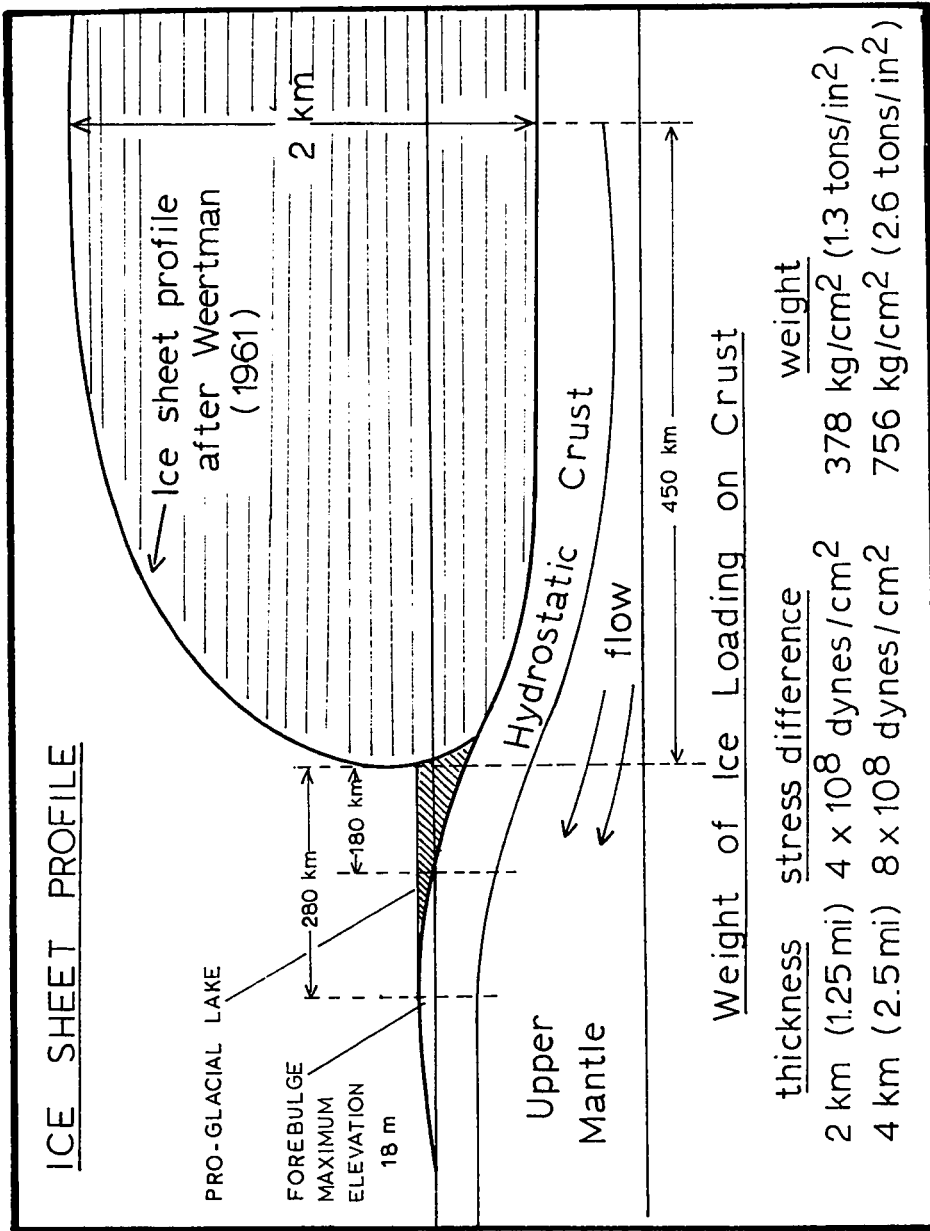


Fig. 31. Profile across an ice front (after Walcott 1970). The ice sheet is approximated by an exponential curve. Note the proglacial lake formed by crustal depression. Normal weight of air pressure on the earth's surface is only 1.03 kg/cm².

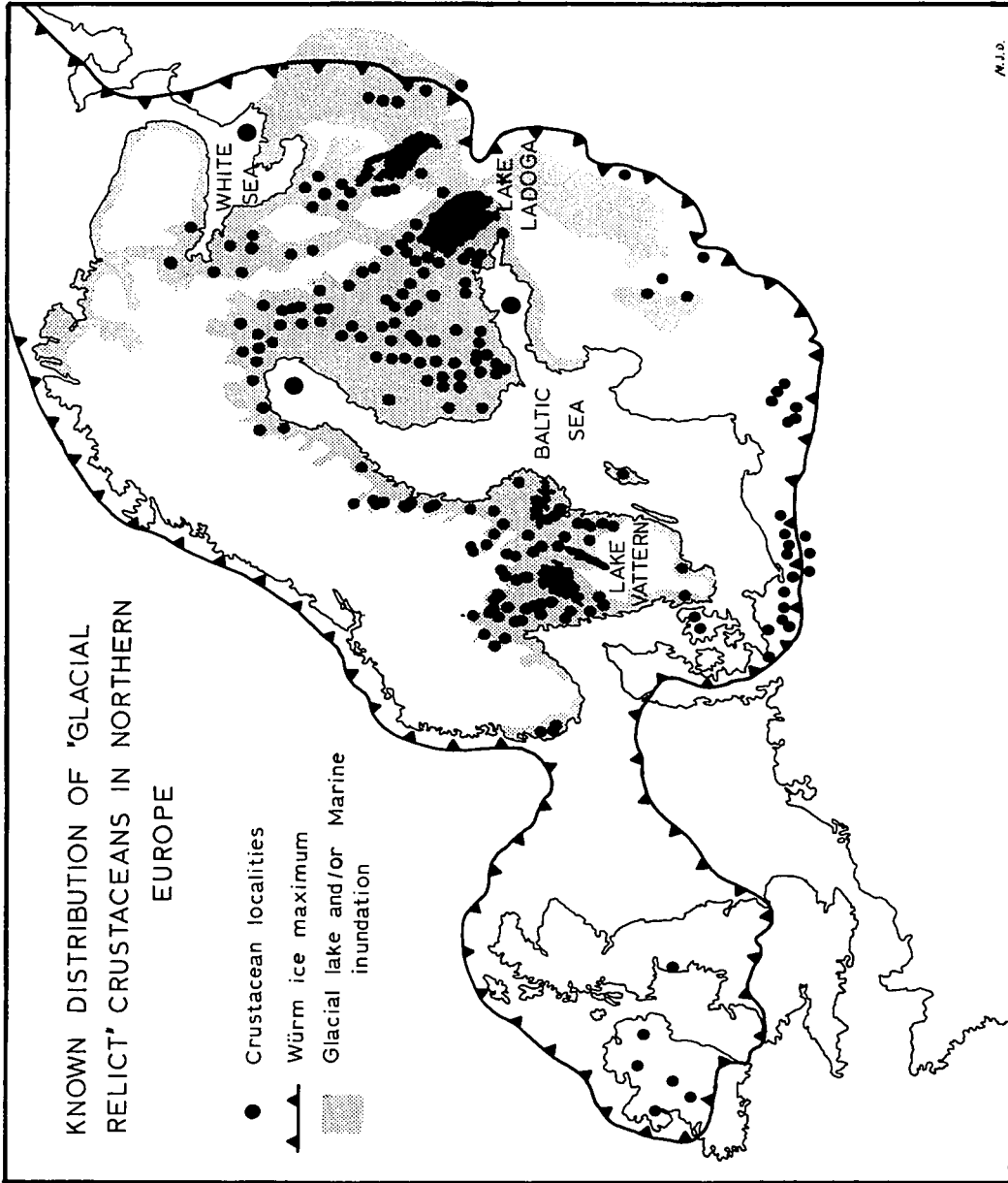


Fig. 32. Distribution of the "glaciomarine relicts" in relation to the maximum extents of Würm glaciation and the glacial lake - marine inundations formed during the retreat of the last ice sheet in Europe (after Segerstråle 1957, 1962; Holmquist 1966).

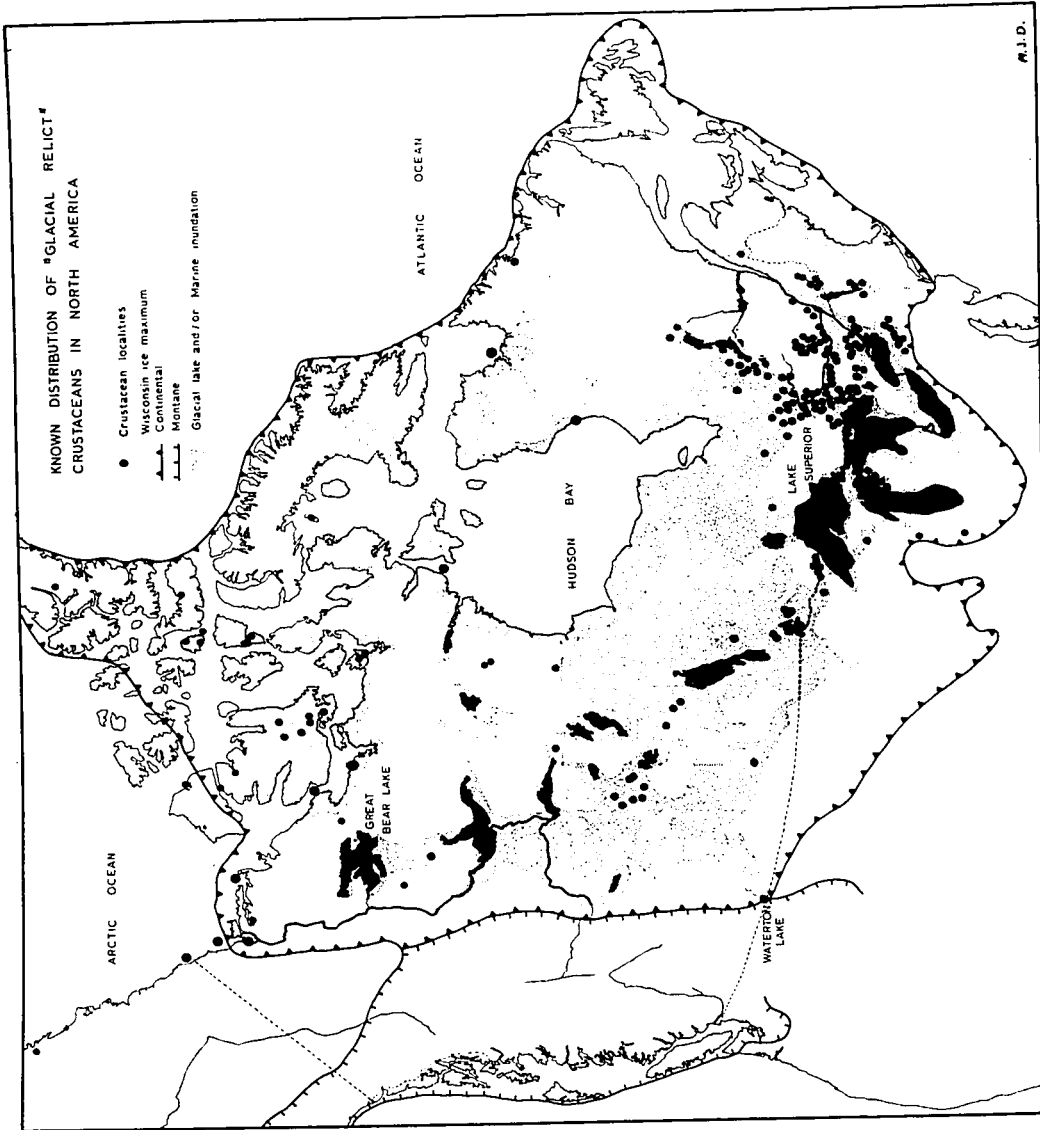


Fig. 33. Distribution of the "glaciomarine relicts" in North America in relation to the maximum extents of Wisconsin glaciation and the glacial lake - marine inundations formed during the retreat of the last ice sheet (after Prest et al. 1968; Ricker 1959; Reed 1963; Johnson 1964; Holmquist 1966; and Dadswell, this study).

With the formation of the proglacial waters Senecella could have joined the rest of the "relicts" and been dispersed inland.

Ricker (1959) thought it necessary for there to have been only one ice center (i.e. in northern Quebec) for the present distribution pattern of the community to have been formed, and he reasoned that ice at a Keewatin center would have blocked dispersal. Even with two centers, however, dispersal inland is possible if the ice advance followed a course similar to the known ice retreat (Prest 1969). Keewatin ice advancing from the north and west, and Labrador ice from the north and east, could have coalesed over central Hudson Bay and trapped a proglacial water body in the southwestern region of the Bay. It is also unnecessary to postulate, as Ricker (1959) did, that the animals must have occurred in the St. Lawrence estuary in order for them to have reached certain eastern lakes. The glacial lake systems and their connections formed during the advance of the last ice sheet are believed to be much the same as those formed during ice retreat (Mörner 1971). This means that even if these species were carried inland at only one point, perhaps in southern Hudson Bay, once they had gained access to the glacial lake systems they could have easily dispersed to the eastern and western limits of the glacial lakes during ice advance and have been in position for transport to refugia around the southern ice margin during maximum glaciation.

The above argument does not necessarily imply that these animals invaded North American fresh waters only as recently as the last ice advance. There were three earlier, major

glaciations and other lesser ones (Prest 1970). Consequently, numerous opportunities have occurred for the "glaciomarine relicts" to disperse inland and the mechanism of inland transport (i.e. proglacial waters) was probably the same no matter in which glaciation these animals gained access to central North America. Evidence, however, of these earlier possibilities has been masked by the last glaciation, of which the present distribution pattern of these organisms in eastern North America is the result, and for that matter, the entire, holarctic distribution pattern of this group can be explained in terms of the last glaciation alone.

POSTGLACIAL DISPERSAL IN EASTERN NORTH AMERICA

The distribution of the deepwater community and the accompanying deepwater fishes (Dadswell 1972) in eastern North America suggests that their major dispersal routes during deglaciation were the interconnected, standing bodies of glacial waters and their outlets. The occurrence of these animals in lakes inundated only briefly by the maximum levels of glacial waters indicates that dispersal closely followed ice retreat.

Names and sequences of glacial waters in the following discussion are taken mostly from Prest (1970). Since North American topographic maps and most geological papers give elevations and distances in the English measurement system, I have used it throughout this section to avoid confusion.

Refugia

Current evidence suggests that during the last maximum glaciation in eastern North America most aquatic organisms survived in refugia south of the ice margin (Frey 1965; Ross 1965; McPhail and Lindsey 1970). Most authors allude to only two refugia, generally in the Mississippi and Atlantic regions (Radforth 1944; Nelson 1968a; Khan and Qadri 1971). There are good indications the deepwater community survived in a Mississippian refugium, since it is known to occur in Green and Geneva Lakes, Wisconsin (Marsh 1893). Both of these lakes are situated next to the driftless area, where proglacial lakes are known to have existed during the Wisconsin maximum (Frye et al. 1965) (Fig. 34A). Geological evidence, however, indicates

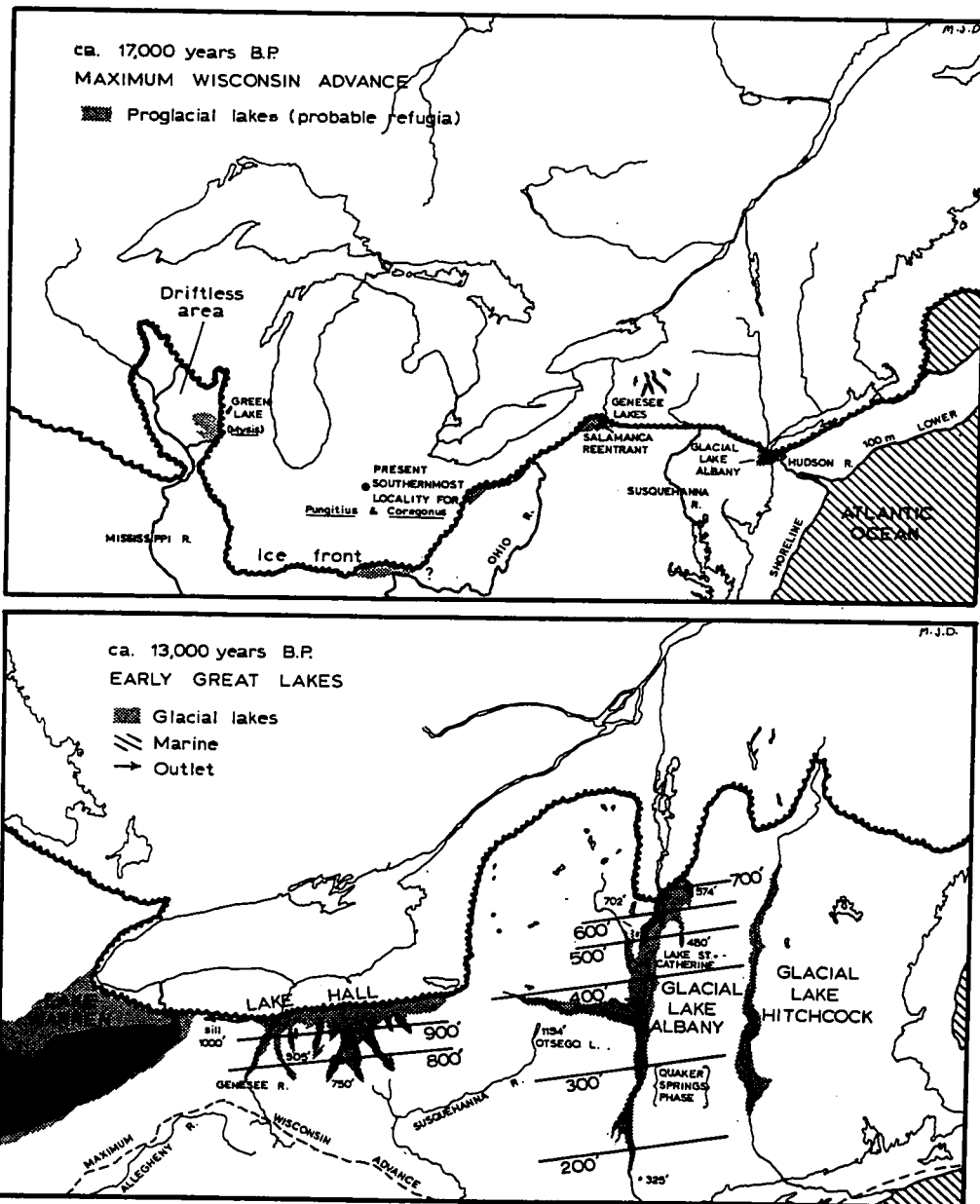


Fig. 34. A. Maximum extent of the last ice advance in eastern North America (after Prest 1970) and possible refugia for the community (after Fairchild 1932; Goldtwaite *et al.* 1965; Frye *et al.* 1965). B. Early glacial lakes in eastern North America with isobases of rebound to present-day elevation (after Fairchild 1932; Goldtwaite *et al.* 1965; Connally 1972). Elevations of present-day lakes and the isobases are in ft. Solid lakes contain the community.

that small proglacial lakes existed in eastern Ohio (Goldthwaite et al. 1965), the upper Genesee River Valley (Salamanca reentrant (MacClintock and Apfel 1944)), and the lower Hudson River Valley (Connally 1972) (Fig. 34A). All of these areas probably served as refugia for the deepwater community.

The absence of the community from lakes in the marine-inundated areas of Maine, New Brunswick, and Newfoundland, as well as the valleys of the Connecticut and Merrimack Rivers (where glacial lakes existed during ice retreat (Brooks and Deevey 1966)) (Fig. 7; Fig. 34A) suggests that no refugia existed east or north of the Hudson Valley. In New England, the advancing ice would have overtopped the Appalachians and the steep downslope gradient would have caused frontal proglacial lakes to drain. Another possibility is that an ice cap already existed on the Appalachians (Prest, personal communication), and with the meeting of the two ice sheets the proglacial lakes were destroyed. In many places, such as the Gulf of Maine, the ice terminus fronted on marine situations that were probably too saline (Kenny 1964) for survival of the community (Fig. 34A). Nor does it seem these animals were able to disperse north from the Hudson Valley in the sea, possibly because of high salinity or temperature.

When ice retreat began, between 17,000 and 14,500 B.P., the community followed in the small proglacial lakes formed along the ice front. As the ice retreated into the Lake Erie basin these small lakes coalesced to form glacial Lake Maumee (Goldthwaite et al. 1965) and with continued ice retreat the

community spread into the Huron basin in the glacial Lake Arkona phase around 13,500 B.P. (Fig. 35).

Finger Lakes Region

Two lines of reasoning substantiate the possibility that a glacial lake in the Genesee River Valley served as the source of the community for the Finger Lakes. First, the community must have been in small regional glacial lakes before the Finger Lakes became connected to glacial Lakes Warren or Iroquois (Fairchild 1932; Goldthwaite *et al.* 1965) because during these later phases, water levels were too low for the community to have gained access to higher lakes such as Hemlock (905 ft) or Skaneateles (867 ft). The community could not have been present in the earlier Finger Lakes (e.g. Newbury phase (Fairchild 1932)) or it would have gained access to Canadice Lake (No. 708. 1012 ft), which was part of the glacial lake at that time. The community probably dispersed from the Genesee Valley glacial lakes into the rest of the Finger Lake basins when these two lake systems joined during the glacial Lake Hall phase about 13,000 B.P. (Fig. 34B) (Prest 1970).

Lake Champlain Region

Whether the community survived in a Hudson Valley refugium is uncertain. Lakes sampled around New York City (Fig. 7) yielded none of the species, but all the sampled lakes were above 300 ft in elevation and Connally (1972) stated that the maximum glacial lake level in this region was only 200 ft. Nevertheless, the community must have been in glacial Lake Albany during the Quaker Springs phase since it is present in

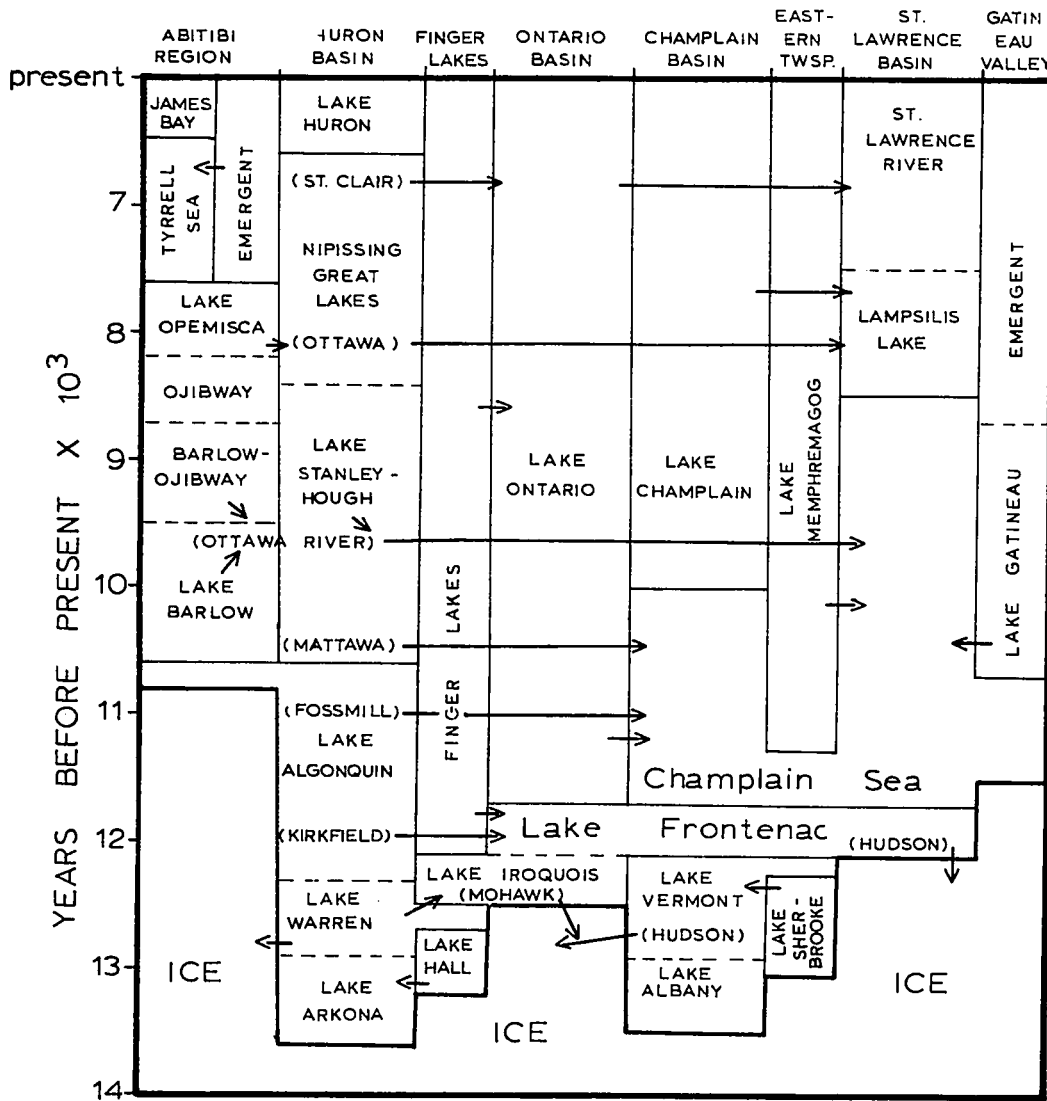
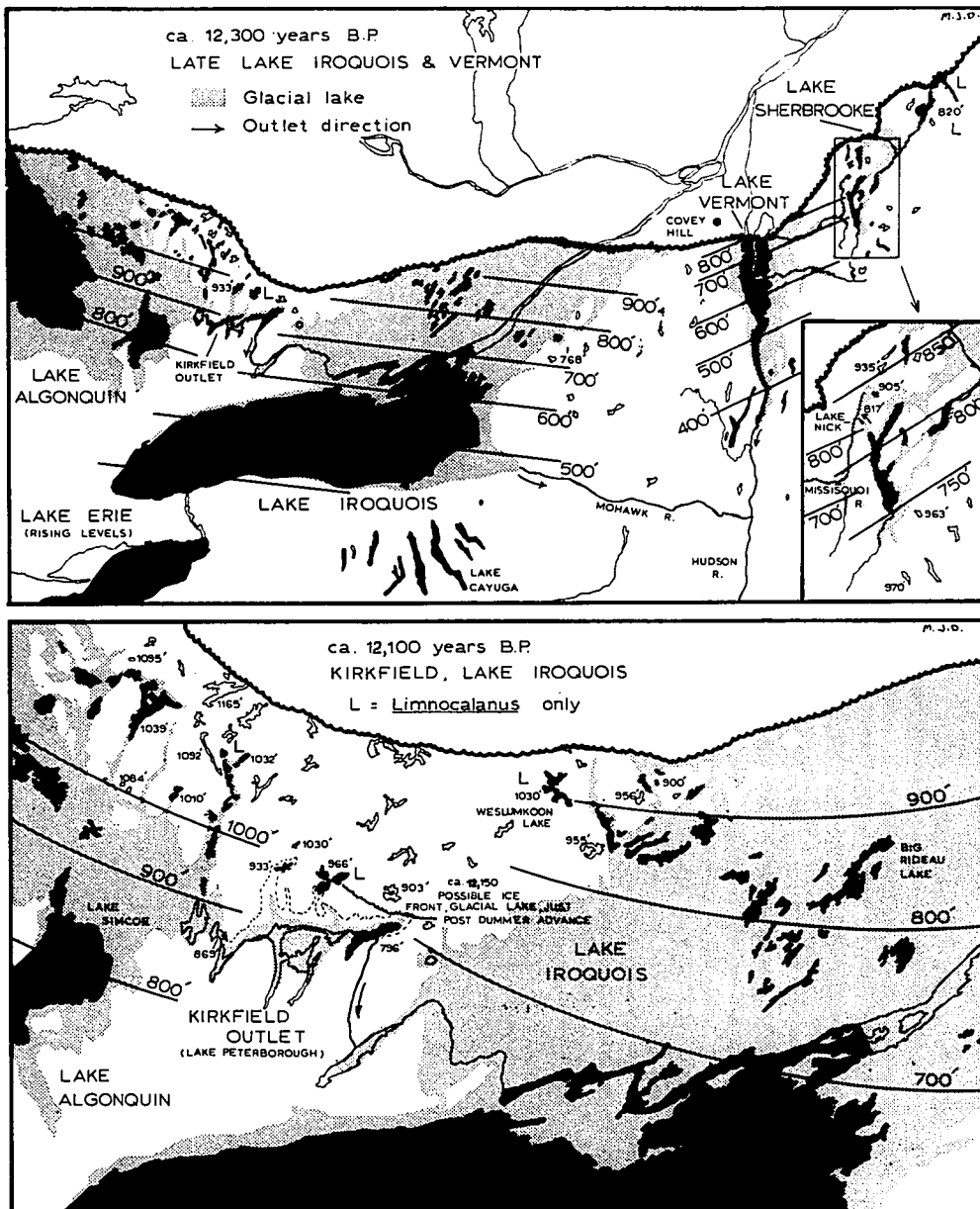


Fig. 35. Sequence and time relationship between the glacial lakes, their spillways, and the marine inundations formed during the retreat of the last ice sheet in eastern North America. Arrows indicate the direction of flow and the destination of the spillways. Correlation is based on Prest (1970).

lakes inundated only by this stage (e.g. St. Catherine ; Fig. 34B). Connally (1972) stated that the Quaker Springs phase existed about 13,000 B.P., but Prest (1970) indicated that the Mohawk Outlet from the Finger Lakes was not operating until 12,800 B.P. This means the community probably survived in a Hudson refugium (possibly glacial Lake Hackensack) unless there was some earlier eastward flow from the Finger Lakes region.

The distribution pattern of the community in the Eastern Townships of Quebec is best related to the outline of the Sherbrooke phase of glacial Lake Memphremagog as given by McDonald (1968). Existing lakes in Vermont, that were inundated by earlier, higher levels of glacial Lake Memphremagog are negative for the community (Fig. 36A, inset; Fig. 7). Eligo Pond (Fig. 42. No. 683), through which the earlier phases of glacial Lake Memphremagog discharged (Hitchcock 1906), is also negative.

The community probably gained access to glacial Lake Memphremagog from glacial Lake Vermont, but McDonald (1968) did not think these two lakes were connected until the late Fort Ann phase of glacial Lake Vermont, by which time the water plane was too low to have introduced the community into the higher lakes in the region where they occur (e.g. Lovering, 803 ft). There is a good possibility, however, that glacial Lake Vermont penetrated up the Mississquoi River and joined with glacial Lake Memphremagog just prior to the Sherbrooke phase. If Chapman's (1937) isobases of the late Coleville phase of glacial Lake Vermont are extended eastward, the level of glacial Lake Vermont is higher than the Lake Nick Outlet



A.

B.

Fig. 36. A. Late glacial Lakes Iroquois and Vermont (after Prest 1970; Coleman 1937) and (inset) glacial Lake Memphremagog (Sherbrooke phase) (after McDonald 1968). B. Hypothetical late phase of glacial Lake Iroquois and glacial Lake Algonquin (after Martin and Chapman 1965). Isobases and present-day lake elevations are in feet. Solid lakes contain the community.

(Fig. 36A). McDonald (1968) noted no evidence of standing water over Lake Nick, but the connection was probably short-lived and any evidence may have been removed by the later flow of water through there. The presence of the community in Lac Orford (No. 307, 905 ft) at the Mississquoi headwaters, and the existence of a large reentrant (calving embayment?) in the ice front when it was in the valley (McDonald 1968), indicate a glacial lake probably existed in the valley.

If the isobases of McDonald's Sherbrooke phase are extended up the St. François River the probability arises that glacial Lake Memphremagog penetrated at least to the level of Lac Aylmer (820 ft) (Fig. 36A) and allowed the community to reach there. The presence of only Limnocalanus and Cottus ricei in Lac St. François (No. 303, 900 ft) indicates only a shallow, transient connection existed with the source area.

Lake Huron - Lake Ontario Region

As the ice front retreated glacial Lakes Algonquin and Iroquois expanded northward carrying the community with them (Fig. 36A). The precise relationship of the present localities of the community to the former extent of glacial Lake Algonquin (Figs. 36A and 36B) was established by Martin and Chapman (1965). The occurrence of the community around Watertown, N.Y., east of Lake Ontario, is restricted to lakes below 700 ft, the highest known level of glacial Lake Iroquois in that area (Coleman 1932).

The occurrence of the community in two of three lakes north of Peterborough, Ontario presents a problem. Crystal

Lake (No. 156, 933 ft) contains most of the community, Mississagua Lake (No. 159, 966 ft) contains only Limnocalanus, and Jack Lake (No. 494, only 903 ft) contains none of the species. For this distribution pattern to have formed, ice must have covered Jack Lake, while at the same time it blocked the Kirkfield Outlet and held glacial lake waters at a high enough level to inundate the other two lakes. The community could have entered the Kirkfield Outlet from glacial Lake Algonquin, when the outlet first opened about 12,500 B.P. (Prest 1970), and then dispersed into the lakes during the Dummer retreat (Fig. 36B). It appears possible that the two lakes containing the community were ice-free, while Jack Lake was still ice-covered because the Dummer ice margin was sharply angled northwest-southeast (Chapman and Putnam 1966) (Fig. 36B). When the glacier retreated from the sill at Stony Lake (796 ft) (Johnston 1916) water levels dropped, becoming too low to penetrate into Jack Lake.

Maximum levels of the northern shoreline of glacial Lake Iroquois have not been mapped toward its northeastward end. To overcome this problem I constructed a hypothetical Iroquois water plane using the known, northwestern Iroquois beaches formed at the time of the Kirkfield Outlet (Johnston 1916; Coleman 1932) and extrapolated a rebound curve northward parallel to the known warped water plane of nearby glacial Lake Algonquin (Fig. 12) (Johnston 1916). When the isobases of this water plane are established on a topographic map of the area, the hypothetical outline of late glacial Lake Iroquois appears as in Fig. 36B. The occurrences of the community are almost

100% within this hypothetical lake boundary. Only Weslemkoon Lake (No. 161, 1033 ft) is outside.

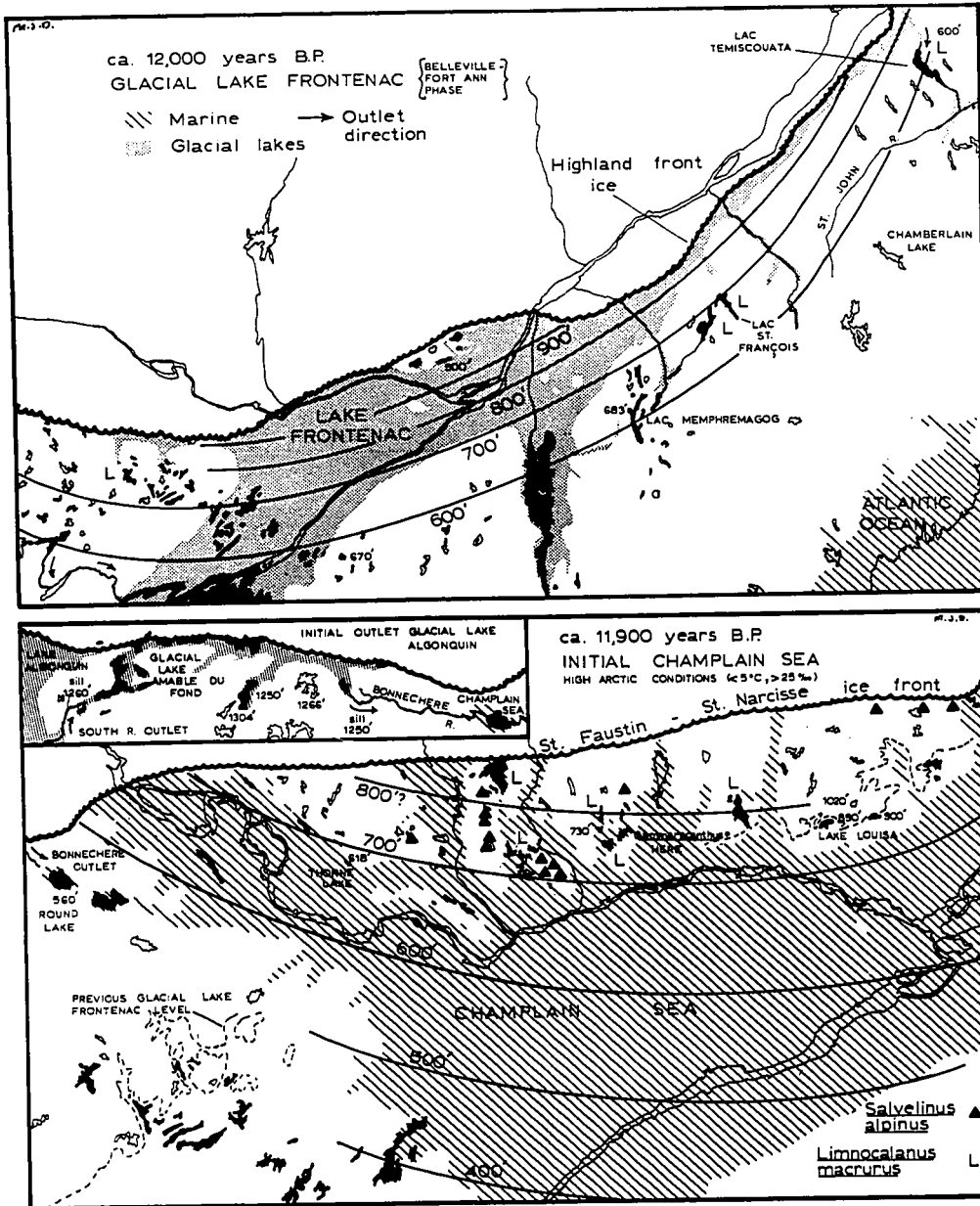
Henderson (1971) did not believe that glacial lake Iroquois extended into the Mazinaw Lake area (no. 167), and attributed the lacustrine deposits there to a small glacial lake held up by a sill at Marble Lake. An examination, however, of 1:50,000 topographic maps of the area revealed it was impossible for this small lake to have existed at the level Henderson gave for the lacustrine deposits; a topographic low at Swamp Creek would have drained the lake below this level. The presence of an outwash boulder train south of Mazinaw Lake was cited by Henderson as evidence that glacial Lake Iroquois regressed while the ice front still covered Mazinaw and the lakes to the north and east. Prest (personal communication) has suggested that the outwash may have been laid down following a small ice readvance into the deep basin of Mazinaw Lake only (after Iroquois had regressed), allowing the community to survive in the adjoining lakes at elevations up to 900 ft. After this ice retreated the community reinvaded Mazinaw from the nearby higher lakes. The occurrence of Limnocalanus in Weslemkoon Lake remains unexplained at the present; perhaps it was introduced there unknowingly by man.

Events in the St. Lawrence Lowland

Around 12,000 B.P. a number of events took place in rapid succession. The ice retreated from Covey Hill and lowered the level of glacial Lake Iroquois, uniting it with glacial Lake Vermont to form the Belleville - Fort Ann phase of glacial

Lake Frontenac (Fig. 37A) (Prest 1970). This lake was maintained in the St. Lawrence Valley by ice blockage of the valley at a point between Quebec City and Rivière du Loup. Ice-calving caused the ice front to retreat rapidly to the Ottawa River and the highlands immediately north of Montreal. The north shore of the Bell^eville - Fort Ann lake phase is unknown, but if Chapman's (1937) isobases for the Fort Ann phase of glacial Lake Vermont are extended northward with the same isobase separation distance as that of the Champlain Sea (Fig. 13B) the 900-ft isobase occurs just north of Montreal (Fig. 37A). The presence of the community in four lakes north of Montreal, but only up to 900 ft in elevation, is probably attributable to this lake phase (e.g. Lac Louisa, No. 295, 890 ft) (Fig. 37B).

The occurrence of Limnocalanus in Lac Temiscouata (Fig. 37A) is problematic and cannot be readily explained on the basis of known geological evidence. This may be a chance occurrence (human transport?) or it may be possible the copepod reached the area from the west through a series of ice-marginal lakes formed along the Highland Front morainic system. Gadd's (1964) statement that "the ice front impinged against the highland at elevations of 700 ft," together with his map of the moraine and the hypothetical isobase situation at this time, makes it possible that a long arm of glacial Lake Vermont may have penetrated to the Rivière du Loup area. Lee (1962,1963) indicated that when the ice front was at Rivière du Loup there was glacial drainage south to the St. John River, and regional topography makes it possible this



A.

B.

Fig. 37. A. Glacial Lake Iroquois-Vermont (Frontenac) just prior to the collapse of the ice dam near Quebec City and the invasion of the sea. B. Early Champlain Sea in the Ottawa - St. Lawrence Valleys. Isobases and present-day lake elevations are in feet. Solid lakes contain the community.

drainage went through Temiscouata. Radiocarbon dates, however, indicate that the sea had penetrated almost to Quebec City by 12,700 B.P. (Prest, personal communication). This would make it impossible, if the date is right, for the glacial lake situation I have outlined in Fig. 37A to have existed at 12,000 B.P. The possibility that Limnocalanus reached Temiscouata via the flowage from the Chaudière Valley to the Upper St. John (Gadd 1964) is ruled out by the copepod's absence from lakes in northern Maine and New Brunswick, all of which were part of a glacial lake that existed in the Upper St. John Valley at the time of the connection (Prest et al. 1968).

The Champlain Sea Episode

At approximately 11,900 B.P the ice retreated from the St. Lawrence Valley south of Quebec City, the Belleville - Fort Ann lake phase drained to sea level, and the ocean then flooded the valley to form the Champlain Sea (Prest 1970). By this time the ice front stood north of the St. Lawrence along the St. Faustin - St. Narcisse Moraine (Parry and MacPherson 1964; Beland 1953) and the northern part of the sea flooded the land up to the present elevation of 700 ft (Johnston 1917; Gadd 1971; Romanelli 1972) (Fig. 37B).

Palaeontological studies have revealed that conditions during the initial stages of the Champlain Sea were high arctic with summer water temperatures below 5°C and surface salinities above 25‰ (Elson 1969; Harington and Sergeant 1972). Because of the proximity of the ice front at this time (Fig. 37B) there was probably a thin surface layer of brackish water along

the northern shore. The occurrence of landlocked arctic char in certain Quebec lakes (Fig. 37B), the remnants of former anadromous populations, is also indicative of arctic saline conditions. Present-day anadromous char populations occur only where summer sea temperatures are below 10°C (Fig. 38).

Some of the "glaciomarine relicts" cannot survive highly saline conditions (see experiments; Segerstråle 1957), and in essence the early phases of the Champlain Sea acted as a barrier to their dispersal. Nevertheless, Limnocalanus and some of the fishes (Dadswell 1972) continued to disperse in the early phase of the sea, probably by brackish surface layers, and Gammaracanthus apparently entered the Sea, during its earliest phase, probably from the Atlantic. Gammaracanthus would have had no trouble dispersing at this time as it is commonly found in salinities as high as 25‰ (Lomakina 1952; Drainville 1970). Heart Lake (No. 287), the only freshwater locality in which Gammaracanthus was found, also contains Limnocalanus and Pungitius, both of which are known to be quite salt-tolerant (Holmquist 1970; Nelson 1968b). The apparent absence of Gammaracanthus from other marine-inundated lakes may be an artifact of collecting. Even in lakes where this species is well known, it is not abundant (Grimas 1969).

Limnocalanus probably dispersed widely in the early phase of the Champlain Sea, but populations survived only locally in areas where maximum dilutions would be expected to have occurred (i.e. river mouths) and were isolated in lake basins in these areas by falling water levels (e.g. Lac Papineau,

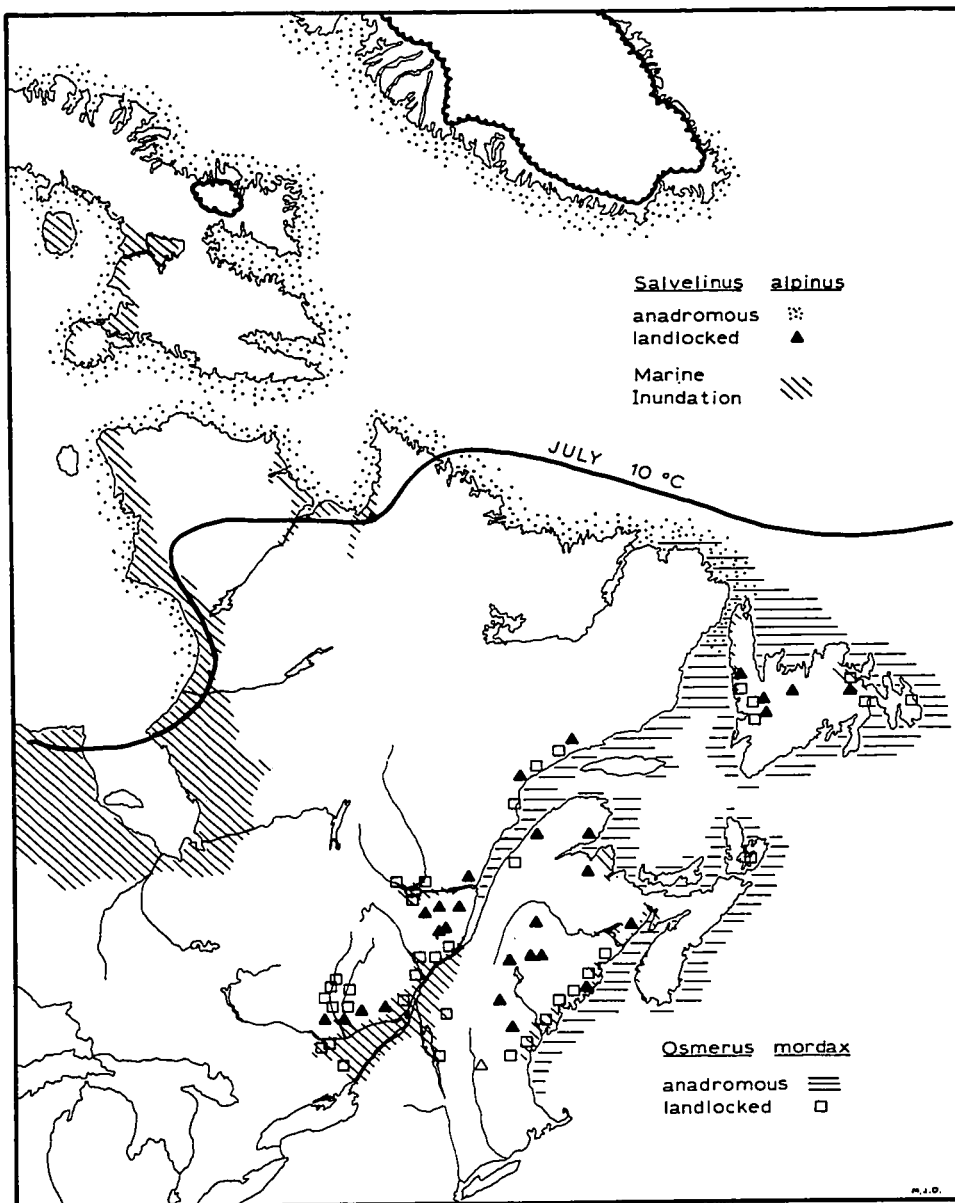


Fig. 38. Present distributions of anadromous and landlocked populations of arctic char (*Salvelinus alpinus*) and smelt (*Osmerus mordax*) in eastern North America (after Legendre 1953; Leim and Scott 1966).

No. 299). Inundated lakes that had broad connections to the sea at this time (e.g. Lac Simon, Fig. 39C) (Faessler 1948a, 1949b) are all negative for Limnocalanus. The salinity in the region of these basins during the period when they were separating from the sea was probably too high for its survival.

Limnocalanus and Myoxocephalus (also quite salt-tolerant (McAllister 1964)) are the only two species of the community known from lakes in the Lièvre Valley. These species and the fishes C. ricei and P. pungitius probably penetrated into the valley before sea level dropped below the 600-ft sill at High Falls, Quebec (Fig. 39B). Once in the valley, they were able to continue dispersing in the glacial lake formed north of this sill (Fig. 39C.)

During the early phases of the Champlain Sea, a brackish water embayment apparently continued to exist in the upper Ottawa Valley (Goldring 1922; Wagner 1970), and the other crustaceans probably survived there (Fig. 39C, Golden Lake). As the Champlain Sea shoaled, the water freshened (Elson 1969), allowing these species to begin dispersal, the initiation of which seems to have been controlled by more than just the salinity tolerance of each species. It seems that dispersal, when it occurred, was nearly simultaneous for all the species, since to reach the Gatineau Valley through standing water, they would have had to disperse through the Champlain Sea, and although M. relicta is more salt-tolerant than either Sene-
cella (see experiments) or the fish Percopsis (Dadswell 1972), their respective distribution patterns in the Gatineau Valley lakes are nearly identical.

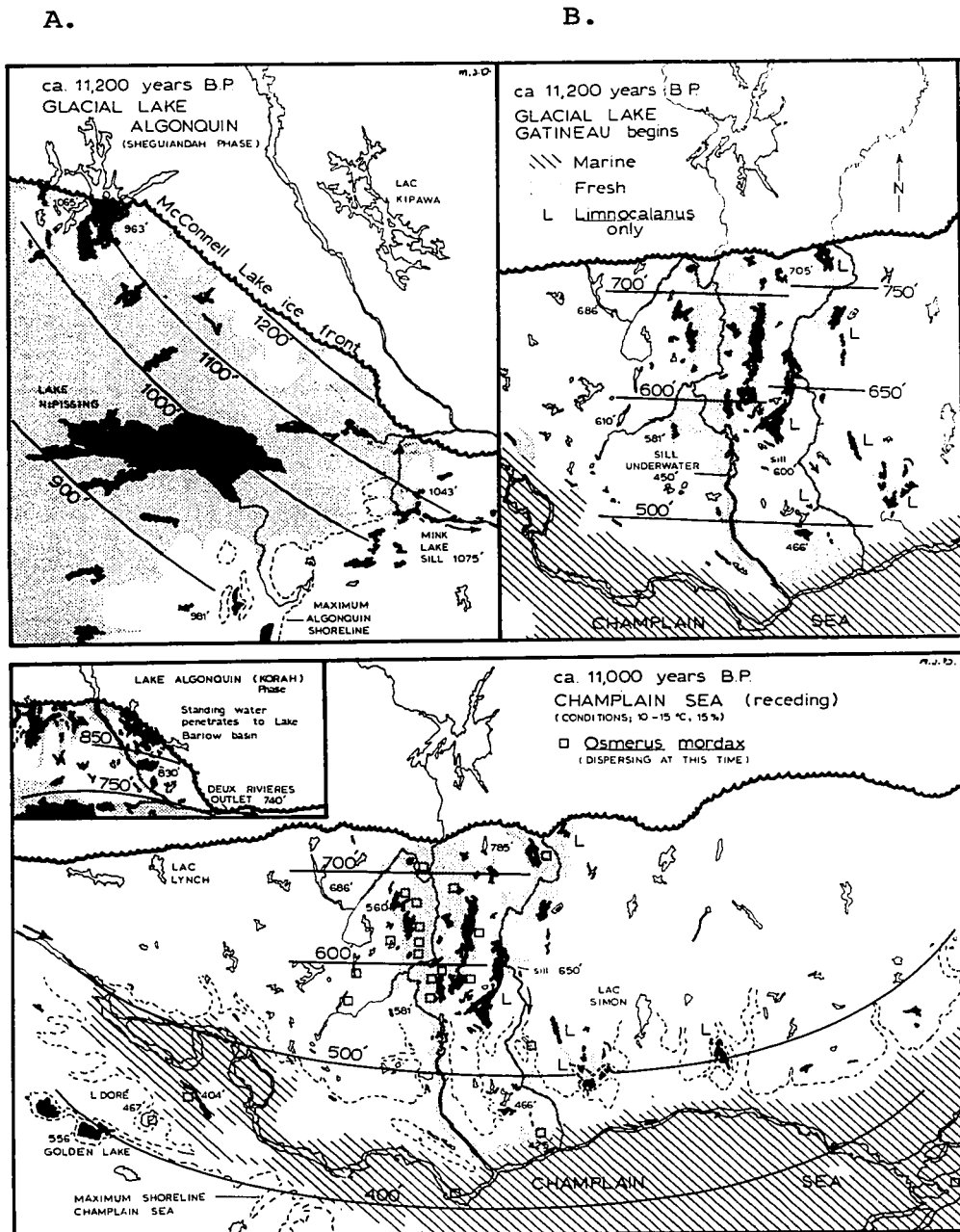


Fig. 39. A. Events in the Temagami - North Bay area, late glacial Lake Algonquin (Boissoneau 1968; ~~Henderson~~ Henderson 1971). B. Early phase of glacial Lake Gatineau. C. Champlain Sea at the time of the smelt invasion (smelt distribution after Dymond 1939; Delisle and Veilleux 1969); (inset), last phase of glacial Lake Algonquin and penetration of the community into the Barlow basin (after ~~Henderson~~ Henderson 1971).

Dispersal probably took place at a time when conditions were tolerable for Senecella (deep salinity less than $15^{\circ}/\text{oo}$). Observations indicate that M. relicta is unable to osmoregulate in sublethal salinities if exposed to light (see experiments). It is possible that as the ice terminus retreated from the northern shore of the Sea, the areas of murky, brackish water were isolated in river mouths and were separated by areas of clear, saline water owing to the rapid precipitation of clay by ions in the sea water (Terasmae 1959). A clear water area such as this may have existed along the Luskville escarpment and acted as a barrier between the upper Ottawa and the Gatineau Valleys until deepwater salinities declined.

Pontoporeia 'affinis' may have begun dispersal slightly before either Mysis or Senecella, since it occurs in three lakes (Fig. 7: Thorne, No. 280; Johnston, No. 281; MacGregor, No. 282) near the Gatineau River at higher elevations than those of lakes inhabited by the other two species. Green (1965) obtained an LD50 of $21.9^{\circ}/\text{oo}$ at 7°C for Pontoporeia from Cayuga Lake. At 7°C , freshwater-acclimated M. relicta has an LD50 of only $19.3^{\circ}/\text{oo}$ (Fig. 26). Also, P. affinis in the Baltic Sea is more salt-tolerant than M. relicta (Segerstråle 1957).

Since the greatest influx of fresh water was probably from the north side of the Champlain Sea (where the glacier was situated) and since dispersal across the sea from southern lakes was probably prevented by high salinities, the probable dispersal route into the Gatineau Valley was across the northern reaches of the Champlain Sea from the upper Ottawa Valley. The hypothetical isobase situation for this period

(Fig. 39B), the constricted neck of the Gatineau Valley, a probable low tidal amplitude (Karrow 1961), and the presence of a 450-ft sill at Low, Quebec blocking deep salt wedge penetration into the valley (Gadd 1971), all point to the probability that a nearly freshwater, standing connection existed between glacial Lake Gatineau and the Champlain Sea. The community probably reached the upper Ottawa down the Fossmill Outlet (Martin and Chapman 1965) and dispersal of the less salt-tolerant species in the Champlain Sea began when water levels were about 600 ft (e.g. Thorne Lake, Fig. 37B). They seem to have reached the Gatineau Valley about 11,200 B.P. when sea level was about 500 ft present-day elevation (Fig. 39B).

Further evidence for this reasoning is found in the present distribution of smelt, Osmerus mordax, in lakes of the Ottawa and St. Lawrence Valleys (Fig. 39C). Anadromous populations of smelt require summer sea temperatures above 10°C (Fig. 38) and this fish was unable to invade the Champlain Sea until 11,000 B.P. when conditions approached those of the present-day Baltic (Elson 1969; Wagner 1978). By 11,000 B.P. sea level in the Ottawa area had dropped to present-day elevation of 450 ft (Mott 1968) (Fig. 39C), and smelt were able to gain access only to lakes in the central Gatineau Valley along with the community. Lakes above 450 ft in the southern portion of the Gatineau Valley and in the upper Ottawa Valley contain the community but no smelt.

As isostatic readjustment continued, the Pagan Falls sill rose above the sea level and separated glacial Lake

Gatineau from the Champlain Sea (Fig. 40B). Glacial Lake Gatineau expanded northward as the ice retreated, reaching a possible present-day elevation of 900 ft at its upper end, and carried the community to the lakes it inundated. Continuing isostatic rebound finally caused the lake to drain, leaving the community in the existing lakes (see Fig. 40B).

The Champlain Sea, during its history, apparently alternated between a dispersal barrier and dispersal route for various species, depending on their individual environmental tolerances. In its earlier phases especially, it exercised a strong influence over the dispersal of aquatic organisms in eastern North America. After 10,500 B.P., sea level in the St. Lawrence Valley dropped below the elevation of any existing lakes and evidence for further eastward dispersal of the less salt-tolerant members of the community does not exist.

Late Glacial Lake Algonquin and Glacial Lake Barlow-Ojibway Events

While the above events were taking place in the St. Lawrence Valley, glacial Lake Algonquin continued to expand northward, and about 11,900 B.P. the first of its northern outlets opened at South River, Ontario (Fig. 37B, inset) (Harrison 1971).

Martin and Chapman (1965) attribute the majority of the community's occurrences in the northern portion of Algonquin Park to the Fossmill Outlet, but they explain its presence in a number of lakes above the outlet level (1075 ft) by "sluicing-up" in a small proglacial lake (to 1250 ft) during a small re-advance of the ice front. There is no evidence to indicate that a readvance occurred at this time (Harrison 1971), but

there is a good possibility that a glacial lake existed in the Fossmill area with maximum levels of 1250 ft, during the operation of the South River Outlet. This glacial lake (early glacial Lake Amable du Fond (Harrison 1971)) could have been held up along the ice front by a sill at 1250 ft just south of White Partridge Lake (Fig. 37B, inset). This outlet would have led down the Bonnechere River.

As the ice front retreated, lower outlets opened, dropping the level of glacial Lake Algonquin (Harrison 1971). By the time the present northern shore of Lake Huron became ice free, water levels stood at a present-day elevation of 1100 ft (Boissoneau 1968), and when the ice front was at the Whiskey Lake Moraine (Boissoneau 1968) the community could have dispersed into lakes in the Sudbury region (Fig. 7: Windy Lake, No. 105, 1093 ft). With further ice retreat, even lower outlets were opened and a large calving embayment opened in the ice front north and west of Fossmill (Harrison 1971). When the ice front stood at the Cartier - McConnell Moraine (Fig. 39A) water levels were only 900-1000 ft north and west of North Bay (Boissoneau 1968). Nevertheless, this was sufficient to allow the community access to the Temagami region (Fig. 39A).

As the ice front continued to retreat in the Temagami area, strong ice flow from Quebec blocked the Ottawa Valley at Deux Rivières (Harrison 1971) and a standing body of water could have extended up the Ottawa River (Harrison, personal communication) (Fig. 39C, inset). If hypothetical isobases are drawn for this water body two facts are revealed: it would have

inundated the lakes in Quebec, next to the Ottawa River south of Lake Temiskaming, which contain the community (Fig. 39C, inset: Lac Beauchêne, No. 96, 840 ft); and a standing water link would have existed between glacial Lake Algonquin and glacial Lake Barlow, allowing the community to disperse into the latter basin.

When the ice withdrew from Deux Rivières, glacial Lake Algonquin drained and glacial Lake Barlow became separate (Fig. 40A). Glacial Lake Barlow extended northward from a sill of morainic material that plugged the Temiskaming trench (Boissoneau 1966), and although its shoreline has not been accurately mapped, it can be approximated. If the elevation of the morainic sill in the Temiskaming trench is assumed to have been at 850 ft (Boissoneau assumes 800 ft), and the standard isobase separation distances are laid off (from Fig. 13B) northward to the ice front as depicted by Prest (1969) for 10,500 B.P., the resulting water plane is as in Fig. 40A. The fit of the known community occurrences to this hypothetical water plane is excellent, especially on the Quebec side of the Ottawa River. The argument is further strengthened by Hughes' (1965) observations of terraces (normally below a maximum lake level) at 985 ft along the Montreal River (at the hypothetical 1000-ft isobase) and at 1025 ft around New Liskeard (near the 1100-ft hypothetical isobase). Vincent (1971) found the upper limit of lacustrine erosion at Ville Marie to be 1000 ft (just north of my 1000-ft isobase).

Between 10,500 and 7500 B.P. glacial Lake Barlow-Ojibway

spread northward and segmented into a series of proglacial lakes (Norman 1937; Prest 1970). The community dispersed northward via this lake series. Its present distribution pattern agrees well with the overall maximum glacial lake coverage given by Prest et al. (1968). As a result of isostatic depression of the region during the existence of the glacial lakes, the occurrences of the community undergo a consistent northeastward rise in elevation, reaching lakes as high as 1350 ft near Chibougamau (Fig. 40C).

When the glacier receded from James Bay these glacial lakes drained, except for a small water body around Lac Mistassini (Prest 1970). This small glacial lake spread northward carrying the community until it reached elevations of 1350 ft north of Lac Albanel (Ignatius 1956), and further expansion was halted by the rapid rise of the Otish Highlands (Fig. 40C: Lac Bethoulat, No. 2, 1330 ft). This ended the eastward glacial lake dispersal of the community in North America.

Further dispersal to the south, however, apparently occurred after this. It seems the upper level of glacial Lake Ojibway barely penetrated into two lakes around 1300 ft in elevation south of Chibougamau (Fig. 7: Malo, No. 15; Rohault, No. 16), and Limnocalanus and the fishes (Dadswell 1972) gained access to them. At first these lakes probably drained northward to James Bay, but isostatic readjustment has diverted their drainage southward down the Chamouchane River. Limnocalanus and the fishes have spread down this river into Lac St. Jean (Fig. 40C).

The alternate dispersal route for Limnocalanus into Lac St. Jean (i.e. down the St. Lawrence and up the Saguenay River) seems unlikely. Not only are water currents against this route (Drainville 1970), but lakes around Lac St. Jean, which were also inundated by the sea, contain no Limnocalanus (Fig. 40C). The presence of Percopsis in Lac St. Jean indicates a primarily freshwater dispersal route was in operation.

The presence of the community in lakes along the parallel Macho-Megiscane River systems also seems attributable to post-glacial rebound (Fig. 40C). The drainage divide in this region is virtually nonexistent and the Bell and Waswanipi River headwaters are strongly interdigitated. It is quite probable that lakes at the present headwaters of these rivers were once within the glacial lake boundaries, and drained northward, but isostatic rebound has diverted their drainage southward, or conceivably some headwater capture has taken place.

Gammaracanthus loricatus occurs in the Saguenay estuary (Drainville 1970). As mentioned earlier this species, unlike the other members of the deepwater community, probably reached eastern North America by dispersing from the Arctic along the east coast of Labrador. At present, it is known from two brackish water localities along the Labrador coast (Dunbar 1954; Carter 1966) and the St. Lawrence estuary (Bousfield and Laubitz 1972). The absence of this species from the Great Lakes and from lake basins that I studied which were inundated by glacial lakes, seems to be more than just an artifact of collecting. The numerous trawls that I carried out, as well

as the many fish food studies (Dryer et al. 1966) and extensive bottom sampling with otter trawls and dredges in the Great Lakes (Teter 1960; Dryer 1965; Henson 1966; Brownell 1970), have failed to find Gammaracanthus. I think it was not present in the refugia south of the ice margin during maximum glaciation and that it did not disperse in the main glacial lake systems.

CONCLUSIONS

Zoogeographers, for justifiable reasons, usually consider the Pleistocene glaciations as a period of destruction that disrupted habitats and caused many extinctions. During the glacial periods, however, unprecedented dispersal opportunities were opened for aquatic organisms and an abundance of lakes not present before the Pleistocene were left behind. In fact, the "glaciomarine relicts" may have evolved their freshwater tolerance in response to conditions present during the Pleistocene, and they appear to have flourished during glacial periods, and to depend on glaciations for inland dispersal.

In eastern North America most of the community's dispersal took place via the glacial lake systems during ice retreat. The importance of glacial lakes for dispersal of deepwater organisms is evident in Fig. 41. Elevation of a lake basin in relation to former glacial lake occurrence is the major factor determining the makeup of the lake's deepwater community. There is a sharp decline in the number of deepwater species as one crosses the former glacial lake shoreline.

Even more striking is the strong similarity between the deepwater communities of lakes in widely separated geographical locations that have been inundated by the main glacial lakes. Although they are separated by 1800 miles, the deepwater communities of Great Slave Lake (Rawson 1951, 1953, 1956) and Thirty-one Mile Lake (Fig. 7: No. 267) have a community coefficient of similarity of 80%. Sam Lake (Fig. 42: No. 573) is only 12 miles from Thirty-one Mile Lake and 340 ft higher,

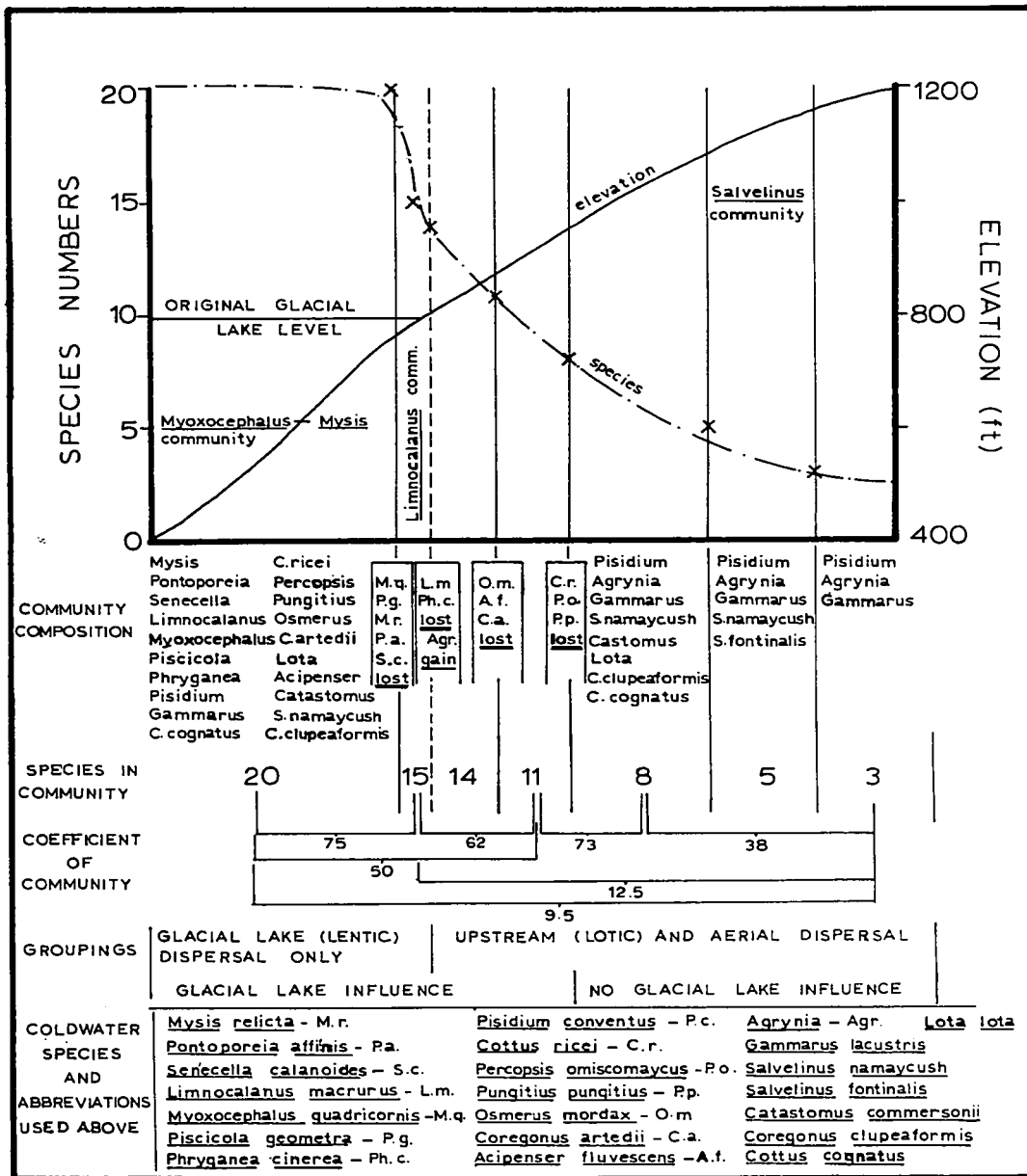


Fig. 41. Change in the species composition of the deepwater community in relation to the elevation of the lake basin and the former glacial lake level across a hypothetical transect of lakes in the Gatineau Valley, Quebec. Note the sharp drop in species number at the former, upper glacial lake level.

but the deepwater community coefficient of similarity is only 14%. Sam Lake was never inundated by glacial waters.

The "glaciomarine relicts" do not form a homogeneous group. Mysis relicta, P. 'affinis', L. macrurus, and Myoxocephalus quadricornis have much the same distribution patterns in brackish and fresh water throughout the Holarctic (Fig. 4). Senecella calanoides, however, is restricted to fresh waters of North America and may have been in fresh water for a longer period than the other species. Gammaracanthus loricatus is primarily a marine form, with a short history of freshwater adaptation, and is restricted to lakes in areas of former marine submergence. Limnocalanus macrurus has dispersed farther east in fresh water than any of the other species in North America and may be able to disperse by means other than standing water connections. In short, they are a group of animals held together mostly by their lack of highly evolved freshwater dispersal mechanisms, and whose distribution pattern is a result of past geological events and present ecological conditions.

I agree with Holmquist (1966) that these species are not relicts. When their distributions are completely established, they will probably be known from lakes and brackish water in an unbroken chain from Quebec, west through the holarctic region to Ireland. This type of distribution pattern is completely unsuitable to Darlington's (1957) definition of a relict. Also, rather than having been left behind by glacial lakes and marine inundations (therefore a relict in the sense of Ekman, cf. Holmquist 1959), one could interpret their

distribution another way; that is, these animals have gained access to fresh water using glacial water systems.

It may be that these are marine organisms that, because of competition from more advanced marine relatives, were becoming relicts in the marine situation, and to avoid organic competition had evolved a more advanced physiological system (holeuryhalinity) to live in very brackish, estuarine situations. This resulted in a certain amount of "pre-adaption" and enabled the animals to survive when introduced to fresh water by glaciation. In fresh water they have found a virtually unoccupied niche (deep water) and have taken advantage of it. They can no more be considered relicts than other ecologically restricted freshwater organisms, such as lake trout, which formerly enjoyed a wider range, but which have become restricted because of ecological conditions. Probably the postglacial range of this group is wider than it has ever been in the past. A better term for this heterogeneous group would perhaps be "glacial opportunists" or "immigrants."

Besides their usefulness in fisheries management, these animals could be used as glacial lake indicators. Because they are restricted to dispersal through standing water, their presence in a lake is conclusive evidence for a former glacial lake connection. By establishing the highest elevation at which they occur in an area, it is possible to determine the highest former level of glacial lakes. This method would be invaluable in inaccessible areas of the north where ground survey work is difficult, and in regions where glacial waters

fronted directly on the ice sheet, leaving no easily discernible geological characteristics.

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Appendix I. Physicochemical characteristics of 716 lakes in the study area, eastern North America. Lake numbers 1-326 are positive for the community; lake numbers 327-357 are negative lakes inside the glacial lake boundaries; lake numbers 358-716 are negative lakes outside the glacial lake boundaries. Abbreviations: No., base map lake number (Fig. 42); Elev., elevation of lake a.s.l. (feet); A_0 , surface area (hectares); z_m , maximum depth (meters); T_m , maximum bottom temperature ($^{\circ}C$); zO_2 , depth dissolved oxygen less than 2 ppm (Meters); TH, total hardness (ppm); pH E-H, pH epilimnion-hypolimnion; SDV, secchi disk visibility (meters); O_2C , oxygen consumption (ppm); Co., color (ppm). All locality names are from Canada and United States Topographic Map Series. Unless otherwise specified all parameters were measured by the author.

No.	Locality	Elev.	A_0	z_m	T_m	zO_2	TH	E	pH	H	SDV	O_2C	Co.	Order
1.	Baudeau	1220	1827	27	9.5	-a	8	6.1	6.0		3.9	9.5	25	II
2.	Bethoulat	1330	1540	24	9.4	-	10	6.2	6.0		3.0	8.5*	30	II
3.	Albanel	1279	33500	48	6.0	-	17	6.6	6.3		3.6	5.3	20	II
4.	Mistassini	1229	100000+	184	4.0	-	26	7.0	6.6		9.0	4.7	30	I
5.	Opataca	1180	5148	13	13.5	-	25	6.8	6.4		3.9	6.0*	20	II
6.	Waconichi	1250	6774	34	9.5	-	42	7.8	7.2		5.7	3.8	5	II
7.	Lymburner	1340	86	24	5.5	-	45	7.4	7.1		6.3	1.0*	5	I
8.	Bourbeau	1358	459	40	4.0	-	76	7.8	7.4		6.6	2.9	5	I
9.	Gilman	1270	134	25	6.0	-	60	7.8	6.7		3.9	4.2	5	II
10.	Chibougamau	1246	17647	56	9.0	-	36	7.2	6.6		5.4	6.7	10	II
11.	Armitage	1310	287	10	13.5	-	20	6.5	6.1		2.7	7.3*	40	II
12.	Antoinette	1250	115	27	6.0	-	50	7.0	6.0		4.8	2.0*	5	II
13.	Caché	1270	220	23	7.2	-	35	7.5	6.4		4.1	4.0*	5	II
14.	Obatogamau	1218	6067	27	7.5	-	20	6.7	5.8		2.8	8.4	30	II
15.	Maló	1320	268	15	9.3	-	15	6.8	6.2		3.0	7.0*	25	II
16.	Rohault	1270	4631	21	10.0	-	15	6.7	6.3		4.1	3.3	10	II
17.	Gabriel	1290	1215	15	13.0	-	10	6.4	6.0		2.9	2.6	30	II
18.	Presqu'île	1185	966	14	11.3	-	20	6.9	6.7		3.0	7.0	30	II
19.	Caopatrina	1198	4086	12	17.0	-	10	6.4	6.3		2.6	7.0*	30	III
20.	de la Surprise	1223	4966	27	9.0	-	12	6.4	6.3		2.8	6.7	40	II

No.	Locality	Elev.	A ₀	z _m	T _m	zO ₂	TH	E	pH	SDV	O ₂ C	Co.	Order
21.	Sylvie	1290	134	18	8.0	-	12	6.3	5.5	2.1	9.0*	50	II
22.	Hébert	1278	2794	15	16.1	-	10	6.2		4.8	4.7	10	III
23.	Lacroix	1270	909	12	17.5	-	12	6.5		2.1	8.9	50	III
24.	Doda	1109	11225	18	12.5	-	15	6.6	6.6	3.3	6.2	30	II
25.	Opemisca	1176	6010	14	11.5	-	20	7.2	7.1	3.0	1.7	30	II
26.	la Tréve	1120	4823	15	12.5	-	15	6.6	6.2	3.3	5.5*	20	II
27.	Renault	990	373	25	6.0	-	14	6.2	5.6	2.4	8.0*	50	II
28.	Goeland	820	29667	11	16.0	-	18	6.6		1.2	6.5*	20	III
29.	Mattagami	796	19618	12	16.0	-	25	6.8		1.1	6.0*	20	III
30.	Waswanipi	830	17704	11	16.0	-	15	6.5		1.5	7.0	30	III
31.	Bachelor	960	928	15	7.5	-	25	6.7	6.1	1.5	6.5*	20	II
32.	Pustimica	925	5435	27	7.0	-	15	6.0	5.9	2.3	5.0*	25	II
33.	Madeleine	1020	1224	12	16.0	-	40	7.2		3.3	5.5*	15	III
34.	Quevillon	940	4105	13	16.0	-	20	6.6		2.1	7.0*	30	III
35.	Cuvillier	1230	952	21	9.3	-	5	5.7	5.5	3.2	7.5*	30	II
36.	Wetetnagami	1205	1732	60	6.0	-	8	6.1	5.6	3.4	5.2	30	II
37.	Maseres	1265	1847	27	8.0	-	11	6.5	5.7	3.4	6.4	40	II
38.	Megiscane	1260	2871	18	15.5	-	10	5.7	5.5	2.2	7.5*	40	II
39.	Valmy	1230	698	39	5.5	-	12	6.1	5.6	3.0	9.0*	50	I
40.	Berthelot	1225	527	18	9.0	-	10	5.9	5.6	2.8	8.0*	45	II
41.	Faillon	1164	2344	82	4.5	-	10	5.7	5.2	2.8	6.5*	30	I
42.	Matchi-Manitou	1120	3550	100	4.0	-	17	6.1	5.6	3.9	5.0*	15	I
43.	Gueguen	1060	3971	14	16.4	-	12	6.5	6.0	1.3	6.9	30	II
44.	Villebon	1070	4058	14	15.0	-	12	6.5	6.2	1.9	7.2	40	II
45.	Granet	1050	3378	17	14.8	15	12	6.2	5.5	2.5	8.4*	30	II
46.	Grand Victoria	1065	8268	11	18.0	-	10	6.1		2.4	5.8	30	III
47.	Parent	990	7943	22	15.0	-	12	6.0	5.8	1.9	7.0*	40	II
48.	Fiedmont	990	823	28	6.0	-	25	6.9	6.2	0.9	4.0*	10	II
49.	Mourier-Lemoine	980	3205	12	14.0	-	24	6.5		1.2	6.0*	20	III
50.	Priessac	958	8690	15	17.0	-	25	6.6		1.5	5.0*	20	III

No.	Locality	Elev.	Ao	z _m	T _m	zO ₂	TH	E	pH	SDV	O ₂ c	Co.	Order
51.	Lois	990	1043	6	15.0	-	35	6.7		1.0	7.0*	20	III
52.	Chicobi	980	1732	6	15.0	-	42	6.7		0.2	8.0*	30	III
53.	Turgeon	950	2000	10	14.0	-	45	7.0		0.7	6.5*	30	III
54.	Macamic	927	4125	11	15.0	-	50	7.5		1.0	7.0*	20	III
55.	Abitibi	868	85760	5	17.0	-	64	8.4		0.1	3.5	10	III
56.	James Bay #	0	-	100	?	?	?	?		?	?	?	
57.	Remi	746	2414	9	15.8	-	120	8.5		1.6	6.0*	10	III
58.	Papakomeka	1005	180	45	5.0	-	70	7.8	6.8	3.2	7.5*	35	I
59.	Clarice	990	297	19	9.0	-	42	7.2	6.2	3.4	4.5*	20	II
60.	Duparquet	896	3617	10	15.0	-	50	7.1	6.7	1.6	6.5*	30	II
61.	Caron	880	1942	67	4.5	-	50	7.4	6.0	3.2	5.9*	20	I
62.	Opasatica	866	4220	42	6.0	-	43	7.6	6.5	1.8	3.5*	10	II
63.	Larder	950	3435	37	6.0	-	80	8.4	7.1	2.1	5.5*	10	II
64.	Mistinikon	1030	803	26	7.0	-	40	7.3	6.1	3.3	6.5*	30	II
65.	Round	886	1148	28	5.8	-	85	8.5	6.6	1.0	6.0	20	II
66.	Raven	950	507	48	4.2	-	35	6.9	6.6	3.2	5.0*	20	I
67.	St. Anthony	990	483	24	6.5	-	26	7.0	5.8	4.2	4.0*	10	II
68.	Kinogami	820	734	36	5.0	-	85	8.3	6.9	2.7	8.3*	40	I
69.	Wendigo	750	388	27	5.8	-	45	7.1	6.2	4.9	4.2*	20	II
70.	Remigny	880	2613	27	6.0	-	32	7.0	6.5	1.1	6.4	30	II
71.	Mountain	930	478	45	8.0	-	40	7.5	6.3	2.7	7.0*	40	II
72.	Mendelssohn	925	433	33	5.5	-	20	6.4	6.0	8.1	3.5*	5	I
73.	Hammond	915	100	24	5.5	18	42	7.5	6.3	6.6	2.0*	5	I
74.	Simard	863	14355	47	7.5	-	15	6.3	5.6	1.2	6.0*	20	II
75.	des Quinze	850	11149	30	8.3	-	15	6.3	6.3	0.8	5.1	20	II
76.	Temiskaming	585	100000+	140	4.0	-	39	7.0	7.2	0.8	2.6*	5	I
77.	Gilles	950	70	28	5.5	-	55	8.0	6.6	6.5	2.3*	5	II
78.	Bay	903	1063	24	6.7	-	24	6.9	6.4	3.3	5.5*	10	II
79.	Kitt	935	80	30	6.0	-	25	6.6	5.8	5.1	5.5*	20	II
80.	Barter	1020	45	30	5.0	-	20	6.1	5.8	5.4	3.0*	5	I

No.	Locality	Elev.	A ₀	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ C	Co.	Order
81.	Lady Evelyn	930	5611	31	7.0	-	20	6.4	5.6	5.7	10	II
82.	Obabika (upper)	932	1000	36	6.0	-	24	6.5	5.9	7.5	5	II
	(lower)		1376	27	7.0	-	24	6.5	6.1	6.0	5	II
83.	Kokoko	975	496	42	6.5	-	38	6.6	5.8	5.1	15	II
84.	Kanichee	990	224	32	4.5	-	30	6.9	6.1	3.9	25	I
85.	Net	980	714	37	5.0	-	35	6.9	6.3	4.2	20	I
86.	Rib	1025	578	47	7.0	-	35	6.9	6.5	6.6	5	II
87.	Rabbit	938	2000	25	9.0	-	35	6.9	6.5	4.8	15	II
88.	Herridge	1043	194	30	4.5	-	27	6.7	6.1	3.6	20	I
89.	Jumping Caribou	1028	404	34	7.5	-	27	6.8	6.0	4.7	10	II
90.	Temagami	962	20000	61	6.0	-	26	6.8	6.6	7.5	10	II
91.	Manitou	872	326	42	5.5	-	28	6.6	6.5	7.5	5	I
92.	Waswiakashi	827	415	24	5.0	-	34	6.8	6.7	5.3	5	I
93.	Cucumber	925	44	24	5.0	-	34	6.8	6.7	5.7	5	I
94.	Red Cedar	914	1868	35	8.5	-	38	6.9	6.4	3.3	25	II
95.	Marten	941	862	49	5.5	-	25	6.4	5.9	3.6	20	II
96.	Beauchêne	840	3205	33	6.5	-	13	6.4	5.7	4.6	10	II
97.	Tee	855	411	55	5.0	-	14	6.2	5.5	5.8	5	I
98.	Kipawa	885	30000	89	5.2	-	15	6.1	5.4	7.5	5	I
99.	Ostabonique	930	2354	41	5.5	-	15	5.9	5.5	4.2	10	I
100.	Cooks	940	145	36	4.9	-	12	6.1	5.5	5.4	5	I
101.	Pomeroy	930	1005	57	5.0	-	18	6.1	5.5	7.9	5	I
102.	St. Amand	940	86	45	5.5	-	20	6.6	5.9	3.9	5	I
103.	Argentier	920	153	25	6.5	-	20	6.6	5.6	5.1	5	II
104.	Wanapitei	876	12519	109	4.8	-	30	6.8	6.7	6.3	10	I
105.	Windy	1093	1200	55	4.3	-	18	6.5	5.9	5.0	5	I
106.	Fairbank	985	653	44	4.2	-	28	7.0	6.3	5.4	5	I
107.	Panache	733	7026	30	8.2	-	26	6.6	6.0	6.9	5	II
108.	Trout	680	800	41	5.5	-	20	6.3	5.5	3.9	20	I
109.	Tomiko	800	1542	24	12.8	22	16	6.1	5.5	3.3	20	II
110.	Tilden	936	396	25	8.9	20	12	5.7	5.4	4.2	20	II

No.	Locality	Elev.	A _o	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ c	Co.	Order
111.	Marin	740	363	42	5.0	-	15	6.5	3.7	3.0*	5	I
112.	Talon #c	636	1293	58	4.5	-	30	6.8	4.2	3.0*	5	I
113.	Smith #	700	183	28								
114.	Turtle #	663	210	50	4.5	-	30	6.9	4.0	3.0*	5	I
115.	Trout	663	1850	74	5.0	-	30	6.9	3.9	3.0*	10	I
116.	Nipissing #	644	83820	51	8.3	40	76	7.4	4.5	5.5*	10	II
117.	Restoule	691	1223	24	6.5	-	25	6.3	3.6	6.0*	20	II
118.	Waukimakog	600	900	29	9.0	-	25	6.7	2.7	6.5*	30	II
119.	Fowke	981	241	51	5.0	-	35	7.3	5.1	3.1*	5	I
120.	Wawashkesh	880	1500	39	6.0	-	20	6.7	3.3	4.5*	10	II
121.	Eagle	1166	901	21	6.5	-	17	6.5	5.1	6.0*	30	II
122.	Bernard	1082	2074	45	5.0	-	26	6.7	3.9	4.5	5	I
123.	Sand #	1110	565	38	6.0	-	20	6.7	4.0	3.8*	5	II
124.	Pickerel	1050	528	33	6.5	-	26	6.5	3.0	5.7*	20	II
125.	Bethune #	1100	111	25	5.0	20	25	6.4	2.5	7.2*	25	II
126.	Doe	956	902	24	6.0	-	25	6.6	3.0	5.9*	20	II
127.	Ahmic #	917	1800	27	7.5	-	24	6.6	3.2	5.0*	10	II
128.	Manitouwabing	700	769	34	6.5	-	25	6.7	2.7	6.6*	20	II
129.	Mill	650	611	38	7.0	-	25	6.3	3.0	6.2*	25	II
130.	Blackstone	655	510	57	5.5	-	25	6.6	6.3	2.4*	5	I
131.	Kashe	796	478	21	7.5	20	15	6.7	3.0	8.0*	30	II
132.	Simcoe	718	76800	43	9.5	35	150	8.5	6.6	1.0	5	II
133.	Ontario #	248	1925120	300	4.0	-	185	8.5	6.0	2.3	5	I
134.	Erie #	572	2542000	57	6.0	30	180	8.5	4.8	3.0	10	II
135.	Huron #	573	6000000	240	4.0	-	110	8.0	8.0	1.5	5	I
136.	Muskoka	739	9493	60	5.5	-	25	6.5	5.4	3.2*	5	I
137.	Rousseau	735	5186	60	4.0	-	24	6.7	6.6	2.0*	5	I
138.	Joseph	735	4268	90	5.0	-	20	6.7	9.6	1.3*	5	I
139.	Skeleton	920	1858	62	5.0	-	26	6.5	9.6	1.0*	5	I
140.	Buck	955	210	24	6.0	-	25	5.7	1.5	9.8	50	II

No.	Locality	Elev.	Ao	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ c	Co.	Order
141.	Vernon	931	1426	32	6.0	-	25	6.1 6.0	3.3	6.8*	30	II
142.	Mary	921	800	54	5.5	-	25	6.6 5.7	3.3	5.5*	20	I
143.	Fairy	931	667	74	5.0	-	22	6.5 5.2	3.6	5.9	20	I
144.	Peninsula	931	650	33	5.5	-	20	6.8 5.6	5.2	4.0*	10	I
145.	Lake of Bays	1034	6104	53	4.0	-	25	6.5 6.1	4.2	4.3*	10	I
146.	Halls	1069	547	69	5.0	-	25	6.3 6.0	7.2	1.8*	5	I
147.	Maple #	1032	331	31	6.5	-	32	6.8 6.1	6.3	3.8*	5	II
148.	Beech	1013	133	28	7.0	-	34	6.9 6.1	5.1	4.3*	5	II
149.	Boshkung	1013	690	60	4.5	-	32	7.2 6.1	6.3	2.9*	5	I
150.	Twelvemile #	1009	345	25	8.0	-	34	7.1 6.2	6.0	2.8*	5	I
151.	Mountain #	1005	309	30	6.5	-	35	7.2 6.1	5.5	3.3*	5	II
152.	Horseshoe	1002	282	21	7.5	20	34	6.7 5.8	6.9	2.9*	5	II
153.	Minden	1000	204	31	7.0	-	35	7.1 6.0	5.5	3.2*	5	II
154.	Bob	924	210	56	5.0	-	34	6.7 5.8	6.9	1.7*	5	I
155.	Big Trout #	1010	190	26	6.5	-	30	6.8 5.5	5.0	4.4*	10	II
156.	Gull	885	996	39	6.5	-	30	7.1 6.3	5.4	2.6*	5	II
157.	Shadow	850	303	22	8.5	15	38	7.1 6.1	5.7	4.7*	10	II
158.	Crystal	933	468	34	5.5	25	102	8.5 6.7	4.8	5.2*	10	I
159.	Mississagua	966	581	34	6.0	-	35	6.9 6.1	4.2	5.5*	20	II
160.	Stony #	769	2000	30	7.5	15	110	8.5 7.0	3.0	5.4*	10	II
161.	Weslemkoon	1039	1933	55	6.0	-	18	6.7 6.1	5.8	3.2*	5	II
162.	Mackie	825	156	22	7.0	-	50	8.0 6.9	6.5	1.5*	5	II
163.	Wensley	860	411	57	5.0	-	60	8.2 7.2	8.9	1.0*	5	I
164.	Big Ohlman	900	38	39	4.5	12	55	8.4 7.1	6.0	3.8*	5	I
165.	Palmerston	890	382	53	5.0	-	103	7.5 6.9	5.7	3.2*	5	I
166.	MacKavoy	885	19	21	6.0	20	60	8.3 6.3	3.9	4.4*	15	II
167.	Mazinaw	870	1572	135	4.0	-	36	7.3 6.6	6.0	5.3	20	I
168.	Shabomeka	895	168	31	5.0	-	44	7.6 6.5	5.4	4.7	10	I
169.	Plevna	895	175	18	7.0	15	95	7.4 6.0	5.5	2.3*	5	II
170.	Cross	787	1540	27	8.0	18	44	6.9 6.2	3.9	4.3	5	II

No.	Locality	Elev.	A0	zm	Tm	zO2	TH	E	PH	H	SDV	O2C	Co.	Order
171.	Mississagagon	878	378	26	5.5	21	102	8.3	7.1	6.6	2.8	5	I	
172.	Kawakamak	854	1043	24	6.7	-	55	8.0	6.7	6.3	3.3*	5	II	
173.	Clarendon	831	2336	21	10.5	15	35	7.5	6.5	4.1	4.8*	10	II	
174.	Silver	570	243	25	7.0	18	154	8.2	7.2	4.2	3.8*	5	II	
175.	Sharbot	638	1438	34	6.5	32	125	7.2	6.8	4.1	5.7*	10	II	
176.	Pike	476	312	42	6.5	16	75	7.3	6.3	4.1	4.1*	10	II	
177.	Crowe	550	476	33	8.0	21	70	8.0	6.8	4.5	3.4	5	II	
178.	Bobs	532	2420	25	6.0	18	110	8.5	6.7	5.1	2.1*	5	II	
179.	Wolfe	447	885	28	7.5	14	130	8.5	7.0	3.9	4.2*	10	II	
180.	Big Rideau	406	3568	108	4.5	-	100	8.5	7.0	4.5	3.3	5	I	
181.	Otter	408	595	34	8.8	12	110	8.5	7.0	3.3	4.0*	15	II	
182.	Canoe	454	230	42	6.1	-	90	8.5	7.0	6.0	1.4	5	II	
183.	Desert	444	378	68	5.0	-	110	7.4	7.3	5.1	2.5*	5	I	
184.	Knowlton	430	156	33	3.9	20	130	8.3	7.0	4.3	3.8	5	I	
185.	Birch	450	193	36	5.9	33	85	8.3	6.9	5.5	1.6*	5	II	
186.	Clear	520	143	57	4.0	-	35	7.1	6.3	8.4	2.0*	5	I	
187.	Buck	434	658	39	6.0	27	90	7.4	6.8	5.1	3.0*	5	II	
188.	Indian	400	268	29	8.9	18	110	8.3	7.2	4.3	3.1*	5	II	
189.	Devil	430	997	40	5.0	30	103	8.0	7.0	5.4	2.1	5	I	
190.	Charleston (BW) (RB)	278	1200	44	11.2	-	130	8.5	7.8	3.7	4.0	10	II	
			500	92	4.5	-	130	8.5	7.5	5.7	3.5	5	I	
191.	Red Horse	280	224	39	4.3	16	135	8.5	7.1	4.2	4.3*	15	I	
192.	Loughborough	410	1782	34	9.5	30	155	8.3	7.2	4.8	2.8*	10	II	
193.	Sydenham	470	398	33	5.5	25	140	7.9	7.0	3.1	4.0*	10	I	
194.	Musktrat	404	1169	56	7.0	45	100	8.4	7.1	1.5	5.5*	20	II	
195.	Golden	556	3531	25	9.9	20	45	8.0	6.9	4.2	6.1	20	II	
196.	Round	560	2944	44	8.0	-	34	6.8	6.0	4.5	4.0	20	II	
197.	Grand #	730	717	38	6.0	-	34	7.5	7.0	4.5	5.0*	10	II	
198.	St. Andrews #	730	89	24	5.0	-	26	7.0	6.5	4.0	6.0*	15	I	
199.	Guthrie #	895	45	33										
200.	Little Carcajou #	780	11	48										

No.	Locality	Elev.	A _o	Z _m	T _m	ZO ₂	TH	pH E H	SDV	O ₂ C	Co.	Order	
201.	Carcajou #	829	82	43									
202.	Greenleaf #	819	61	72									
203.	Eustache #	900	40	100									
204.	White Partridge #	1155	563	45	5.0	-	34	7.5	7.0	3.0	7.0*	30	I
205.	Cartier #	590	260	21									
206.	Ottawa River	400	-	150	4.5	-	35	6.7	6.3	4.3	4.5*	20	I
207.	McSourley #	650	28	33									
208.	Waterloo #	907	178	28	5.0	-	20	7.0	6.0	3.9	5.8*	20	I
209.	Wendigo #	1040	160	28	6.0	-	20	7.0	6.0	4.2	5.0*	10	II
210.	Papineau #	995	230	24									
211.	Lauder #	1043	200	35									
212.	Guillmette #	1073	64	33									
213.	Radiant #	914	627	36									
214.	Cedar #	1007	2560	58	8.0	-	34	6.7	6.7	4.0	5.2*	5	II
215.	Hogan #	1250	1230	29									
216.	Gilmour #	1022	162	25									
217.	Laurie #	1026	63	28									
218.	Gouinlock #	1125	69	46									
219.	Couchon #	1066	271	43									
220.	Whitebirch #	1080	62	28									
221.	Mink #	1034	222	43									
222.	Kioshkokwi #	993	1024	39									
223.	Wilkes #	1129	1434	32									
224.	Threemile #	1250	402	37									
225.	Biggar #	1222	366	31									
226.	Waskigomdg #	1215	1331	32									
227.	Big Gibson #	500	48	38									
228.	Nottawissi	795	1254	36	5.5	-	20	6.4	5.6	4.2	5.3*	20	I
229.	Kettle	810	60	57	5.0	-	10	6.0	5.6	6.9	3.3*	5	I
230.	Crevier	800	409	30	5.0	25	35	7.3	6.4	4.5	5.2*	10	I

No.	Locality	Elev.	Ao	zm	Tm	zO2	TH	E	pH	H	SDV	O2C	Co.	Order
231.	Maguerite	810	557	48	5.0	-	15	6.3	5.9		7.5	2.0*	5	I
232.	Cobble	800	71	21	5.0	15	15	6.2	5.6		3.5	8.0*	30	I
233.	Petawaga	750	2233	44	6.0	-	10	6.3	5.8		5.1	2.0*	8	II
234.	Baskatong	732	20000+	82	5.1	-	10	6.5	6.0		3.6	5.5	20	I
235.	Chopin	830	485	30	7.6	-	11	6.3	5.4		2.9	5.1	20	II
236.	Polonais	810	1015	40	5.3	-	15	6.6	5.6		3.6	5.6	20	I
237.	Piscatosine	732	2005	50	5.5	-	20	6.6	5.9		4.2	6.0*	20	I
238.	Tapani	818	578	24	6.7	-	23	6.9	6.3		3.0	4.6	20	II
239.	Chinard	900	120	57	4.2	-	16	6.6	5.5		6.0	3.4	6	I
240.	Gravel	880	133	36	5.6	-	25	7.0	6.0		3.9	2.8	10	I
241.	Moreau	788	406	33	5.5	-	40	7.7	6.2		4.6	2.5*	10	I
242.	des Ecorces	753	516	37	5.8	-	35	7.7	6.2		1.9	4.3*	20	II
243.	Pope	830	174	30	6.0	-	30	6.6	5.5		4.6	6.5	20	II
244.	Gatineau	850	54	30	5.0	25	38	6.9	6.1		6.9	2.5	5	I
245.	des Iles	660	1472	39	8.0	-	45	8.0	6.6		3.9	3.0	10	II
246.	du Cerf	680	1305	72	4.5	-	35	7.2	6.8		5.4	3.1*	5	I
247.	Corbeau	710	182	57	5.0	-	35	7.1	6.6		4.2	4.5*	10	I
248.	Serpant	690	187	60	4.0	-	45	7.4	6.7		5.7	4.0*	10	I
249.	O'Neil	650	80	37	5.5	-	40	7.3	6.5		5.7	2.5*	5	I
250.	Poisson Blanc	660	4420	75	5.0	-	30	6.9	6.3		7.8	2.0*	5	I
251.	Leamy	790	18	28	4.6	-	16	6.5	5.5		2.1	8.5*	40	I
252.	Serpant	840	41	24	4.6	-	17	6.5	5.5		3.3	7.1*	20	I
253.	Quinn	785	49	28	4.2	25	15	6.7	5.5		3.8	6.8*	20	I
254.	de la Vieille	810	301	28	4.8	-	18	6.6	5.5		4.2	6.2*	20	I
255.	Tomasine	758	393	28	8.0	-	10	6.4	5.5		4.0	6.0*	20	II
256.	Savary	790	403	55	4.2	-	8	6.7	5.5		5.1	5.1*	10	I
257.	Rond	739	547	29	8.5	-	18	6.2	5.5		4.1	6.3*	15	II
258.	Désert	740	1554	42	7.0	-	20	6.5	5.9		5.4	4.5*	8	II
259.	Bras Coupé	755	675	49	5.0	-	30	6.8	6.4		5.7	4.6	5	I
260.	Lytton	745	221	30	7.5	-	25	6.6	5.5		6.5	3.8	5	II

No.	Locality	Elev.	A _o	z _m	T _m	zO ₂	TH	E	pH	SDV	O ₂ C	Co.	Order
261.	Pocknock	580	231	36	5.5	-	35	7.0	6.3	5.7	2.9*	10	I
262.	Grand Cèdres	560	740	37	8.0	-	70	7.3	7.1	6.0	2.4*	5	II
263.	Petit Cèdres	555	257	37	6.0	-	75	7.3	7.1	6.3	2.5*	5	II
264.	Murray	612	269	24	7.0	12	45	7.5	6.5	2.8	5.0*	20	II
265.	à l'Achigan	653	128	25	4.5	20	62	7.3	6.3	6.0	6.4	20	I
266.	Kensington	710	298	39	5.0	30	68	7.2	6.4	6.3	2.0*	5	I
267.	Thirty-one Mile	540	3867	33	5.2	-	72	8.3	6.7	6.7	1.0	5	I
268.	Vert	626	150	96	4.0	80	95	8.5	7.4	12.2	0.5	5	I
269.	Bangall	625	109	43	5.0	40	78	8.5	6.7	7.8	3.2	5	I
270.	Pemichangan (s)	555	868	35	5.5	15	85	8.5	6.9	6.4	4.0	5	I
	(d)		1000	54	4.5	-	85	8.5	6.7	7.9	2.8	5	I
271.	Heney	470	1230	32	7.0	20	75	8.5	6.5	4.9	3.0*	10	II
272.	Bitobi	490	208	29	5.0	25	35	7.0	6.0	3.9	6.2*	10	I
273.	Cameron	480	149	24	5.0	20	45	7.1	6.3	3.8	5.2	10	I
274.	Roddick	483	501	45	5.0	40	80	8.5	6.5	7.3	2.2	5	I
275.	Blue Sea	541	1440	59	5.5	-	90	8.5	7.0	6.0	2.3	10	I
276.	Paquin	590	155	48	4.5	36	95	8.5	6.8	10.0	3.0	5	I
277.	Profond	580	94	33	4.4	25	55	8.0	6.0	7.8	2.5	5	I
278.	Danford	581	115	34	6.0	20	86	8.1	7.0	6.3	2.4*	5	II
279.	Gruice	542	150	37	5.0	-	55	8.3	6.6	5.6	2.0*	8	I
280.	Thorne	618	86	29	5.4	25	60	7.6	6.5	6.0	1.8*	5	I
281.	Johnston	503	54	34	5.0	25	70	7.8	6.0	3.3	5.5*	20	I
282.	MacGregor	466	538	43	7.5	-	62	7.5	7.0	5.1	3.0*	8	II
283.	McFee	669	69	48	4.0	45	35	6.7	6.0	8.7	2.9*	5	I
284.	Dodds	633	53	42	4.0	38	26	6.8	6.4	8.1	1.5*	5	I
285.	Echo	774	514	60	4.5	-	35	7.0	6.3	9.6	1.0*	5	I
286.	St. Sixte	740	141	45	5.0	-	35	6.8	5.5	6.0	4.3	10	I
287.	Heart	670	105	41	5.5	-	45	7.1	5.5	5.7	3.0*	5	I
288.	Britannique	715	154	60	4.5	-	35	7.4	6.3	6.6	1.5*	5	I
289.	Lady	760	95	45	4.5	-	35	6.8	6.0	9.3	0.8*	5	I
290.	Hawk	745	151	39	4.5	-	35	6.9	6.1	8.7	1.4*	5	I

No.	Locality	Elev.	Ao	z _m	T _m	zO ₂	TH	E	pH	H	SDV	O ₂ C	Co.	Order
291.	Gull	730	115	39	4.5	33	51	7.4	6.5	9.6'	2.4	10	I	
292.	la Blanche	590	711	14	10.0	12	35	6.8	6.0	2.7	5.0*	10	II	
293.	Papineau	525	963	81	4.5	-	25	6.8	6.0	10.7	3.2	5	I	
294.	Whitefish	490	49	16	5.0	-	34	6.9	6.2	3.6	5.0*	20	I	
295.	Louisa	890	364	33	5.4	20	20	7.0	6.0	6.0	4.2	5	I	
296.	Barron	910	87	31	5.5	-	16	6.5	5.6	3.0	6.3*	40	I	
297.	Connelly	680	104	19	6.0	-	24	6.8	5.6	3.9	4.5*	20	II	
298.	l'Achigan	690	665	21	6.0	-	25	6.7	6.2	4.8	2.8*	10	II	
299.	des Piles	543	503	66	4.5	-	14	6.5	6.2	10.2	1.0*	5	I	
300.	St. Jean	312	20000+	68	4.5	-	15	6.2	5.9	2.7	7.8	30	I	
301.	Sagueny Estuary	-	-	60	1.0	-	20ppt	8.5		3.0	1.0*	5	-	
302.	Temiscouata	490	5502	66	4.0	-	55	7.6	7.4	2.9	2.9	5	I	
303.	St. François	900	3456	37	4.0	-	43	6.8	6.5	2.1	8.6	40	I	
304.	Aylmer	820	2528	30	4.9	-	36	6.9	6.0	2.0	8.8*	40	I	
305.	Grand Brompton	780	729	44	7.0	-	30	6.5	6.0	3.9	6.3	10	II	
306.	Massawippi	570	1572	82	4.0	-	102	8.0	7.3	4.5	3.4	5	I	
307.	Orford	920	95	47	4.0	30	55	7.0	6.7	8.1	1.7	5	I	
308.	Lovering	803	426	25	9.5	-	38	6.6	5.5	3.6	6.7	10	II	
309.	Memphremagog	683	7737	117	5.0	-	70	7.5	6.9	5.7	2.1	5	I	
310.	ChAMPLAIN	62	120000	120	4.0	-	45	8.0	7.0	3.9	3.0	5	I	
311.	Dunmore	571	396	30	6.5	-	40	7.8	6.5	3.9	4.0*	10	II	
312.	Sunset	498	80	36	5.5	-	35	7.0	6.2	9.0	1.5*	5	I	
313.	St. Catherine	480	500	21	7.0	15	55	8.0	6.0	5.4	3.0*	10	II	
314.	George	322	11280	56	5.0	-	42	6.9	6.0	9.0	1.0	5	I	
315.	Sylvia	670	113	42	5.0	-	130	8.2	7.1	8.4	1.0*	5	I	
316.	Lake of the Woods	300	71	25	6.0	20	45	7.4	6.6	4.2	4.0*	10	II	
317.	Sixberry	345	42	27	5.5	20	40	7.6	6.4	2.8	5.2*	15	I	
318.	Millsite	301	200	22	6.0	-	40	7.2	7.0	5.7	1.0*	5	II	
319.	Green #	419	27	59	7.2	20	150	8.0	6.8	9.0	1.0*	5	II	
320.	Skaneateles	867	3584	90	6.3	-	110	8.0	7.8	9.3	2.0	5	II	

No.	Locality	Elev.	A ₀	Z _m	T _m	zO ₂	TH	E	pH	H	SDV	O ₂ C	Co.	Order
321.	Owasco #	710	2560	48	7.3	-	110	8.4	7.8	4.2	3.0	10		II
322.	Cayuga #	381	16800	120	4.1	-	104	8.5	8.0	6.3	2.0	5		I
323.	Seneca #	444	17100	180	4.0	-	110	8.3	7.7	9.0	2.5*	5		I
324.	Keuka	750	2000	48	4.8	-	110	8.4	7.6	4.5	2.5*	5		I
325.	Canadaigua #	686	4250	75	4.3	-	120	8.3	7.9	4.5	2.0*	5		I
326.	Hemlock	905	800	27	6.0	20	95	7.8	7.4	3.0	4.5*	10		II
Negative lakes within glacial lake boundaries.														
327.	Commanda	850		30	3.9	10	85	8.3	6.5	6.0	2.5*	5		I
328.	Nellie	900		24	6.0	15	35	7.3	6.4	3.7	4.3*	20		II
329.	Perry	1050	106	28	6.0	14	70	8.5	7.0	7.8	1.0*	5		II
330.	Nighthawk	890	8523	5	18.0	-	70	8.0		0.5	2.0*	5		III
331.	Kenogami	1030	1000	6	18.0	-	43	8.0		1.3	4.0*	10		III
332.	Castagnier	980		3	20.0	-	24	6.7		0.4	6.3*	30		III
333.	Malarctic	960		25	17.0	-	33	6.7		1.0	6.0*	30		III
334.	Descelles	930		30	9.2	20	12	5.7	5.5	2.0	9.8*	50		II
335.	Brisbois	830		18	8.5	10	20	6.7	5.5	3.0	8.6	40		II
336.	Wakimika	950		18	9.0	-	23	6.3	5.6	6.0	3.0*	5		II
337.	Tee	890	131	21	7.5	-	28	6.4	5.5	3.9	5.3*	20		II
338.	Capreol	990		28	5.0	-	20	5.5	5.0	6.9	1.3*	5		I
339.	Little Panache	812		24	5.0	21	45	8.3	6.0	4.5	3.5*	5		I
340.	Kawayaymog	1250		13	15.8	10	25	6.9	6.0	2.8	7.4*	30		II
341.	Otter	676	500	42	5.0	-	17	6.6	5.6	3.9	5.8*	20		I
342.	Clearwater	850	71	28	6.0	25	15	6.5	5.3	6.6	2.8*	10		II
343.	Round	655		10	20.0	-	110	8.5		2.4	6.3*	5		III
344.	Coxvale	850		16	7.0	10	40	6.8	6.0	4.0	4.7*	10		II
345.	Clear	400	170	33	8.5	8	120	8.5	6.3	4.8	2.2*	5		II
346.	Lower Beverly	300	638	24	7.5	10	145	8.3	7.3	2.1	4.8*	10		II
347.	Calabogie	505		36	19.5	-	50	7.0		3.1	5.5*	10		III
348.	Esturgeon	820		27	5.0	?	22	6.5	5.6	5.4	3.9*	10		I
349.	Bois Franc	540		20	4.0	10	80	8.3	6.7	5.4	7.2	20		I
350.	Green	480		22	6.0	10	70	8.0	6.5	4.2	2.3	5		II

No.	Locality	Elev.	A ₀	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ c	Co.	Order
351.	Gilmore	490		36	4.5	17	55	8.5	4.9	2.0	5	I
352.	Plumbago	425	56	27	4.2	13	60	7.9	2.4	4.4*	10	I
353.	Litchfield	588		24	4.0	16	35	7.8	3.0	5.9*	20	I
354.	Gilmour	600		21	5.5	12	65	8.0	3.3	8.4*	30	I
355.	Venosta	530		21	6.8	16	75	8.5	6.6	2.3*	5	II
356.	Manitou	520	40	24	4.5	18	140	8.5	4.6	2.8	10	I
357.	Saratoga	204	1765	28	6.0	15	85	7.2	4.8	5.4*	10	II
Negative lakes outside glacial lake boundaries.												
358.	Naacocane	1785		19	8.2	-	15	6.8	6.9	2.3*	5	II
359.	Vallard	1700		13	13.0	-	10	6.5	3.0	6.8*	30	III
360.	Base Camp	2300		13	11.0	-	15	6.5	2.7	7.5*	40	II
361.	Indicator	1700		22	9.0	-	8	6.1	2.4	8.3*	40	II
362.	Petit Temiscamie	1460		43	7.5	-	8	6.0	4.4	5.5	25	II
363.	Temiscamie	1380		31	9.5	-	12	6.2	3.0	5.4	25	II
364.	Kallio	1420		18	9.0	-	36	7.4	4.1	1.3	5	II
365.	Tournemine	1380		10	12.5	-	15	6.5	3.3	7.0*	30	II
366.	Coldwater	1530		35	6.0	-	10	6.0	3.3	5.0*	20	II
367.	File-axe	1480		13	12.0	-	15	6.6	3.6	8.0*	40	II
368.	Margonne	1425		15	10.0	-	25	6.7	4.2	5.8*	20	II
369.	Ida	1400		5	17.5	-	20	6.5	2.1	9.5*	50	III
370.	Vimont	1330		25	8.5	-	20	6.5	4.5	5.0*	15	II
371.	Dufresne	1270		6	14.5	-	17	6.8	2.1	9.0*	50	II
372.	Charron	1310		6	16.0	-	10	5.5	1.5	8.8*	45	III
373.	Nicabeau	1260		18	15.5	-	20	6.8	2.9	7.2*	30	II
374.	Aigremont	1320		14	11.9	-	15	6.5	3.3	6.5*	30	II
375.	d'Eglis	1195		24	7.7	-	10	6.4	2.5	6.0*	30	II
376.	Argenson	1106		27	10.0	-	12	6.3	3.6	6.5	30	II
377.	Chamouchouane	1240		11	12.0	-	8	6.0	2.0	8.5*	40	II
378.	Poutrincourt	1280		10	16.5	-	10	6.3	3.0	6.2	40	III
379.	Robert	1302		20	11.0	-	8	6.0	2.0	7.5*	50	II
380.	Nemagousse	1450		35	6.5	-	12	6.3	4.8	4.6	20	II

No.	Locality	Elev.	A ₀	Z _m	T _m	zO ₂	TH	pH		SDV	O ₂ C	Co	Order
								E	H				
381.	Baptiste	1425		13	8.0	-	10	6.1	6.1	3.5	6.0*	30	II
382.	Gouin	1310		20	10.0	-	8	6.0	6.0	3.8	5.5*	20	II
383.	Pascagama	1380		15	15.5	-	10	5.7	5.5	2.0	7.8*	40	II
384.	Mesplet	1279		5	18.0	-	12	6.5		1.8	6.5*	30	III
385.	Maude	1290		16	12.0	-	8	5.5	5.0	1.8	9.7*	50	II
386.	Attic	1290		23	7.0	-	10	6.3	5.6	4.5	5.8*	30	II
387.	Hickey	1190		16	5.5	-	15	6.3	6.1	2.1	9.2*	50	I
388.	Castonguay	1290		29	6.5	-	8	5.5	5.0	2.0	6.6	40	II
389.	Desforges	1250		18	7.3	-	12	6.1	5.5	7.0	1.3*	5	II
390.	Augier	1290		27	5.4	-	8	6.0	5.5	5.5	2.9*	10	I
391.	Charrette	1270		55	5.0	-	8	5.9	5.6	6.0	2.3	5	I
392.	Valets	1279		18	11.0	-	10	5.5	5.3	4.5	4.6*	20	II
393.	Martin	1480		19	15.5	-	5	5.5	5.0	6.3	1.5*	5	II
394.	Yser	1340		30	6.0	-	10	5.6	5.3	8.7	1.1*	5	II
395.	Denain	1300		31	6.0	-	10	5.6	5.3	7.5	1.2*	5	II
396.	Camachigama	1190		43	6.0	-	12	5.8	5.5	6.0	2.7*	5	II
397.	Dozois	1135		27	8.5	20	8	5.7	5.5	2.7	5.6	30	II
398.	Cabonga	1188		28	8.5	21	12	6.4	5.5	4.0	5.1*	20	II
399.	O'Sullivan	1300		53	6.0	-	15	5.8	5.5	6.9	2.3*	5	II
400.	Lenotre	1220		33	6.5	-	15	6.0	5.5	4.8	3.5*	10	II
401.	Lecointre	1350		24	8.5	-	10	5.9	5.5	3.2	6.7*	30	II
402.	Mitchinamecus	1240		35	6.5	-	10	6.0	5.7	3.5	4.2	10	II
403.	Transparent	1080		36	5.0	-	10	6.1	5.5	11.0	0.5	3	I
404.	Byrd	1200		34	8.0	-	12	6.0	5.5	5.1	3.5*	10	II
405.	Dumoine	850		50	5.5	-	10	6.1	5.5	3.9	5.2*	10	II
406.	Rabbit	1070		18	12.0	-	10	5.5	5.0	3.3	4.0	10	II
407.	Nodier	1030		30	6.0	-	15	5.8	5.5	2.5	5.5	20	II
408.	Kenogamissi	1015	1600	26	10.0	20	40	7.2	6.0	3.0	7.2*	30	II
409.	Muskasenda	1050	624	42	5.0	-	30	7.0	6.0	3.2	6.0*	20	I
410.	Watabeag	1090	2140	32	8.0	-	88	8.0	6.7	5.7	3.3*	5	II

No.	Locality	Elev.	A ₀	Z _m	T _m	zO ₂	TH	PH E H	SDV	O ₂ C	Co.	Order
411.	Mattagami	1080		50	5.7	-	35	7.5	2.7	7.0*	30	I
412.	Duncan	1100	1118	30	6.0	-	30	7.1	3.3	4.6*	20	II
413.	Longpoint	1030	372	20	7.0	13	35	7.3	3.6	5.8*	20	II
414.	Isabel	1375	197	33	5.0	-	24	6.7	9.0	1.2*	5	I
415.	Banks-Makobe	1190	3200	27	7.5	-	10	5.5	10.5	1.3*	3	II
416.	Gowganda	1110	1033	32	7.0	-	25	6.7	4.0	5.6*	20	II
417.	West Shining	1250		20	6.5	-	25	6.5	3.3	6.4*	30	II
418.	Onaping	1350		35	7.0	-	15	6.7	5.4	3.4*	10	II
419.	Smoothwater	1220	1300	85	4.0	-	15	5.9	16.2	0.1*	0	I
420.	Florence	1250		24	6.0	-	15	5.0	8.4	1.0*	5	II
421.	Yorstan	1025		32	7.0	-	20	5.6	10.2	3.2*	10	II
422.	Emerald	1040	560	35	5.0	-	30	6.5	8.5	1.7	5	I
423.	Eaglerock	1040	120	30	5.5	-	28	6.4	9.0	2.6	5	I
424.	Gull	1055	1297	50	5.3	-	26	6.3	7.8	1.8	5	I
425.	Turtleshell	1030	150	33	5.5	-	20	6.3	7.5	2.4	5	I
426.	Turner	1070	50	24	7.0	-	12	5.5	9.0	2.3*	5	II
427.	Anima-Nipissing	1070	1416	69	5.0	-	25	6.3	10.5	1.0	5	I
428.	Friday	1171	320	20	8.5	-	30	7.1	5.1	3.4*	5	II
429.	Lowell	1050	89	45	4.8	-	35	6.8	7.0	4.2	5	I
430.	Upper Twin	1050	178	45	4.8	-	35	7.1	6.3	3.5*	5	I
431.	Spring	1040	69	58	5.0	-	20	7.0	10.2	0.5*	3	I
432.	McConnell	1035	208	35	6.5	-	20	7.0	9.3	1.0*	5	II
433.	Gordon	913		25	5.2	-	20	5.8	5.1	3.5*	10	I
434.	White	895		42	5.8	-	15	6.4	6.5	3.4	10	II
435.	aux Sables	1010		11	11.5	-	14	6.5	2.7	9.0*	50	III
436.	Soufflot	1040		30	6.5	-	8	5.5	4.8	2.1	5	II
437.	la Truite	1122		33	7.4	-	12	5.5	6.0	1.1	5	II
438.	Lescot	1042		35	5.5	-	12	5.7	4.8	3.9	5	I
439.	Sandean	1015		27	5.6	-	15	5.7	4.5	3.5*	5	I
440.	Ogascan	1030		30	7.8	-	15	5.5	4.5	3.6	10	II

No.	Locality	Elev.	Ao	Zm	Tm	zO ₂	TH	pH E H	SDV	O ₂ C	Co.	Order
441.	des Loups	995		30	8.5	-	12	5.7 5.5	3.6	5.3	10	II
442.	Sasaginaga	1020		26	7.8	-	12	5.6 5.5	6.5	1.2	5	II
443.	Regenzie	945		33	7.0	-	15	6.1 5.6	5.5	2.3*	5	II
444.	Kikwissi	960		36	7.8	-	15	5.5 5.5	6.7	1.5	5	II
445.	Pants	890		24	8.9	-	12	5.8 5.3	4.2	2.7	5	II
446.	Booth	895		30	8.0	-	17	6.3 6.1	8.1	3.3	5	II
447.	Smith	890		75	4.5	-	15	6.6 6.0	9.0	1.0*	5	I
448.	Windy	930		30	5.1	-	15	6.5 5.5	8.1	1.4*	5	I
449.	Douglas	870		20	5.0	15	26	7.0 6.0	5.5	4.5*	10	I
450.	Petit Beauchêne	855		42	5.2	-	20	6.9 5.7	5.7	2.5	5	I
451.	Sairs	890		39	6.5	-	12	6.3 5.6	4.2	5.4*	20	II
452.	Sand	1080		25	8.0	-	17	6.5 5.6	4.2	4.0*	10	II
453.	Bleu	1075		57	6.5	-	15	6.1 6.0	7.5	1.0*	5	II
454.	Caughnawana	1075		24	7.0	-	15	6.1 6.0	7.8	1.0*	5	II
455.	Loon	1090		30	5.5	-	15	6.0 5.5	6.9	2.3*	5	I
456.	Memewith	840		36	7.0	-	15	6.5 5.5	5.1	2.8*	5	II
457.	Timber	1035	150	27	6.0	20	16	6.0 5.5	5.5	1.9*	5	II
458.	Transparent	975	93	36	4.4	-	18	6.5 5.8	8.7	1.5	5	I
459.	McCracken	980		40	6.0	-	15	6.0 5.5	6.0	2.8*	5	II
460.	Smyth	1325	46	23	5.0	20	20	6.2 5.5	5.0	4.2*	10	I
461.	Sweny	1220	134	35	5.5	-	26	6.5 5.8	6.9	1.5*	5	I
462.	Proudfoot #	1180	125	28	5.0	-	25	6.4 5.8	6.5	1.8*	5	I
463.	Butt #	1475		30	4.0	-	20	7.0 6.0	6.6	1.0*	5	I
464.	Burntroot #	1304		30	4.0	-	20	7.0 6.0	6.6	1.0*	5	I
465.	McCraney #	1431		30	4.0	-	20	7.0 6.0	6.6	1.0*	5	I
466.	Smoke #	1380		45	6.0	-	10	6.5 6.5	6.6	3.0*	5	II
467.	Canoe #	1379		26	6.0	-	10	7.2 6.6	4.8	3.5*	5	II
468.	Big Trout #	1322		50	6.0	-	12	6.5 6.0	4.0	3.5*	5	II
469.	Opeongo	1323	6000	45	7.0	-	15	6.5 6.0	3.6	3.0	10	II
470.	Two Rivers #	1289		33	5.0	-	20	6.3 5.8	3.2	6.0*	10	I

No.	Locality	Elev.	Ao	zm	Tm	zO ₂	TH	E	pH	SDV	O ₂ c	Co.	Order
471.	Louisa #	1445											
472.	Bella	1180	337	35	6.5	-	25	6.8	5.5	3.3	3.5*	5	II
473.	Camp #	1370		45	5.0	-	25	6.7	5.6	3.8	3.0*	5	I
474.	Harp	1090	71	33	5.5	-	24	6.7	5.5	6.0	2.5*	5	I
475.	Oxtongue	1195	246	27	6.5	-	15	6.1	5.8	2.2	7.8*	30	II
476.	Livingstone #	1160		33	6.5	-	10	6.0	5.7	4.6	4.5*	10	II
477.	Kawagama	1165		70	5.0	-	13	6.5	6.5	8.4	1.5*	5	I
478.	Kennisis #	1212	1344	72	4.5	-	15	6.7	6.0	9.7	1.0*	5	I
479.	Redstone #	1195	1179	80	4.0	-	20	6.8	5.8	8.6	1.0*	5	I
480.	Little Hawk	1180	256	80	5.0	-	25	6.2	6.0	7.2	1.4*	5	I
481.	Raven #	1148		45	5.0	-	25	6.4	6.1	5.8	1.7*	5	I
482.	St. Nora	1092	841	35	6.5	-	26	6.6	5.6	6.6	1.8*	5	II
483.	White Pine	1100	76	22	6.0	-	25	6.5	5.5	4.5	4.0*	10	II
484.	Clear	1084	99	25	6.0	-	17	6.5	5.8	6.3	2.3*	5	II
485.	Kashagawigamog	1043	820	38	5.5	-	42	7.2	6.6	5.7	1.3*	5	I
486.	Koshlong	1137	396	35	5.5	-	15	6.4	5.5	6.3	2.3*	5	I
487.	Drag #	1161	900	55	4.5	-	15	6.8	5.5	8.0	2.0*	5	I
488.	Haliburton #	1183	998	52	4.5	-	30	7.0	6.0	5.0	3.0*	5	I
489.	Baptiste	1157	1952	31	8.0	-							
490.	Paudash #	1120	640	33	4.5	-	70	7.5	6.3	4.8	4.3*	10	I
491.	Eels	1180	884	30	5.5	-	35	6.7	5.7	3.3	5.8*	20	I
492.	Salmon	1030	161	32	5.5	20	90	8.2	6.7	8.1	1.2*	5	I
493.	Chandos	1054	1360	42	5.5	-	55	7.3	6.3	4.5	2.5*	5	I
494.	Jack	903	608	40	5.0	-	70	8.5	6.9	3.9	3.4*	10	I
495.	Oak	853	650	24	7.0	12	60	8.0	6.6	3.6	3.5*	10	II
496.	Dickey	1014	96	55	4.5	-	76	8.2	6.8	5.0	6.0	20	I
497.	Wollaston	1050	348	30	4.9	-	80	8.5	7.0	3.5	3.0*	5	I
498.	Limerick	1030	690	28	6.3	-	115	8.5	7.2	4.5	3.7	5	II
499.	Ashby	1150	242	27	5.5	-	30	7.1	6.0	5.7	4.0	10	I
500.	Ashden	1120	134	25	5.0	20	100	8.5	6.8	7.5	2.4	5	I

No.	Locality	Elev.	A _o	Z _m	T _m	ZO ₂	TH	pH E H	SDV	O ₂ C	Co.	Order	
501.	Buckshot	956	434	33	6.0	-	35	6.9	6.2	5.7	4.1	10	II
502.	Mosque	1025	136	33	5.0	20	50	7.6	6.5	5.5	4.3*	10	I
503.	Skootamatta	955	1271	30	6.5	-	25	6.8	5.7	4.0	6.0	20	II
504.	Galeairy #	1278		24	5.0	-	30	6.8	5.9	4.2	6.0*	10	I
505.	Louisa #	1300		60	4.0	-	34	8.0	6.5	7.5	1.0*	5	I
506.	Papineau #	1039		60	5.0	-	20	6.5	6.0	7.0	1.0*	5	I
507.	Clear #	755	2399	40	5.0	-							I
508.	Bark #	1027	6000	72	5.0	-	26	7.0	6.5	7.5	2.0*	5	I
509.	Kameniskeg	928	2172	42	5.5	-	26	7.0	6.5	4.2	5.0*	10	II
510.	Paugh	990	740	50	4.5	-	34	7.5	7.0	4.2	4.5*	10	I
511.	Victoria	1270		45	4.5	-	20	6.8	6.0	5.0	4.0*	10	I
512.	Aylen #	1170		70	5.5	-	25	7.0	6.5	7.5	2.0*	5	I
513.	Lavieille #	1266		45	4.5	-	29	7.0	6.0	4.2	5.0*	10	I
514.	Lost	1150		37	6.0	-	20	6.8	5.0	5.7	1.0*	5	II
515.	Stevens	901		36	6.0	-	20	7.0	6.2	6.0	2.1*	5	II
516.	Vert	895		30	6.0	25	20	6.8	6.0	7.2	1.0*	5	II
517.	St. Patrick	870		60	6.5	-	10	6.5	6.0	9.5	1.2*	5	II
518.	Lynch	890		75	6.5	-	12	6.6	6.0	9.0	1.0*	5	II
519.	aux Vers	880		65	4.5	-	8	6.2	6.0	12.9	0.5*	3	I
520.	Pappin	760		33	5.0	-	10	6.5	5.5	4.8	3.0*	10	II
521.	Trout	750		28	6.0	-	20	6.5	6.0	5.7	2.8*	5	II
522.	Jim	681		24	7.5	-	28	7.5	6.2	4.0	5.9*	30	II
523.	Vert	550		20	4.5	15	50	7.6	6.4	6.0	2.0*	5	I
524.	Bark	1183		37	6.0	-	12	6.4	5.7	5.0	4.5*	10	II
525.	Roland	1225		20	8.0	15	16	6.3	6.0	4.6	5.0*	20	II
526.	Embarrass	1157		45	4.1	-	8	6.2	5.5	4.5	5.3*	10	I
527.	du Rocher	1085		55	4.8	-	15	6.3	5.5	6.9	2.0*	5	I
528.	Buckshot	1020		37	4.2	-	12	6.5	5.5	4.9	4.0	5	I
529.	Ross	810		18	6.2	15	18	6.9	5.6	6.2	1.3*	5	II
530.	Corbeau.	900		36	5.4	-	8	6.5	5.5	4.8	4.0*	10	I

No.	Locality	Elev.	A0	zm	Tm	zO2	TH	PH E H	SDV	O2C	Co.	Order
531.	Gilmore	850		24	5.0	-	15	6.6	4.8	4.0*	15	I
532.	Gagamo	890		22	7.5	-	10	5.6	3.0	5.6*	20	II
533.	la Croche	852		24	6.0	-	15	5.7	4.3	5.2*	15	II
534.	Cole	800		22	6.0	12	12	6.0	3.6	6.7*	30	II
535.	Royal	535		27	6.0	-	15	6.0	5.0	3.4*	5	II
536.	Caroline	1025		36	5.3	-	12	5.6	6.0	1.5*	5	I
537.	Clearwater	780		25	4.5	-	16	6.4	6.0	2.3*	5	I
538.	Green	825		30	4.5	-	15	6.5	5.4	3.2*	5	I
539.	à la Tortue	730		20	7.0	15	20	6.7	5.1	4.5*	20	II
540.	Pythonga	686		78	5.6	-	15	6.7	6.3	4.9	10	I
541.	David	716		33	6.0	-	16	6.6	8.4	2.0*	5	II
542.	Abatis	899		27	6.4	-	16	6.6	4.5	1.9	10	II
543.	Usborne	796		28	4.3	-	20	6.1	3.5	6.9	10	I
544.	Conway	725		32	5.0	-	20	6.5	4.5	2.3*	5	I
545.	Mer Bleue	680		33	7.2	-	35	7.0	4.8	3.0*	10	II
546.	Latourelle	640		18	5.5	15	70	8.5	5.4	6.0*	5	I
547.	des Iles	630		21	5.5	18	60	8.5	6.3	6.7	5	I
548.	Patterson	800		25	6.5	-	15	6.8	5.4	2.4	5	II
549.	Cayamant	640	680	57	7.0	-	35	7.2	4.8	3.0	10	II
550.	Hook	890		42	4.0	-	25	7.1	10.5	0.5*	3	I
551.	Lamarsh	640		32	4.2	15	17	7.0	7.5	2.3*	5	I
552.	Petit Cayamant	610		48	5.8	-	35	7.0	5.7	4.5*	20	II
553.	Laforêt	825		18	4.3	15	27	6.7	7.0	2.3*	5	I
554.	Dumont	851		55	4.3	-	27	6.6	10.5	1.2	5	I
555.	Squaw	803		42	4.0	-	35	6.8	6.6	3.2	5	I
556.	Hickey	738		55	4.0	-	30	7.5	6.3	2.5*	5	I
557.	Huddersfield	770		22	4.5	-	27	6.4	3.9	4.0*	5	I
558.	Leslie	658		33	4.2	-	25	7.4	3.4	4.5*	10	I
559.	MacCraig	647.	80	30	4.2	18	35	7.6	6.0	1.5*	5	I
560.	Hughes	646		20	6.5	10	25	6.9	4.5	5.2*	20	II

No.	Locality	Elev.	Ao	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ C	Co.	Order
561.	Otter	638		22	12.3	15	32	7.0	4.4	5.3*	20	II
562.	Johnson	645		34	4.0	18	55	7.6	5.1	2.3*	5	I
563.	Mechan	647		42	4.0	12	112	8.6	4.3	5.0*	5	I
564.	Charrette	1200		18	5.0	-	20	6.5	2.4	7.0*	30	I
565.	Harrington	560		21	7.0	10	45	7.0	6.3	3.0	5	II
566.	Sinclair	784		36	5.0	25	75	8.4	4.2	4.8	5	I
567.	Isabel	797		33	5.6	-	60	7.8	9.0	3.5*	5	I
568.	Cabaret	799		25	6.5	-	60	7.0	2.4	7.5*	30	II
569.	Bernard	564		20	6.2	13	76	8.1	5.4	3.5*	10	II
570.	Meach	555		23	6.0	14	46	7.0	5.4	4.0	5	II
571.	Little Trout	895		33	4.5	25	30	7.2	8.7	1.0*	5	I
572.	à la Truite	990		80	4.0	-	18	6.0	8.4	2.3*	5	I
573.	Sam	880		60	5.0	-	20	6.2	7.5	1.8*	5	I
574.	Normandeau	1150		40	5.0	-	15	6.4	6.9	1.8*	5	I
575.	Ecluse	890	120	42	5.5	-	25	6.8	6.6	2.3*	5	I
576.	Wakefield	539	352	54	4.5	40	52	7.9	4.8	4.0*	5	I
577.	Grand	516	530	40	7.5	-	60	7.2	8.1	3.0*	5	II
578.	Long	790		33	5.0	12	45	7.0	6.3	4.5*	5	I
579.	Clay	667	440	40	7.5	-	50	7.5	2.0	6.3*	10	II
580.	Vert	825		42	4.5	24	55	6.7	8.4	1.5*	5	I
581.	Lathbury	990		35	4.5	-	33	6.3	6.9	3.0*	5	I
582.	O'Hara	695		45	4.5	-	95	8.0	6.9	1.5*	5	I
583.	Babiche	1015		32	6.0	-	25	6.8	5.5	4.5*	10	II
584.	Perras	980		53	5.0	-	25	6.8	7.5	2.0*	5	I
585.	Pimodon	1050		32	6.0	-	20	6.5	6.0	3.0*	5	II
586.	Quinn	740		40	5.0	-	27	6.9	6.9	2.5*	5	I
587.	Winding	990		36	6.0	-	12	6.3	5.7	3.0*	5	II
588.	Kiamika	862		43	6.0	-	26	7.0	4.2	5.5*	10	II
589.	des Cornes	980		33	5.5	-	20	6.4	6.0	4.5*	5	I
590.	Major	925		36	5.4	-	17	6.7	4.6	5.3	10	I

No.	Locality	Elev.	A0	Zm	Tm	ZO2	TH	E	pH	SPV	O2c	Co.	Order
591.	Laluge	1020		28	5.5	-	15	6.8	5.9	4.5	5.5*	10	I
592.	Iveteaux	915		27	5.0	-	12	6.4	5.4	3.3	3.6	5	I
593.	Dieppe	1240		30	5.5	-	15	6.0	5.5	3.6	6.3*	20	I
594.	Bondy	960		105	4.0	-	10	5.9	5.7	8.5	1.0*	5	I
595.	Douaire	1125		32	6.5	-	8	5.8	5.6	5.3	1.2*	5	II
596.	Nominique	812		35	4.5	-	26	6.6	6.6	6.3	4.0	5	I
597.	Chaud	850	640	33	5.4	-	26	5.9	5.9	4.2	5.6	10	I
598.	Petit Nominique	813		30	6.0	15	20	6.3	6.0	3.3	3.8	10	II
599.	Montjoie	875	1203	75	4.5	-	15	6.4	5.8	8.4	1.5*	5	I
600.	Labelle	812		60	4.0	-	26	6.6	6.4	5.4	3.7	10	I
601.	Tremblant	747		62	4.5	-	12	6.0	6.0	5.5	3.9	5	I
602.	Simon	652	3200	105	6.5	-	30	6.6	6.0	8.7	1.0*	5	I
603.	Désormeaux	722	289	45	7.0	-	35	7.2	6.0	4.8	3.5*	5	II
604.	Viceroy	694		27	6.0	-	35	7.4	6.0	6.3	2.4*	5	II
605.	Cross	690		30	4.5	-	30	5.7	5.5	4.8	4.5*	10	I
606.	Beavin	593	358	27	5.6	22	35	6.8	6.0	4.2	4.2	10	I
607.	Sixteen Island	930	358	54	5.0	-	25	6.8	6.0	5.7	3.0*	5	I
608.	Anne	1020	113	25	5.5	21	16	6.7	5.8	4.5	4.2*	10	I
609.	Bark	711	645	48	4.0	30	15	6.3	5.2	4.5	2.6	5	I
610.	St. Joseph	1199	143	32	6.0	-	17	6.6	5.5	2.8	6.5*	20	II
611.	Manitou	1273	394	23	5.5	-	18	6.7	5.6	3.0	5.0*	10	I
612.	Masson	1100		45	4.5	-	18	6.7	5.6	3.3	6.0*	20	I
613.	Wexford	1192		24	5.5	-	19	6.8	5.9	4.2	4.5*	10	I
614.	Archambault	1281		40	4.5	-	12	5.9	5.9	5.7	3.0	5	I
615.	Chertsey	990	152	33	5.0	-	18	6.8	5.9	5.1	3.8*	5	I
616.	Cloutier	730		24	5.5	-	25	7.0	5.9	4.5	4.5*	10	I
617.	des Français	550		24	5.0	20	25	6.9	5.7	3.5	5.0*	10	I
618.	Maskinonge	467		27	7.0	-	15	6.1	5.5	3.3	4.3	10	II
619.	Long	580		30	4.5	-	20	6.7	5.5	4.5	4.0*	5	I
620.	Goulet	519		30	4.2	12	16	6.8	5.5	3.3	4.5*	5	I

No.	Locality	Elev.	A _o	z _m	T _m	zO ₂	TH	E	pH	H	SDV	O ₂ c	Co.	Order
621.	la Pêche	555	320	40	4.1	-	27	6.6	5.5		3.6	4.0	5	I
622.	Isaïe	540		24	6.5	-	15	6.5	6.0		5.0	4.0*	5	II
623.	Edouard	913	174	30	6.0	-	8	5.8	5.0		5.0	4.9	10	II
624.	Saccomie	910		65	5.5	-	10	6.3	5.5		14.5	0.5*	3	I
625.	L'eau Claire	815		72	5.5	-	12	6.5	5.5		6.9	2.0*	5	I
626.	Wapazigonke	725	584	27	6.0	-	10	6.4	5.7		6.6	1.8	5	II
627.	Dauphinaus	925	200	30	5.0	-	10	6.1	5.0		4.5	2.0	5	I
628.	Atikagamac	560	184	28	4.3	-	15	6.4	5.5		3.0	4.4	5	I
629.	Caribou	1300	387	35	5.7	-	10	6.3	5.3		9.3	2.0	5	I
630.	Taureau	1190		25	6.0	-	15	5.9	5.7		2.7	8.1*	30	II
631.	Clear	1350		50	5.0	-	15	6.6	6.3		6.6	4.0*	10	I
632.	Normand	1350	920	60	5.0	-	10	6.3	6.0		4.2	5.5*	10	I
633.	Kempt	1350		48	6.0	-	10	6.0	5.8		4.8	5.0*	10	II
634.	Harper	801		68	4.5	-	12	6.4	6.0		4.5	4.5*	5	I
635.	Wayagamac	887		35	5.0	-	10	6.2	6.0		6.3	3.5*	5	I
636.	à Beauce	705		26	6.0	-	25	6.4	6.3		4.5	5.0*	10	II
637.	Mekinac	525	2341	125	4.0	-	10	6.2	6.2		4.1	4.5*	5	I
638.	du Missionnaire	520		42	6.5	-	18	6.3	6.1		6.0	4.0	5	II
639.	du Jesuite	670		33	6.0	-	15	6.3	5.8		4.8	3.0*	5	II
640.	aux Sables	520		35	6.0	-	12	5.8	5.5		1.5	2.5	5	II
641.	Blanc	480		45	5.0	-	15	5.5	5.5		3.0	6.0	20	I
642.	St. Joseph	520		35	4.0	-	15	5.5	5.5		4.5	5.0*	20	I
643.	Jacques Cartier	2500		100	4.9	-	8	5.6	5.4		3.9	6.3	20	I
644.	des Commissaires	900		25	9.5	-	9	6.2	5.8		5.5	5.0*	20	II
645.	Kenogami	500		75	5.0	-	15	5.7	5.6		1.3	9.0*	50	I
646.	Jim	690	432	42	5.0	-	10	5.8	5.6		2.0	7.5*	30	I
647.	aux Rats	625		26	5.5	-	10	5.5	5.0		2.4	7.3*	30	I
648.	La Mothe	820		50	5.0	-	15	6.5	6.0		2.5	6.5*	20	I
649.	Labreque	440		27	6.5	-	26	6.8	6.2		3.0	5.5*	10	II
650.	Matapedia	514		33	5.5	-	85	8.0	7.8		3.0	4.0*	5	I

'No.	Locality	Elev.	A _o	Z _m	T _m	ZO ₂	TH	E	pH	H	SDV	O _{2c}	Co.	Order
651.	Humqui	700		37	4.2	-	85	8.0	7.4		4.2	2.8*	5	I
652.	Petit Macpes	500		33	5.8	-	85	8.4	7.6		4.5	3.0*	5	II
653.	St. Simon	390	572	20	9.9	-	42	7.2	7.1		2.7	5.0*	10	II
654.	Squatek	525		47	5.8	-	60	7.3	7.0		5.4	1.8*	5	II
655.	Merumticook	650		55	5.5	-	51	7.5	7.1		4.8	3.2	5	I
656.	Long	620	1664	22	8.6	20	36	7.4	7.0		3.6	5.5*	10	II
657.	Pohenegamook	650	856	35	4.0	-	38	6.5	6.4		2.4	4.0*	10	I
658.	de l'Est	1050		29	4.4	-	26	7.4	6.3		3.0	5.5*	20	I
659.	Long	620	2400	45	5.3	-	42	7.0	6.7		1.0	4.5*	15	I
660.	Eagle	574		40	4.0	-	35	6.7	6.5		2.4	6.0*	30	I
661.	St. Froid	581		30	4.5	-	25	6.6	6.4		2.7	6.0*	30	I
662.	Pushineer	1200		15	5.0	-	20	6.9	6.0		4.5	1.8*	5	I
663.	Grand	50	16240	30	7.0	-	30	6.8	6.0		2.4	5.5*	20	II
664.	Utopia	55		20	10.0	-	20	6.0	5.5		3.3	6.0*	30	II
665.	Tunk	200	804	60	5.0	-	30	7.0	6.0		10.8	1.0*	5	I
666.	Green	150	1210	40	7.0	-	30	6.3	5.5		4.0	6.5*	20	II
667.	Chamberlain	945	4433	45	4.8	-	18	6.3	6.3		4.2	7.2	30	I
668.	Moosehead #	1050	33100	75	4.5	-	16	6.5	6.0		5.0	4.5*	10	I
669.	Megantic	1294	2650	45	4.0	-	30	6.5	6.3		3.6	3.0	15	I
670.	William	650		27	5.0	15	68	7.8	6.6		1.2	5.0*	5	I
671.	Elgin	880		33	4.0	-	36	6.8	6.5		3.6	5.0*	20	I
672.	Nicolet	1150		40	4.0	-	26	6.5	6.4		7.8	1.0*	5	I
673.	Montjoie	890		20	8.0	15	30	6.4	6.0		3.6	6.0*	30	II
674.	Bowker	1110		45	5.0	-	25	6.5	6.3		8.1	0.0	5	I
675.	Stukely	935		30	6.0	-	38	6.6	6.5		5.1	2.5	5	II
676.	Lyster	1550	170	45	5.9	-	37	7.0	6.7		5.1	2.1	5	II
677.	Big Averill	1684	339	30	5.5	-	15	6.1	5.8		6.3	4.5*	5	I
678.	Salem	963		21	7.0	15	50	8.0	7.2		3.3	6.5*	20	II
679.	Seymour	1279	702	50	5.0	-	40	7.2	7.0		6.9	3.5*	5	I
680.	Willoughby	1170	600	81	5.0	-	45	7.3	7.2		11.2	0.7*	3	I

No.	Locality	Elev.	A0	Z _m	T _m	ZO ₂	TH	pH		SDV	O ₂ C	Co.	Order
								E	H				
681.	Crystal	970	272	31	5.0	-	38	7.2	6.9	3.3	5.0*	25	I
682.	Caspian	1400	315	42	5.0	-	70	8.0	7.1	6.9	2.0*	5	I
683.	Eligo	881	47	30	6.0	20	85	8.3	7.1	5.1	3.0*	5	II
684.	Rangley	1520	2400	30	7.0	-	10	6.8	6.0	9.0	1.0	5	II
685.	Thompson	500	1740	27	9.0	-	30	6.7	6.0	5.5	2.0*	5	II
686.	Sebago	250	11630	96	4.0	-	35	7.0	6.5	10.5	0.7*	3	I
687.	Winnepesaukee #	480	18000	54	5.0	-	20	6.5	6.0	6.5	2.0*	5	I
688.	Sunapee #	1200		60	4.5	-	15	6.5	6.0	8.0	1.0*	5	I
689.	Chazy	1531	794	25	6.0	-	24	6.8	6.0	4.2	5.0*	10	II
690.	Upper Chateaugay	1310		20	6.0	-	30	6.7	6.4	3.0	6.0*	20	II
691.	Taylor	1370		27	5.5	-	26	6.6	5.8	5.0	2.5*	5	I
692.	Upper St. Regis	1600		21	6.0	15	15	6.4	5.6	3.0	6.5*	20	II
693.	Placid	1850		42	5.0	-	20	5.8	5.7	10.2	1.0*	5	I
694.	Upper Saranac	1571	2035	27	5.5	-	20	6.8	5.9	3.3	7.0*	20	I
695.	Tupper	1542	1920	27	6.0	-	12	5.5	5.0	3.5	6.5*	15	II
696.	Trout	780		27	7.0	20	36	7.1	6.6	4.0	5.0*	10	I
697.	Massawepie	1550		24	5.0	15	15	6.5	5.5	5.7	4.0*	5	I
698.	Portaferry	859	20	27	5.5	20	32	6.9	6.7	3.6	6.0*	20	I
699.	Bonaparte	768	512	24	6.5	-	75	7.8	7.3	4.2	4.5*	10	II
700.	Brantingham	1235	138	18	6.5	15	15	6.2	6.0	3.6	7.0*	30	II
701.	Fourth Fulton	1707		21	6.0	-	20	6.5	6.3	4.8	5.5*	10	II
702.	White	1422	84	23	6.0	15	20	6.5	6.1	7.8	2.0*	5	II
703.	Schroon	702	1692	45	5.0	-	24	6.8	6.3	4.5	4.4*	10	I
704.	Trout	759	100	23	5.0	20	26	6.2	6.0	4.5	4.5*	10	I
705.	Canada	1542	210	35	5.0	-	12	5.4	5.0	5.1	4.0*	10	I
706.	Hedges	535	30	23	5.5	12	136	8.5	7.1	2.1	5.5*	5	I
707.	Otsego	1194	1600	50	5.0	-	145	8.5	7.9	4.8	3.5*	5	I
708.	Canadice	1012	256	27	6.5	25	60	7.2	6.9	2.0	4.0*	5	II
709.	Sylvan	325		42	5.5	-	144	8.5	7.9	3.6	3.5*	5	I
710.	Gilead	498		35	5.5	-	43	7.0	6.8	7.8	1.0*	5	I

No.	Locality	Elev.	A _o	z _m	T _m	zO ₂	TH	pH E H	SDV	O ₂ c	Co.	Order
711.	Glenida	508	76	30	6.0	20	80	8.0	9.0	1.0*	5	II
712.	Sterling	750	126	33	4.5	-	24	6.5	6.3	2.0*	5	I
713.	Wawayanda	525	90	33	6.0	-	40	7.0	2.4	5.6*	20	II
714.	Western Brook	125		210	9.2	-	9	7.0	9.0	3.6	5	II
715.	Rocky Harbour	50		20	11.0	-	70	7.6	2.7	9.8	20	II
716.	Deer	17		6144	6.0	-	10	6.5	2.7	9.0	30	I

a no depth with oxygen less than 2 ppm at time of survey

* estimated by graphical analysis (Fig. 43).

physicochemical data obtained from literature or regional biologist's files.

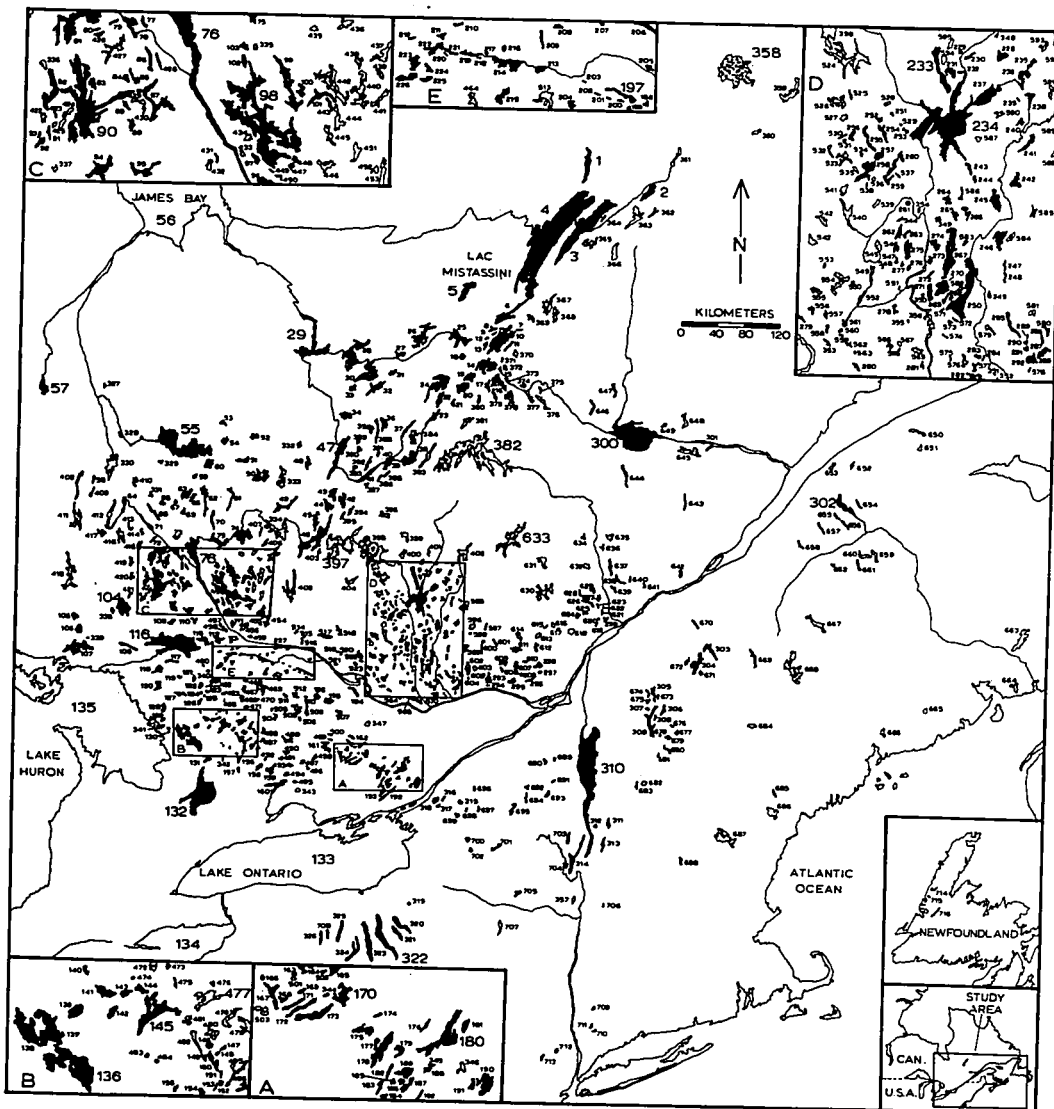


Fig. 42. Base Map of study area illustrating lakes considered in the study. Numbers refer to localities in Appendix I. Solid lakes and numbers are localities in which one or more species of the deepwater community are known. Open lakes are ecologically suitable lakes lacking the deepwater community. Latitudes of study area: 53°N - 41°N ; Longitudes, 82°W - 57°W .

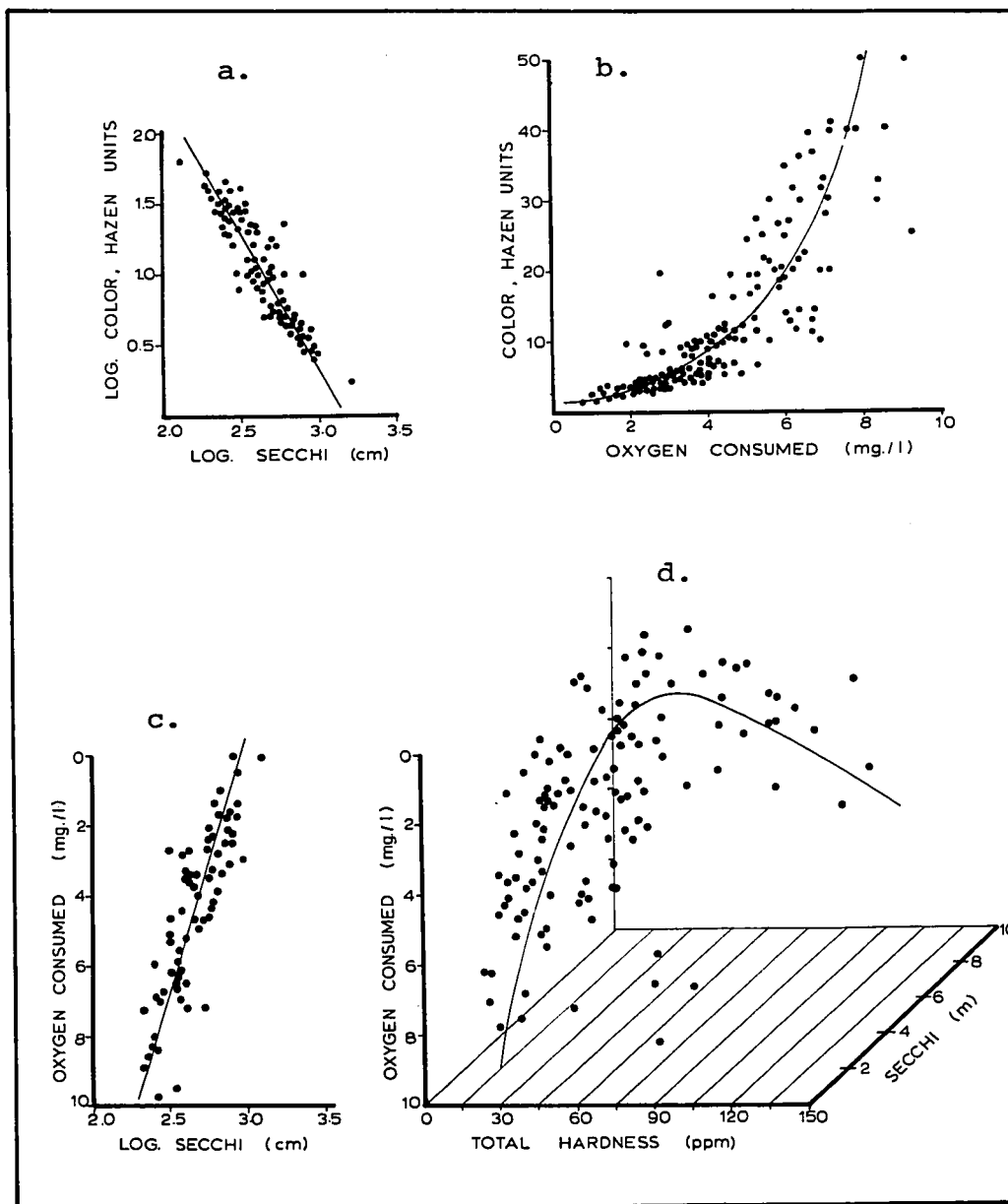
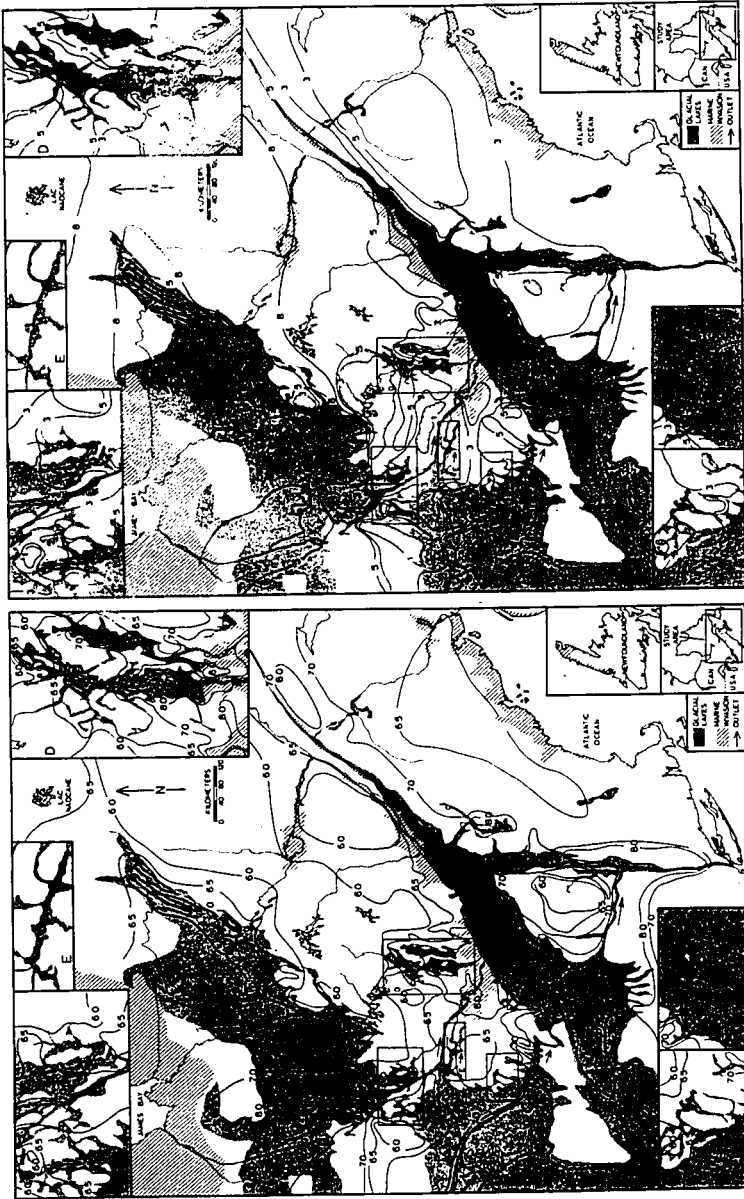


Fig. 43. Relationship between: (a) log of color and log of secchi visibility, (b) color and oxygen consumed, (c) oxygen consumed and log of secchi visibility, (d) oxygen consumed, total hardness, and secchi visibility in the 150 study lakes with complete chemical analysis. Graphs were used to estimate O_2c and Co in study lakes without complete chemical analysis.



A.

B.

Fig. 44. Distribution of (A) surface pH, (B) oxygen consumption (dissolved organic matter) in the study lakes, in relation to the distribution of former glacial lakes. Oxygen consumption values are in ppm.

APPENDIX II

Distributions of the deepwater fishes captured
during the course of this study.

For the reprint by M.J. Dadswell entitled Postglacial dispersal of four deepwater fishes on the basis of new distribution records in Eastern Ontario and Western Quebec, which forms part of Appendix II, see pocket at the back.

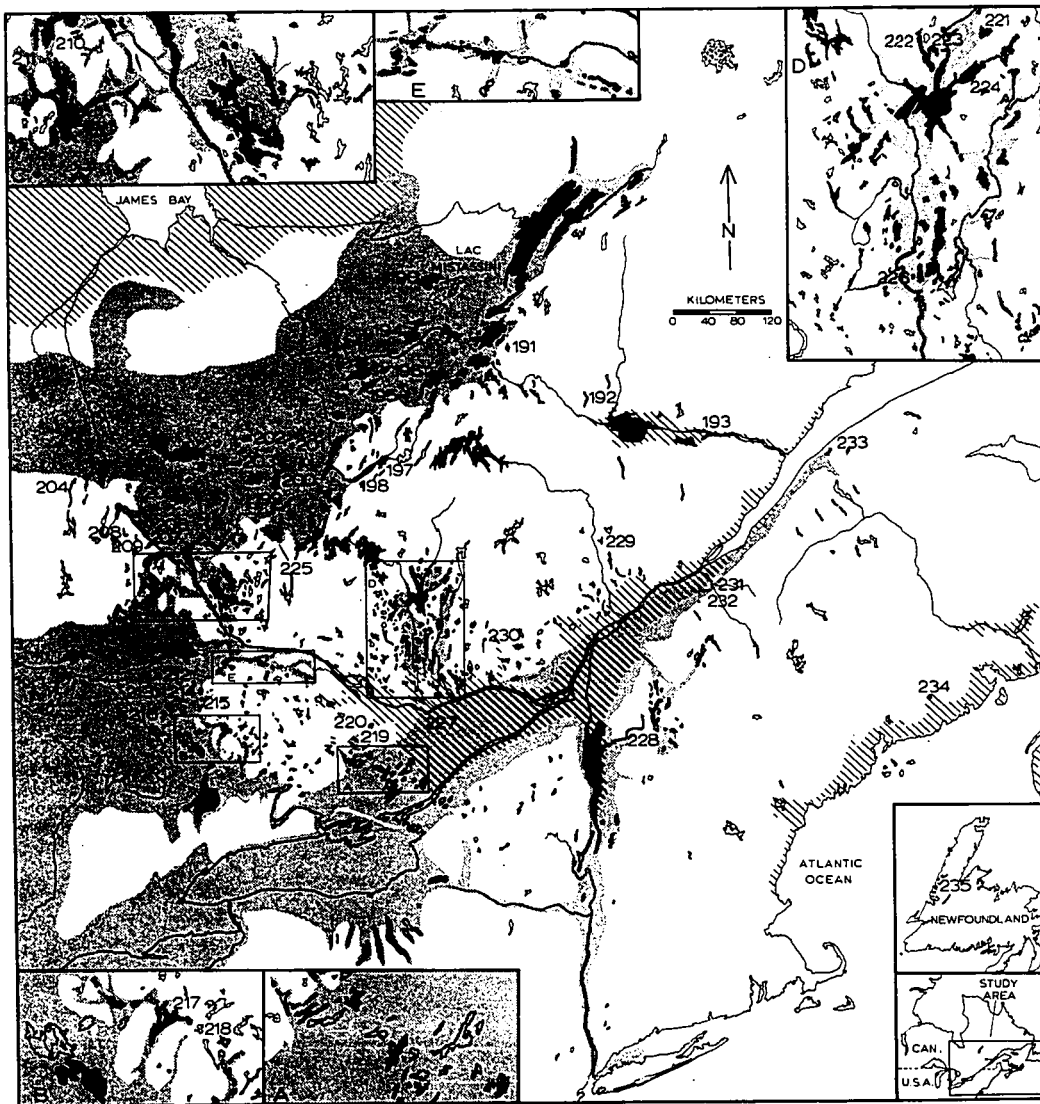


Fig. 45. Localities (solid lakes and numbers) in which one or more of the four fish species were found during 1972. Numbers refer to localities in Table 2, continued from Fig. 2 (Dadswell 1972). Open lakes are those sampled in which none of the fishes were found.

Table 1. continued...

Localities, found during 1972, in which one or more of the four deepwater fish species are known. Number of locality in table is used to show geographical position of record in Fig. 45. Plus sign (+) indicates presence of species. Sources of records are as follows: new records (n.rec.); previously unpublished records from Service de la Faune de Quebec (SFQ); Ontario Department of Lands and Forests (ODLF); previously published records (authors name and date of publication). Unless otherwise specified all localities refer to lakes.

No.	Locality	<u>Cottus</u>		<u>Myoxocephalus</u>		<u>Pungitius</u>		<u>Percopsis</u>		Source of record
		<u>ricei</u>		<u>quadricornis</u>		<u>pungitius</u>	<u>omiscomaycus</u>			
190.	*Assinica	-		-		+		-		SFQ
191.	Vimont	-		-		-		+		n. rec.
192.	Jim	+		-		+		+		SFQ
193.	Saguay Estuary	-		-		+		-		Legendre (1961)
194.	la Tréve	+		-		-		+		n. rec.
195.	Pustimica	-		-		-		+		n. rec.
196.	Bachelor	+		-		-		+		"
197.	Maude	-		-		-		+		"
198.	Faillon	-		-		-		+		"
199.	Mourier-Lemoine	+		-		-		+		"
200.	Malarctic	-		-		-		+		"
201.	Castagnier	-		-		-		+		"
202.	Chicobi	-		-		-		+		"
203.	Lois	-		-		-		+		"
204.	Kenogamissi	-		-		-		+		"
205.	St. Anthony	+		-		-		-		"
206.	Kinogami	-		-		-		+		"
207.	Mountain	-		-		-		+		"
208.	Longpoint	-		-		+		+		"
209.	Mendelssohn	+		-		-		-		"

* numbering follows after Dadswell (1972). It is not the same as the relict crustacean base Map. i.e. Fig.

Table 1 . continued...

No.	Locality	<u>Cottus</u> <u>ricei</u>	<u>Myoxocephalus</u> <u>quadricornis</u>	<u>Pungitius</u> <u>pungitius</u>	<u>Percopsis</u> <u>omiscomaycus</u>	Source of record
210.	Lady Evelyn	+	-	-	-	n. rec.
211.	Wakimika	-	-	+	-	"
212.	Wauquimakog	-	-	-	+	"
213.	Wahwashkesh	+	-	-	-	"
214.	Bernard	-	-	-	+	ODLF
215.	Pickerel	+	-	-	-	n. rec.
216.	Manitouwabing	+	-	-	-	"
217.	Lake of Bays	-	-	-	+	ODLF
218.	Little Hawk	-	-	+	-	ODLF
219.	Wensley	+	-	-	-	n. rec.
220.	Calabogie	-	-	-	+	n. rec.
221.	Nottawissi	-	-	+	+	"
222.	Petawaga	-	-	+	+	"
223.	Maguerite	-	-	+	-	"
224.	Piscatosine	-	-	-	+	"
225.	Descelles	-	-	-	+	"
226.	Green	-	-	+	-	"
227.	Ramsey Creek	-	-	-	+	"
228.	Massaquoi River	-	-	-	-	Richardson (1935)
229.	à Beauce	+	-	-	-	n. rec.
230.	Labelle	-	-	+	-	n. rec.
231.	Riviere Etchemine	-	-	-	+	SFQ
232.	Riviere Chaudiere	-	-	-	+	SFQ
233.	Simon	-	-	+	-	n. rec.
234.	Tunk	-	-	+	-	"
235.	Berry Point	-	-	+	-	"

References

Legendre, V. 1961. Les poissons de la Fjord Saguenay. Nat.
Can. 88: 129-147.

Richardson, L. R. 1935. The freshwater fish of southeastern
Quebec. Ph.D. thesis, McGill University, Montreal.

Appendix III

CHEMICAL ANALYSIS

Instant Ocean Synthetic Sea Salts:

At 15°C has the following ionic composition, in ppm.

Cl	18400	MoO ₄	0.7
Na	10200	S ₂ O ₃	0.4
SO ₄	2500	Li	0.2
Mg	1200	Rb	0.1
K	370	I	0.07
Ca	370	EDTA	0.05
HCO ₃	140	Al	0.04
H ₃ BO ₃	25	Zn	0.02
Br	20	V	0.02
Sr	8	Co	0.01
PO ₄	1	Fe	0.01
Mn	1	Cu	0.003

Postglacial Dispersal of Four Deepwater Fishes on the Basis of New Distribution Records in Eastern Ontario and Western Quebec

M. J. DADSWELL

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DADSWELL, M. J. 1972. Postglacial dispersal of four deepwater fishes on the basis of new distribution records in eastern Ontario and western Quebec. *J. Fish. Res. Bd. Canada* 29: 545-553.

Occurrences in 130 new localities in eastern Ontario and western Quebec are given for the fishes *Cottus ricei*, *Myoxocephalus quadricornis*, *Pungitius pungitius*, and *Percopsis omiscomaycus*. A total of 189 localities for these fishes is now known within this area. The distributions of these species are closely associated with the maximum extent of the large, interconnected, Wisconsin glacial lakes, their outlet channels, and areas inundated by postglacial marine waters. Although all four fishes dispersed primarily by means of the proglacial waters between 17,000 and 6000 years ago, *C. ricei*, *P. pungitius*, and *Percopsis omiscomaycus* have dispersed short distances beyond the glacial lake-marine boundaries and are probably still dispersing as drainage systems adjust themselves to postglacial rebound. Dispersal was probably north and eastward from a Mississippian refugium.

DADSWELL, M. J. 1972. Postglacial dispersal of four deepwater fishes on the basis of new distribution records in eastern Ontario and western Quebec. *J. Fish. Res. Bd. Canada* 29: 545-553.

La présence de *Cottus ricei*, *Myoxocephalus quadricornis*, *Pungitius pungitius*, et *Percopsis omiscomaycus* a été constatée dans 189 localités de l'est de l'Ontario et de l'ouest du Québec. De ces observations 130 sont nouvelles. La distribution de ces poissons coïncide avec l'étendue maximum du grand système des lacs glaciaires apparus après l'âge Wisconsin, de leurs décharges et des régions inondées par les eaux mer grossies par la fonte des glaciers. Bien que la dissémination de ces poissons se fasse probablement surtout par les lacs d'origine glaciaire il y a 6000-17,000 années, *C. ricei*, *P. pungitius*, et *Percopsis omiscomaycus* ont également tendance à se disséminer un peu en amont de leurs limites. La dissémination était probablement vers le nord et vers l'est à partir du refugium du Mississippi.

Received April 14, 1971

THE distribution and biology of many fishes in eastern Canada, particularly those occurring in deep water, are poorly known. This factor has prevented a complete discussion of their zoogeography in the few broad geographic studies (Radforth 1944; Legendre 1953; Scott 1967) that have been done.

During a study of the distributions of glacial relict crustaceans in eastern Canada, *Cottus ricei* (spoonhead sculpin), *Myoxocephalus quadricornis* (fourhorn sculpin), *Pungitius pungitius* (ninespine stickleback), and *Percopsis omiscomaycus* (trout-perch) were frequently captured. In eastern Ontario and western Quebec, these fishes were previously known largely from the Great Lakes, James Bay, and a few widely scattered lakes (Martin and Chapman 1965; Magnin 1965; Delisle and Van

Vliet 1968). This paper presents new records that close some of the gaps in the literature on the distributions of these four fishes, thereby allowing discussion of their postglacial dispersal routes.

The glacial lakes and marine transgressions shown in the study area (Fig. 1) are the maximum extents of all glacial waters during retreat of late Wisconsin ice and, with some modifications by the author, are basically those of Prest et al. (1968) and Bois-soneau (1968). The presence of a glacial lake in the Gatineau Valley, Que., (Fig. 1 and 3) that is here named glacial Lake Gatineau, was noted by Antevs (1928); its boundaries are given tentatively on the basis of distributions of the relict crustaceans (M. J. Dadswell unpublished data). These glacial lakes did not occur synchronically, but rather in sequence from south to north 17,000-6000 years ago (Prest 1970).

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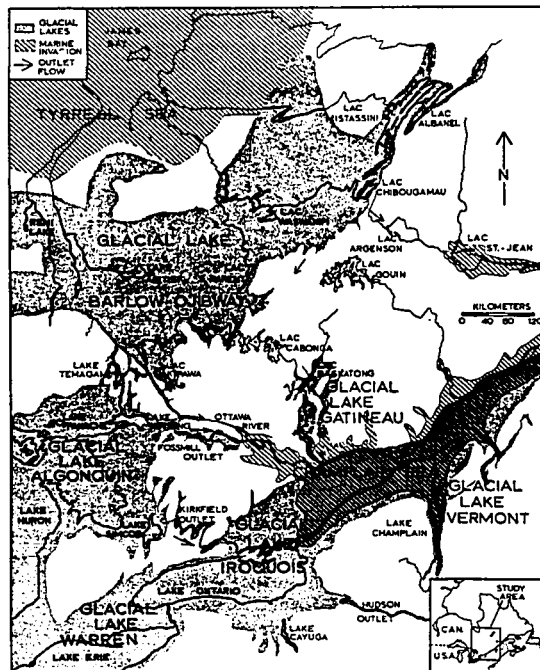


FIG. 1. Maximum extent of the late Wisconsin glacial lakes and marine transgressions (adapted from Prest et al 1968; Boissoneau 1968) in the study area. Glacial Lake Fort Anne and glacial Lake Iroquois joined to form glacial Lake Frontenac and occupied the St. Lawrence lowlands prior to the Champlain Sea transgression (Prest 1970).

Materials and Methods

As the major study was concerned with distributions of relict crustaceans, the sampling methods were directed towards their capture. The main sampling gear was a small otter trawl, 3.5 m across the footrope and 5.5 m long. Mesh size was 38 mm throughout, with an inner 2-m bag of 3-mm mesh in the codend. The trawl was towed along the bottom with a ratio of tow rope to depth of 3:1, at speeds from $\frac{1}{2}$ to 3 kph. Fishing depths were determined using an electronic depth sounder.

In each lake the vertical distributions of temperature and oxygen were first determined, and from these the best trawling depth for the capture of crustaceans selected. Two slow-speed tows of 5–7 min duration were then made at the selected depth, usually 20–50 m. If time permitted, tows were made in shallower water, or deeper water, or both, expressly to capture fish. All trawling was done during daylight.

In all, 372 lakes were sampled with the otter trawl. In 20 of the lakes a 5-m minnow seine was used over sandy beaches after nightfall to obtain trout-perch.

Series of the fish specimens from all localities have been deposited at the National Museum of Natural Sciences, Ottawa, and the Royal Ontario Museum, Toronto.

Distributions Records

A total of 130 new localities were obtained for the four species. One or more of these fishes were found in 101 (53%) of the 191 sampled lakes considered to be within the glacial lake–marine boundaries (Fig. 2 and 3). On the other hand, one or more were taken in only 29 (15%) of the 181 lakes sampled that were considered to be outside the boundaries (Fig. 2 and 3). Furthermore, 84% of the 189 known localities for these fishes in eastern Ontario and western Quebec are within the glacial lake–marine boundaries (Table 1; Fig. 2 and 3). Of 69 lakes in areas inundated only by the maximum levels of the glacial lakes, 51 (75%) were found to contain one or more of these fishes. In only a few instances were any of the fishes found more than 5–10 m above, or more than a few kilometers beyond, the limits of glacial waters. The maximum distance of dispersal upstream to lakes so far known from this study is 60 km, and the maximum known elevation above maximum glacial lake level reached by these fishes is 36 m (Lac Cabonga, no. 63 Fig. 2). In regions where considerable dispersal beyond the glacial lake–marine boundaries has occurred, either the topography is low or the streams are slow and meander through sand plains.

Cottus ricei was the most commonly captured fish and was found in 88 new localities (Table 1). This brings to 100 the known localities for this fish within the study area (Fig. 4). The new localities extend the known distribution of *C. ricei* 700 km eastward in Canada to the northern end of Lac Mistassini. This species is now known to occur in Lake Abitibi; Dymond and Hart (1927) recorded it only from a tributary of the lake.

Although I did no collecting in rivers, there are only two known captures of *C. ricei* from running water in the study area, and in southeastern Canada this fish appears to be predominantly lacustrine. In western Canada this species is commonly found in rivers (McPhail and Lindsey 1970). This apparent difference in habitat may be due to a lack of sampling with an otter trawl in western lakes, or a lack of knowledge of the fishes in the large rivers flowing into James Bay, or both.

In deep, stratified lakes, *C. ricei* was found at depths of 15–50 m and at temperatures ranging from 8–4 C. In these lakes it was moderately abundant, and an average of 2–4 specimens were taken per trawl run. Some lakes (e.g. Lac des Iles, no. 149

Fig. 3) yielded 35 specimens per tow from depths of 40 m. In the shallow, turbid lakes of the Ontario-Quebec clay belt the species was very abundant (50 or more per tow) at depths of 5-10 m and at temperatures as high as 18 C.

Myoxocephalus quadricornis was taken in only five new localities, and these records bring to 11 the known localities for this fish within the study area (Fig. 4 and Table 1). The known distribution now extends into the basin of glacial Lake Barlow-Ojibway. This species was always found at depths of 25 m or more, the average capture depth being 50 m. As in northwestern Canada (McPhail and

Lindsey 1970), all of the lakes where this species was found also contained the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Temperatures where it occurred were always below 8 C, although some of the lakes where it was found (Heney, no. 169; Thirty-one Mile, no. 167 Fig. 3) were not particularly oligotrophic, having both moderate dissolved solids (75 ppm) and low oxygen tensions below 30 m (2 ppm or less).

Myoxocephalus quadricornis appears to be sporadically distributed in eastern Canada, and the lack of records obtained may not simply be a result of incomplete sampling. When this species was

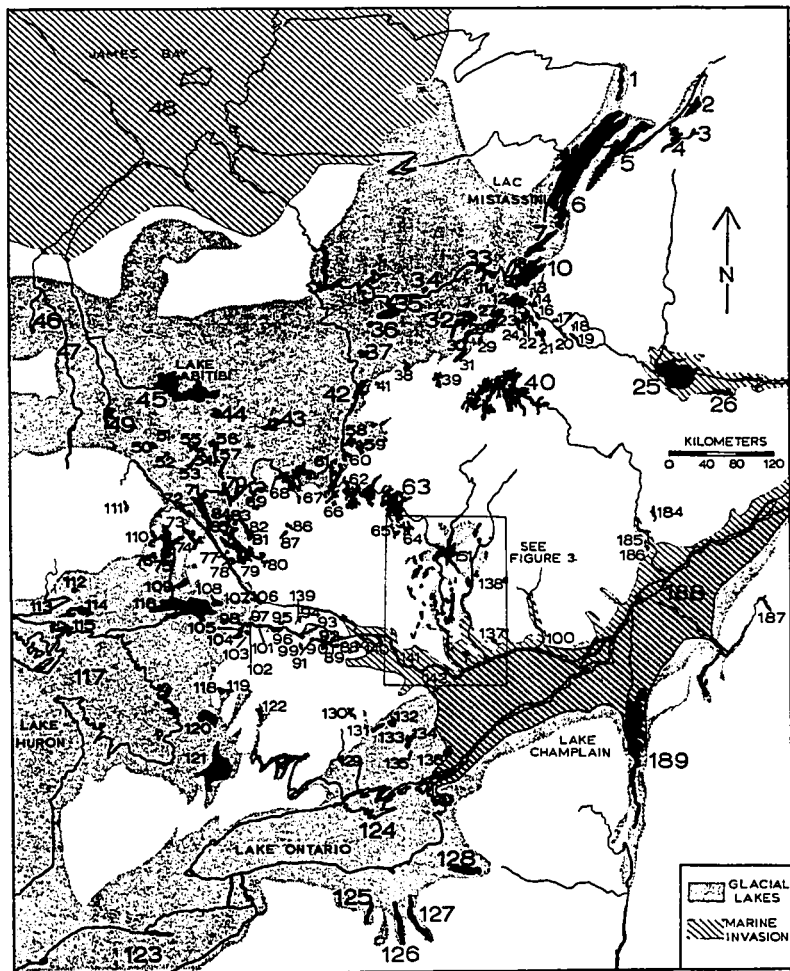


FIG. 2. Localities (solid lakes and numbers) in which one or more of the four species have been found. Numbers refer to localities in Table 1.

TABLE 1. Localities in which one or more of the four deepwater fishes were found. Number of locality indicates position of record in Fig. 2 and 3. Plus sign (+) indicates presence of species. Sources of records are as follows: new records (n. rec.) in this paper; previously unpublished records from Service de la Faune de Québec (SFQ), Ontario Department of Lands and Forests (ODLF), Royal Ontario Museum (ROM), and the National Museum of Natural Sciences (NMC); previously published records (author's name and date of publication). Unless otherwise specified all localities refer to lakes.

No.	Locality ^a	C. <i>ricei</i>	M. <i>quadricornis</i>	P. <i>pugetius</i>	P. <i>omiscamycus</i>	Source of record	No.	Locality ^a	C. <i>ricei</i>	M. <i>quadricornis</i>	P. <i>pugetius</i>	P. <i>omiscamycus</i>	Source of record
1.	Baudeau	+			+	n. rec.	97.	Lauder				+	N. V. Martin (pers. comm.)
2.	Bethoulat	+			+	"	98.	Boulter				-	"
3.	Petit Temiscamie	+			+	"	99.	White Partridge				-	"
4.	Temiscamie	+			+	"	100.	Rivière du Nord				-	NMC
5.	Albanel	+		+	+	"	101.	Davenport				+	ROM
6.	Mistassini	+			+	"	102.	Kitchikowi			+	+	N. V. Martin (pers. comm.)
7.	Wazonkichi	+			+	Richardson (1944)							
8.	Gilman	+			+	n. rec.	103.	Threemile				+	"
9.	Caché	+			+	"	104.	Wasigomog				+	"
10.	Chibougamau	+			+	"	105.	Wilkes				+	"
11.	Presqu'île	+			+	"	106.	"Unnamed"				+	ODLF
12.	Obalagamau	+			+	"	107.	Kearney				+	ODLF
13.	Dufresne	+			+	"	108.	Trout			+	+	ODLF
14.	Charron	+			+	"	109.	Tomiko					n. rec.
15.	Malo	+			+	"	110.	Obabika	+			+	ODLF
16.	Nicabau	+			+	"	111.	Smoothwater	+			+	n. rec.
17.	Aigremont	+			+	"	112.	Fairbank				+	ROM
18.	D'Égils	+			+	"	113.	Spanish River		+		+	ROM
19.	Argenson	+			+	"	114.	Panache				+	n. rec.
20.	Chamouchouane	+			+	"	115.	Lumsden				+	Beamish (MS 1970)
21.	Poutrincourt	+			+	"	116.	Nipissing				+	ROM
22.	Rohault	+			+	"	117.	Huron		+		+	Hubbs & Lagler (1964)
23.	Gabriel	+			+	"						+	ROM
24.	Robert	+			+	Legendre (1933)	118.	Vernon	+			+	ROM
25.	St.-Jean	+			+	SFQ	119.	Fairy	+			+	n. rec.
26.	Kenogami	+			+	n. rec.	120.	Muskoka	+			+	ROM
27.	Caopatrina	+			+	"	121.	Simcoe	+			+	ROM
28.	de la Surprise	+			+	"	122.	Twelve-Mile	+			+	ROM
29.	Sylvie	+			+	"	123.	Erie	+			+	Hubbs & Lagler (1964)
30.	Hébert	+			+	"						+	"
31.	Lacroix	+			+	"	124.	Ontario	+			+	Greely (1928)
32.	Doda	+			+	"	125.	Canandaigua	+			+	"
33.	Opemisca	+			+	"	126.	Seneca	+			+	"
34.	Renault	+			+	"	127.	Cayuga	+			+	"
35.	Waswanipi	+			+	Magnin (1965)	128.	Oneida	+			+	"
36.	Madelaine	+			+	n. rec.	129.	Moira River	+			+	NMC
37.	Quevillon	+			+	"	130.	Westmooon	+			+	n. rec.
38.	Weinagami	+			+	"	131.	Kashwakamak	+			+	"
39.	Mespiet	+			+	"	132.	Cross	+			+	"
40.	Gouin	+			+	"	133.	Crow	+			+	"
41.	Desforges	+			+	"	134.	Bobs	+			+	"
42.	Parent	+			+	"	135.	Dessert	+			+	"
43.	Preissac	+			+	"	136.	Charleston	+			+	"
44.	Duparquet	+			+	"	137.	Heart	+			+	"
45.	Abitibi	+			+	Dymond & Hart (1927)	138.	Nomininque	+			+	"

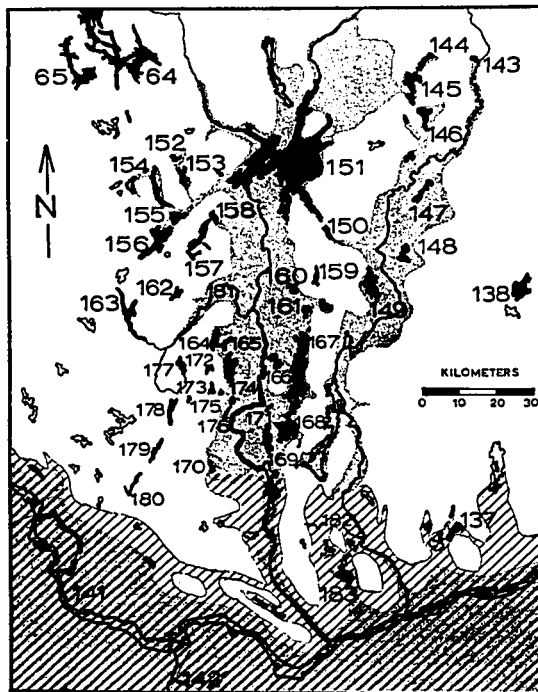


FIG. 3. Maximum extent of the Champlain Sea (cross-hatching; Elson MS 1960) and the later combined Champlain Sea and glacial Lake Gatineau (shading; M. J. Dadswell unpublished data) in the Gatineau Valley region. Solid lakes were found to contain one of more of the fishes, open lakes are those sampled in which none of the fishes were found. Numbers refer to localities in Table 1.

found in a lake it was always taken readily and in large numbers. The size of some populations is indicated by the following catch data: Fairbank Lake, 18 per tow; Raven Lake, 15 per tow; Roddick Lake, 33 per tow.

Pungitius pungitius was captured in 36 localities. This brings to 53 the known localities for this fish within the study area (Fig. 4 and Table 1). The known distribution in central Quebec is extended to Lac Albanel.

The ninespine stickleback was usually found in depths from 5–20 m; this agrees with depth distributions found by Reckahn (1970) in South Bay, Lake Huron, and Nelson (1968a) in Illinois for this species. Specimens were occasionally caught as deep as 40 m and as shallow as 1 m. *Pungitius pungitius* was especially abundant in lakes with much submerged aquatic vegetation (Kaswakamak, no. 75; 70 per

tow). Catches of this species in 10–30 m of water usually consisted of 2–5 fish per tow.

Percopsis omiscomaycus was collected from 58 new localities. This brings to 108 the known localities for this fish within the study area. *Percopsis omiscomaycus* was found in shallower water than the other three species. The average depth range was 5–15 m, although the fish was captured at 20 m and was commonly taken with a seine over beaches at night if water temperatures were not higher than 21 C. Therefore, during the summer in southern Canada it would be restricted to depths in or below a thermocline, and it is for this reason that I consider it a deepwater fish. Sixty specimens were taken in one tow in Nighthawk Lake (no. 49 Fig. 2); but the average trawl catch in most lakes was 10.

Postglacial Dispersal

The distribution of these four fish species in southeastern Canada suggests that the major routes of dispersal following deglaciation were the interconnecting standing bodies of proglacial waters and their outlets. Their occurrence in 75% of the lakes in areas covered only by the maximum levels of proglacial waters indicates that dispersal closely followed the ice retreat. In support of this hypothesis, it can be stated that all four species are essentially coldwater, lacustrine forms with a limited ability to move upstream. In the ensuing discussion, names and sequences of glacial lakes are greatly simplified from the more complete discussion by Prest (1970).

Current evidence indicates that during Wisconsin glaciation in eastern North America these fishes survived in a Mississippian refugium (Nelson 1968a; McPhail 1963; McPhail and Lindsey 1970). *Pungitius pungitius* and *Percopsis omiscomaycus* are the only two of the four species now known from that area, but *C. ricei* and *M. quadricornis* occur in Lake Michigan just to the north (Hubbs and Lagler 1964).

As Wisconsin ice in eastern North America began retreating approximately 17,000 years ago (Prest 1970), the fishes, following the ice closely, presumably spread first from the Mississippian refugium into glacial lakes Chicago and Warren and thence (Fig. 1) into glacial lakes Algonquin and Iroquois. The Finger Lakes in New York State were probably reached through the connection they had with the late stages of glacial Lake Warren (about 12,500 years ago, Prest 1970).

They probably dispersed into the Muskoka-Haliburton lakes around 11,800 years ago, when glacial Lake Algonquin inundated that region (Prest 1970). Martin and Chapman (1965) have shown that this same means was used by the relict crustaceans to invade the area.

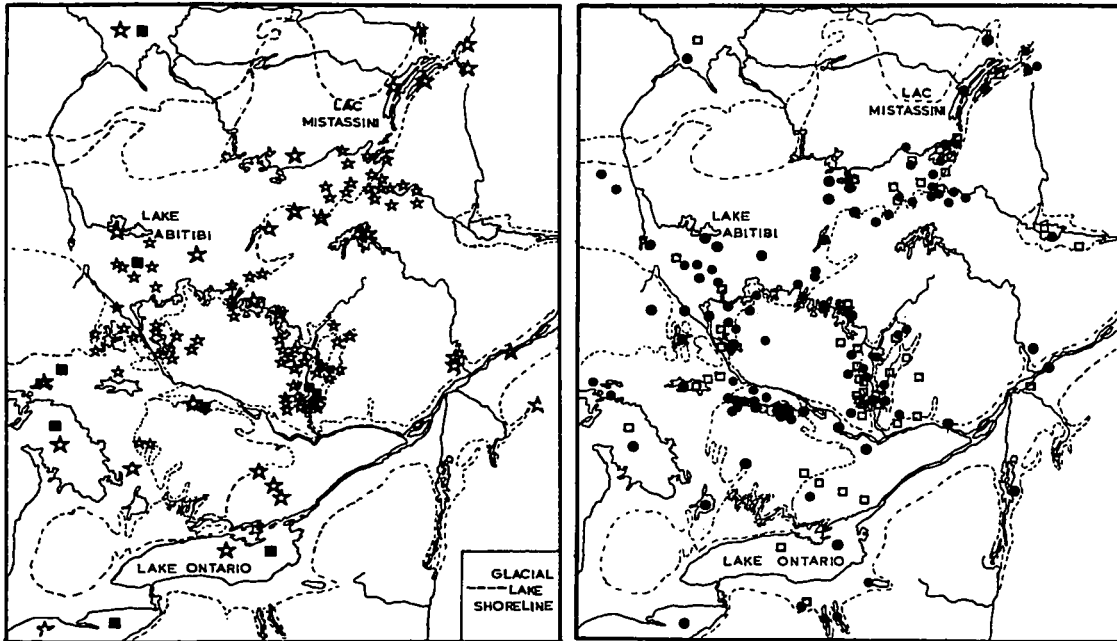


FIG. 4. Known distributions of *Cottus ricei* (stars), *Myoxocephalus quadricornis* (closed squares), *Pungitius pungitius* (open squares), and *Percopsis omiscomaycus* (closed circles) in the study area.

Two routes were available for fishes to disperse into the Lake Champlain area: one down the Hudson Outlet of glacial Lake Iroquois proper (about 12,000 years ago), and the other to the north of the Adirondacks when glacial lakes Iroquois and Fort Anne became connected (Fig. 1) during the Belleville-Fort Anne phase of glacial Lake Frontenac (Prest 1970).

Dispersal into the Ottawa and Gatineau valleys could also have taken place by two routes. Both of these were in existence between 11,500 and 9500 years ago (Prest 1970): one across the Champlain Sea from the south and the other from glacial Lake Algonquin via the Fossmill Outlet (Fig. 1). This latter route has been proposed by Martin and Chapman (1965) to explain the distribution pattern of the relict crustaceans and by Delisle and Van Vliet (1968) to explain the presence of *M. quadricornis* in the Gatineau Valley. The large numbers of records (Fig. 2 and 4) in the Fossmill area for all four species indicate that this route was used extensively for fish dispersal. On the other hand, *Pungitius pungitius* is also present on the Atlantic seaboard and conceivably could have dispersed into the Gatineau from the east as did the smelt (Delisle and Veilleux 1969). This does not seem likely,

however, as *P. pungitius* from the Gatineau Valley conforms to McPhail's Mississippian form (1963).

The present day distribution patterns of these fishes, their dispersal abilities, and the limited salinity tolerances of some of them indicate that all four species simultaneously invaded the Gatineau Valley via a brackish or fresh body of standing water. *Percopsis omiscomaycus* apparently has the lowest salinity tolerance of the four species (Nelson 1968b; McAllister 1964; Ryder et al. 1964), but its distribution pattern in the Gatineau Valley is nearly the same as that of the other fishes (Fig. 4), indicating that it dispersed into the Gatineau Valley at about the same time. Due to higher salinity tolerance, *Pungitius pungitius* and *C. ricei* may have been able to invade the area slightly earlier, as indicated by their presence in higher level lakes east of the Gatineau Valley (Fig. 3), which were covered only by more saline stages of the Champlain Sea (Elson MS 1960).

Since the greatest influx of fresh water was probably from the north side of the Champlain Sea (where the glacier was situated) and since dispersal across the sea from southern lakes was probably prevented by high salinities (Elson MS 1960), the probable dispersal route into the Gatineau Valley

was down the Fossmill Outlet and across the northern reaches of the Champlain Sea. The time of dispersal was probably about 10,000 years ago when the Champlain Sea was shoaling and freshening in the northern end (Prest 1970). The distributions of the relict crustaceans in the study area (M. J. Dadswell unpublished data) indicate that a standing body of water linked the Gatineau and Ottawa valleys at this time (Fig. 3).

Dispersal into the Temagami region could have taken place by way of late stages of glacial Lake Algonquin and early stages of glacial Lake Barlow, which alternately flooded this area about 10,000 years ago (Boissoneau 1968). Dispersal into the Barlow-Ojibway basin could have taken place through this same double flooding as well as by way of the Temiskaming reentrant which briefly linked glacial lakes Algonquin and Barlow by standing water around 10,000 years ago (Boissoneau 1968). They probably then dispersed through the various stages of glacial Lake Barlow-Ojibway northwards and eastwards, and reached the maximum limit of the glacial lake system north and east of Lac Mistassini (Fig. 2) about 7500 years ago (Prest 1970).

Considerable short-distance, secondary dispersal of these fishes, excepting *M. quadricornis*, has occurred beyond the glacial lake boundaries, especially along the southern Barlow-Ojibway shoreline (Fig. 2). The additional dispersal in that area may be due to cooler stream temperatures, low topography, and a shifting of Arctic drainage to Atlantic drainage due to isostatic rebound. This isostatic shifting of drainage is especially evident at the headwaters of the Chamouchane River just south of Chibougamau (Fig. 2), and there has been extensive spread of these fishes over the divide in this area.

The distributions of these fishes indicate that their primary means of dispersal in eastern Canada were proglacial lakes and their outlets. Dispersal upstream to lakes has played a secondary role. Most dispersal took place between 17,000 and 6000 years ago, and except in cases of drainage shifts due to isostatic rebound or stream capture, their distributions have remained static since that time.

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