THE DISTRIBUTION OF FISHES IN THE THUNDER BAY AREA OF NORTHWESTERN ONTARIO SINCE DEGLACIATION, WITH SPECIAL REFERENCE TO THE DARTERS (GENUS *Etheostoma*) AND THE SIBLEY PENINSULA

by

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in partial fulfillment of the requirements for the
Degree of Master of Science

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ABSTRACT

The prevailing theory explaining fish distribution in the western Lake Superior basin states that recolonization was from south to north following the retreating ice margins. Postulated access to post glacial Lake Superior is via the St. Croix River. However, as the ice masses retreated north of Lake Superior, several ice dams held back glacial Lake Agassiz. These were successively removed. Lake Agassiz, which covered much of Manitoba and northwestern Ontario, then catastrophically overflowed into the Superior basin. This allowed fish to gain access to western areas.

The Sibley Peninsula and Thunder Bay area provide key evidence for studying the process of fish recolonization. A survey documenting the fishes of Sleeping Giant Provincial Park on the Sibley Peninsula allowed comparison of this area with previously surveyed areas (Isle Royale National Park and Quetico Provincial Park). The distribution of two darters, the Iowa (*Etheostoma exile*) and the johnny (*E. nigrum*), suggested that the Thunder Bay area was recolonized from both the south and northeast by utilizing Agassiz outlets.

Creek chub (*Semotilus atromaculatus*), rock bass (*Ambloplites rupestris*) and common shiner (*Notropis cornutus*) are found at the edge of their range near or in the Kaministiquia basin suggesting either their late movement from the south into Lake Superior or low colonization powers. Colonization from the south is also suggested by johnny darter populations in the Kaministiquia basin.

Geographic variation among johnny darter populations reveal that the Kaministiquia basin populations are meristically unique compared to those from other nearby areas. Kaministiquia basin johnny darters are typically the scaly form and possess a high number of preoperculomandibular pores. Iowa darter populations do not exhibit much variation in meristic characters but, similar to johnny darters, do exhibit disjunct distribution throughout the Thunder Bay area.

Temperatures selected by Iowa darters during temperature selection trials were always cooler than those selected by johnny darters. Preference for cooler temperatures, along with survival in the Missouri refugium, allowed earlier movement northward following deglaciation. Iowa darters, inhabiting areas proximate to early Agassiz overflows, were deposited on both the Sibley Peninsula and Isle Royale.

Analysis of rivers based on ichthyofaunal resemblance suggests Kaministiquia basin rivers and those to the south are very similar, likely due to similar points of origin for their ichthyofauna. Similarly, ichthyofaunal resemblance among Sibley Peninsula rivers suggests a common origin.

Effects of isostatic rebound reveals that the Sibley Peninsula contains more species than Isle Royale and the Huron-Porcupine Mountains if basin morphology is taken into account. Lakes on the Sibley Peninsula were elevated and isolated even later than those of Isle Royale. Deep basins on Isle Royale allow for the existence of many large openwater species and cold adapted smaller species which can not inhabit the shallow lakes of the peninsula.

Fishes now inhabiting the Sibley Peninsula and Isle Royale likely arrived in those areas during Agassiz discharges. It is suggested that the prevailing theory of the recolonization of the Lake Superior basin must be revised since Lake Agassiz overflows likely provided a means for fish to move into, rather than through, the Superior basin.

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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The distribution of certain fish species is of interest to both the professional and the layman. Documenting the distribution of fishes through surveys enables fishery biologists and the fishing public to manage and utilize the resource. Additional physical, chemical and ecological data (e.g. p.H., temperature, or habitat preferences) gathered during fish surveys point out factors governing distribution. Through integration of this knowledge, insights are gained into: the general life history of a species, their tolerances, and their distributional range. Such knowledge can be applied to: predetermine the success of introducing a species into a new area; plot the reduction or expansion of range of various populations; follow the expansion of exotics (e.g. rainbow smelt (*Osmerus mordax*)); determine lakes suitable for commercial baitfishermen; and provide data useful in environmental hearings. An inventory of the distribution and ecological requirements of various species provides basic baseline data necessary to both monitor and manage a major commercial and recreational resource.

Fish distribution provides many insights into past climatic and geologic changes on the earth. Past climates resulted in glacial events in the recent past that eliminated all fish life in the Thunder Bay area and helped mould the present day landscape and drainages. Glacial retreat created the temporary pathways used by fishes during their reinvasion of this area.

Pleistocene climatic changes brought on glacial events that had additional, far reaching effects. Glaciers eliminated the ancestral Hudson Bay stream system that had been in effect for thousands of years and that had likely given rise to many fish species (Cross *et al.*, 1986; Robison, 1986). Representatives of what are presently considered strictly northern families were displaced southward. They survived in refugia located proximate to the furthest recent advance of the glaciers (Burr and Page, 1986; Robison, 1986). These fish were displaced southward by both direct displacement resulting from ice movement and changes in ecological factors e.g. temperature and precipitation (Robison, 1986). Precipitation decreased since moisture was bound up in the glacial ice. This reduced stream flow. Hence, large streams became both smaller and less turbid. This may have provided an advantage for species preferring to live in small, clear streams (Burr and Page, 1986).

As rising temperatures rendered the majority of temporary southern areas uninhabitable, these cold adapted (northern) species followed the glacial retreat north (Robison, 1986). Furthermore, abundant precipitation and runoff increased both stream flow and turbidity. Populations of fish, adapted to life in small, clear streams, were either eliminated or isolated through habitat reduction. Fossil evidence for these southern refugia is not always present. However, the disjunct distribution of several "northern" species within isolated southern areas provides compelling evidence lending credence to this scenario (Burr and Page, 1986; Cross *et al.*, 1986).

Isostatic uplift followed deglaciation and played a major role in directing the repopulation of many areas. Presently operative insurmountable barriers could be crossed immediately following deglaciation and before isostatic uplifting was initiated or completed (Burr and Page, 1986). The present day absence of some fish from certain areas stems from the fact that they were originally located at too great a distance from the retreating ice. Regional variation in the rates of uplift contributed to this phenomenon.

Present day fish distribution in Ontario results from a combination of past glacial (including geological) and ecological processes now modified by the continuous influence of man. Many fish species have been introduced (either intentionally or unintentionally) into areas from which they were formerly excluded, mainly by geological land forms (i.e. barrier falls). The historical absence of Atlantic salmon (*Salmo salar*) and the sea lamprey (*Petromyzon marinus*) in the upper Great Lakes are two good examples of past geological barriers functioning effectively to limit distribution.

Ecological factors can be equally important. Brook trout (*Salvelinus fontinalis*) are absent from the southern U.S. while largemouth bass (*Micropterus salmoides*) are not found in northern Canada. Both are rather extreme, but suitable, examples of climate at work. In these instances, the physiological (i.e. thermal) tolerances of the species are mainly responsible for their presence or absence in an area (Moyle and Cech, 1988). However; those fish species found at their distributional limits often pose puzzling questions concerning their absence in seemingly suitable proximate areas.

Distribution and Present Recolonization Theory

The question often arises as to why a species may be absent from a certain portion of its range even though seemingly suitable conditions exist for its maintenance. Frequently, a species will display a discontinuous "leapfrog" distribution pattern. Large gaps separating areas of habitation result in disjunct populations. A species may be excluded by barrier falls or simply because of its late arrival from a refugia to a recently uplifted area. However, except for introduced species, which typically show disjunctions or sharp distributional edges, disjunct distribution patterns of native species are of special interest and importance to zoogeographers.

Fish biologists and zoogeographers are particularly interested in how and when a species began the route it used to recolonize formerly glaciated areas.

Indeed, the effects of Pleistocene glaciation on the distribution of fishes has been subjected to many analyses (Radforth, 1944; Underhill, 1957: Bailey and Smith, 1981; Legendre and Legendre, 1984; Hocutt and Wiley, 1986). While few disagree that past glacial events are one of the principal factors shaping the present distribution of fishes in previously glaciated areas, much debate still occurs as to the number and location of refugia utilized by certain species and the exact routes utilized for recolonization. Zoogeography particularly asks why some fishes were excluded from certain areas.

Known ecological processes often directly influence the presence or absence of fishes in certain areas (e.g. Edwards *et al.*, 1982). Loss of previously suitable habitat is thought to be a prime cause of disjunct distributions (Brown and Gibson, 1983). However, widespread successful introduction of gamefishes, such as the smallmouth bass (*Micropterus dolomieui*) and walleye (*Stizostedion vitreum*), into areas in which they were previously absent, attests to the ability of many fishes to survive in areas from which they were originally excluded (Moyle and Cech, 1988). In such cases, and likely many others, the deciding factor as to whether a species is currently present or absent depends almost entirely on whether some former historical event affected certain geological landforms. Ecological factors such as: available habitat; competition with other species; or temperature tolerance are likely of less importance. Most likely ecological conditions change several times over in any given area before it becomes entirely suitable for a particular species. In many cases, such changes negligibly impacted past and present fish distribution. This is because of a fishes ability to gradually adapt to a slowly changing environment. Often, swift and radical environmental changes induced by man produce the maximum disruptions to their adaptive adjustments (Burr and Page, 1986).

In the Thunder Bay area of Ontario there are very few eutrophic but many dystrophic lakes (Wetzel, 1983). The majority of lakes and rivers retain the ecological conditions that have existed since deglaciation. Most successional changes have been gradual. Few, if any, extinctions of fish species have likely occurred in this area due to radical ecological changes (the paddlefish (*Polyodon spathula*) may be an exception (Hubbs and Lagler, 1983)). Localized extinctions due to interspecific competition, cultural eutrophication, habitat alteration or gradual oxygen depletion in shallow lakes and small streams are possible. The time since deglaciation in this area has been relatively short (9000 BP (Before Present)). Most species currently found in this area have had many opportunities to expand their ranges, especially in Lake Superior tributaries which have been only accessible since deglaciation. The absence of a particular species from a given location in the Thunder Bay area may be due to physiological intolerance to certain ecological factors or their exclusion from the area by a physical barrier (geologic landform).

Present theories of fish recolonization into the Thunder Bay area suggests that fish followed the edge of northward retreating glaciers (Radforth, 1944; Bailey and Smith, 1981; Crossman and McAllister, 1986). This theory purports to explain the present south to north distribution exhibited by most fish species in Ontario. The majority of fish now inhabiting the Thunder Bay area probably entered from southern refugia, e.g. the Mississippi Valley. Those fish inhabiting this area are believed to have moved northward through the area of the St. Croix River and, possibly, through the Au Train-Whitefish channel, into a precursor of Lake Superior (Underhill, 1986). Upon entering an early stage of Lake Superior, fish are assumed to have followed the shoreline northward, moving into whatever suitable habitats were encountered. Isostatic uplift and the physical characteristics of some streams may have limited the dispersal and abundance of late arriving species as well as those possessing limited tolerances for the initial harsh environment provided within the early Lake Superior basin (Bailey and Smith, 1981). Some species, especially those arriving from the east, are thought to have moved through this area and into the north and west. They are postulated to have gained access into glacial Lake Agassiz (covering much of Manitoba and northwestern Ontario) via the present day Lake Nipigon basin (Underhill, 1957; Bailey and Smith, 1981; Stewart and Lindsey, 1983) (Fig. 1).

The Study Area

The fish fauna of Isle Royale, a large island in western Lake Superior, was extensively surveyed early in the century (Hubbs and Lagler, 1949). This happened well before sport fishermen could make bait fish introductions. The lakes and fish fauna of Isle Royale have been compared with those of the Huron-Porcupine Mountains in Michigan (Hubbs and Lagler, 1949). The area west of Thunder Bay, encompassing Quetico Provincial Park has also been surveyed (Crossman, 1976). These surveys provide a basis for comparisons with closely proximate areas having similar geological histories. One such area is the Sibley Peninsula including Sleeping Giant Provincial Park.

The Sibley Peninsula lies approximately 26.0 km (kilometres) east of the City of Thunder Bay. The peninsula lies due north of Isle Royale National Park and the Huron-Porcupine Mountains, Michigan and east of Quetico Provincial Park (Fig. 2). The investigation of presence or absence of fish species on the Sibley Peninsula provides a means for directly comparing nearby areas. Recolonization processes, resulting in the establishment of a fish fauna in a new study area, are best revealed by comparison with adjacent areas. This survey will assist in establishing which alternate routes were available for recolonization at different

Figure 1: Diagram illustrating prevalent concepts about theoretical routes used by fish to recolonize the Lake Superior basin and eastward movement by utilizing Lake Agassiz outlets.

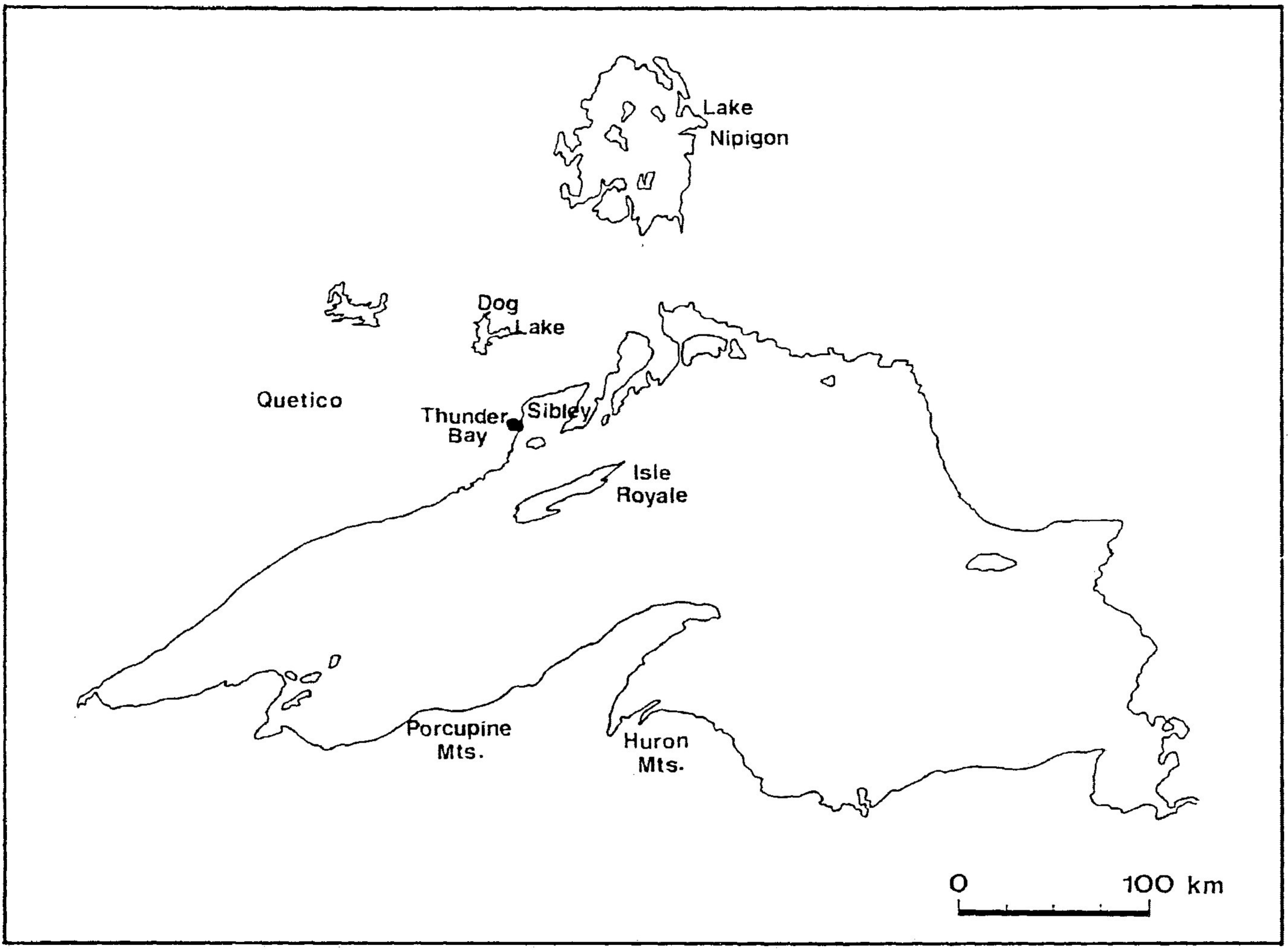

Figure 2: Map of major areas discussed; Sibley Peninsula, Isle Royale, the Quetico region and the Huron and Porcupine Mountains.

times between areas located within different catchments.

The Thunder Bay area, especially the Sibley Peninsula, may hold the key to understanding the recolonization process in Lake Superior. Of prime importance is the suspected re-advance of glacial ice into Thunder Bay via the Marquette lobe approximately 9,900 BP (Farrand and Drexler, 1985). This resulted in the Thunder Bay area and the Sibley Peninsula becoming a portion of the most recently deglaciated area within the entire Great Lakes basin.

This makes Sleeping Giant Provincial Park, located on the Sibley Peninsula, an ideal location for studying the reinvasion of fish species following deglaciation. Several introductions (both failures and successes) of game fish were made into its relatively remote lakes by the Ontario Ministry of Natural Resources (OMNR), however the park never developed as a popular sport fishery due to the inaccessibility of many lakes and the present prohibition on the use of motor vehicles (OMNR, 1973). The access to many or most lakes is gained only by long walks on footpaths. This limits the use of "bait fish" since any species transported for angling purposes would die. Therefore, the fish distribution on the Sibley Peninsula likely represents natural recolonization and the possibility of unintentional past bait fish introductions are nearly nonexistent. As darters (genus *Etheostoma*) are generally not used as bait, their presence on the peninsula, is likely to be totally natural.

The Study Species

Two darter species were chosen as possible indicators of recolonization routes used following glacial retreat; the Iowa (*Etheostoma exile*) and johnny (*E. nigrum*) darters. Both are small in size, lack swim bladders (and hence have weak swimming abilities), and have a very low probability of being an introduced bait fish (Page and Swofford, 1984). Their restricted movements should exclude them from having as widespread a distribution as larger and/or more mobile species, e.g. *Catostomus commersoni* or *Culaea inconstans* which are ubiquitous within the study area (Scott and Crossman, 1973; Hartviksen and Momot, 1989). Darters inhabit mainly shallow water and are susceptible to capture by minnow traps and seines (Becker, 1983; Page, 1983). Their presence can therefore be easily detected.

Prior to the study, their known general distribution consisted of localized, isolated populations (Kuehne and Barbour, 1983; Lee *et al.*, 1980). Their distribution within this area was well within their known range limits (Page, 1983). The puzzling occurrence of two populations of Iowa darters on the northeast end of Isle Royale was noted by Hubbs and Lagler (1949). This confounded any attempts to explain their distribution since Isle Royale lies approximately 20.0 km from the nearest mainland. Iowa darters are absent from the mouths of most Lake Superior tributaries and are locally absent in many areas near the City of Thunder Bay. Furthermore, only johnny darters occur in the Kaministiquia basin (Kaministiquia River and tributaries, McIntyre River (ROM (Royal Ontario Museum) records)).

Etheostoma exile has the most northern and western distribution in Canada of any member of its genus (Scott and Crossman, 1973; Page, 1983). *Etheostoma exile* is the most common darter in the Quetico region (Crossman, 1976) but is relatively rare north of the Albany River in Ontario (Ryder *et al.*, 1964) and present in only two lakes on Isle Royale (Hubbs and Lagler, 1949). *Etheostoma exile* is often considered a glacial relict (Scott and Crossman, 1973).

Etheostoma nigrum is less widespread in Canada than *E. exile* but is the most common and most northerly distributed of all darters in Ontario (Scott, 1967; Scott and Crossman, 1973). It is more common north of the Albany River than *E. exile* (Ryder *et al.*, 1964) but seemingly less common than *E. exile* in the Quetico region (Crossman, 1976). It is not present on Isle Royale (Hubbs and Lagler, 1949). *Etheostoma nigrum* is considered a generalist and less restricted in habitat preference than *E. exile* (Phillips *et al.*, 1982; Becker, 1983; Kuehne and Barbour, 1983).

Glacial Activity in the Thunder Bay Area

The Thunder Bay area was glaciated on four occasions during the Pleistocene Epoch (Robison, 1986), however; only the latest Wisconsin advances are of immediate interest. Advances prior to the Wisconsin certainly effected the present day landscape and interspersed northern and southern ichthyofauna. However, the more recent Wisconsin advances eliminated any fishes previously living in this area. Within the Wisconsin period, it is particularly the very recent Marquette re-advance that directly influenced the recolonization of present day inhabitants of this area.

The most recent glacial advance (approximately 9,900 BP) covered the Thunder Bay area with an ice lobe extending from east of the Sibley Peninsula to, or near, the site of the Marks Moraine located west of the city (Burwasser, 1977). This makes the Thunder Bay region, especially the Sibley Peninsula, of utmost importance to understanding the impact of this Marquette re-advance (Farrand and Drexler, 1985).

This Marquette lobe, together with a lobe that formed the Dog Lake Moraine, likely met to confine a large waterbody called Lake Kaministikwia (Farrand and Drexler, 1985). Lake Kaministikwia, considered to be contemporary with the expanding Lake Duluth (a Lake Superior precursor), alternately drained into Lake Agassiz and served as its outlet (Burwasser, 1977; Clayton, 1983; Teller, 1985; Farrand and Drexler, 1985). A short time after this re-advance (9,700 BP) the ice then began a very rapid, final retreat (Farrand and Drexler, 1985). As the ice retreated northward from the Thunder Bay area (approximately 9,500 BP), the successive removal of a series of five ice dams, previously impounding Lake Agassiz, produced a series of catastrophic overflows into another Lake Superior precursor (developing Lake Minong) via present day Lake Nipigon and nearby channels (Teller and Thorleifson, 1983) (Fig. 3). Teller and Mahnic (1988) suggest that these initial Agassiz overflows entered the Lake Superior basin via the Wolf-Wolfpup spillways. Later overflows entered mainly from areas further east. Both today, as in glacial times, the Wolf-Wolfpup channels are situated above the eastern channels (e.g. Black Sturgeon, Nipigon, Cash). The result is that later inflows to Lake Minong followed spillways other than the Wolf-Wolfpup. The higher western outlets functioned only during initial overflows and possibly later during catastrophic overflows from Lake Agassiz (Teller and Mahnic, 1988).

The disjunct distribution of Iowa and johnny darters in the Thunder Bay area may in part be due to a rapid glacial re-advance. This eliminated all fish from the area. This was quickly (200 years) followed by an early movement of Iowa darters from Lake Agassiz into the Thunder Bay area during the aforementioned catastrophic overflows. Adjacent streams and lakes located at various distances within the Thunder Bay area were then recolonized at various times by different routes. Few authors, except Bailey and Smith (1981) and Owen *et al.* (1981), have alluded to the possibility that the Agassiz to Superior connection could have been used as a route for recolonizing Lake Superior. However, recent geological research on Lake Agassiz and the Marquette advance and their influence on the Great Lakes (Teller and Thorleifson, 1983; Teller and Mahnic, 1988; among others) provides information not available to earlier zoogeographers and forces a reconsideration of this possibility. If indeed some fishes reinvaded from Lake Agassiz, then currently held theories on the origin of the Lake Superior ichthyofauna

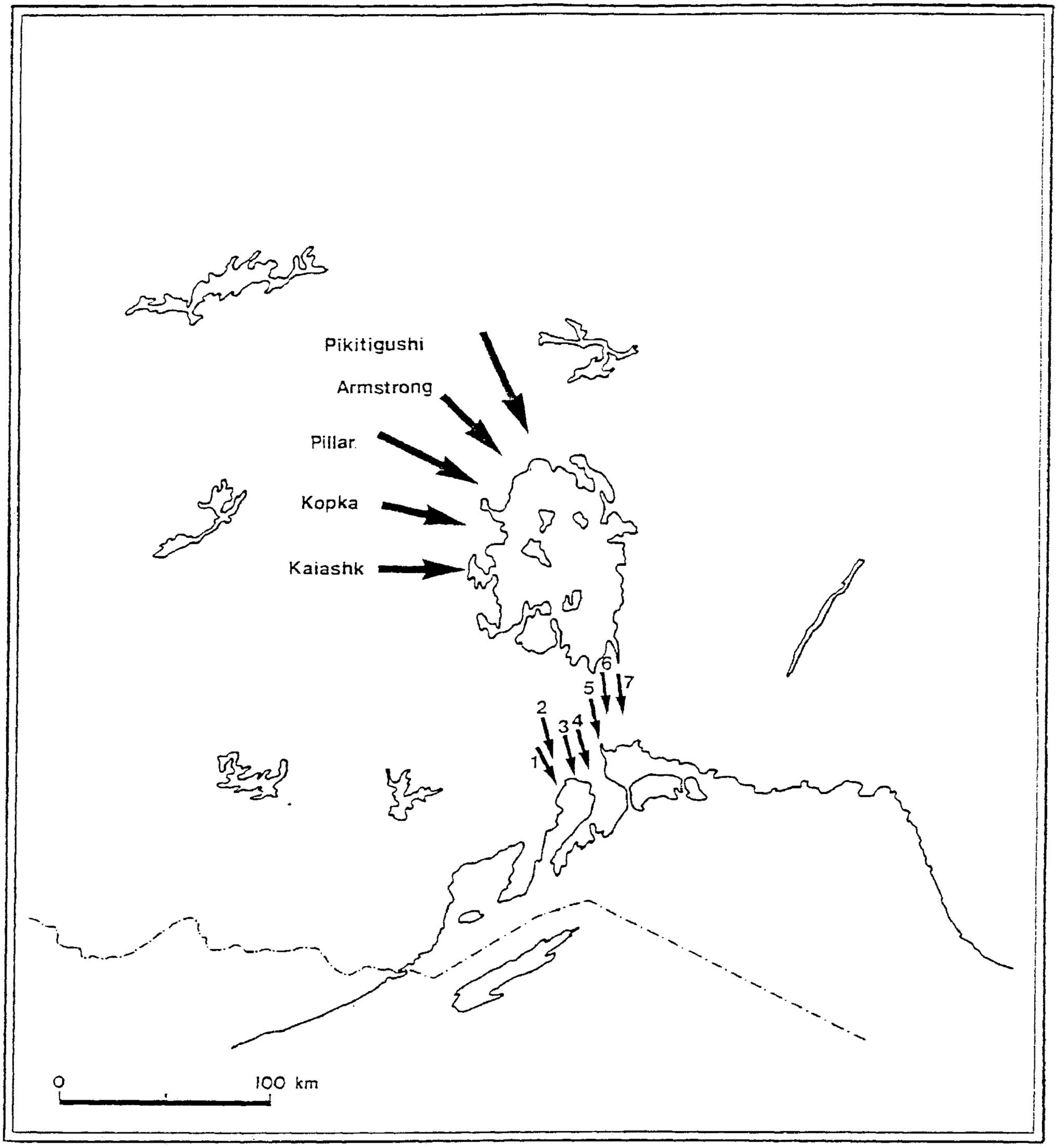

Figure 3: Location of major Lake Agassiz overflow channels into the Nipigon basin and Lake Superior. Earliest Agassiz overflows occurred via the Kaiashk spillway. Nipigon to Superior spillways are; (1) Wolf, (2) Wolfpup, (3) Shillabeer, (4) Black Sturgeon, (5) Nipigon, (6) Cash and (7) Pijitiwabik (adapted from Teller and Thorleifson, 1983).

must be revised.

Other Benefits of the Study

In addition to revising ideas concerning the recolonization of the Lake Superior basin, this study provides a complete ichthyofaunal inventory of a provincial park adjacent to a large urban population. The management of any resource first depends on knowing the extent of the resource (Pearse, 1988). Most lakes and streams in the Thunder Bay area have not been surveyed by the OMNR. What little information does exist on the fishes of the Sibley Peninsula deals mainly with sport fish. Many of the previous identifications of its' small fish were suspect (W. Momot, Lakehead University, pers. comm.). Provincial parks are generally closed to all types of resource extraction; fishing seems the exception. Yet Sleeping Giant Provincial Park had only limited information concerning the status of its fishery resource (OMNR, 1973). The documentation of the fishes of the Sibley Peninsula is of great importance for assessing any future ecosystem changes whether man made or natural. Another desire was to increase visitor awareness of the aquatic inhabitants of the park. Although seldom seen, fishes are a great example of faunal diversity serving as general indicators of the aquatic ecosystem's health. The number of failed sport fish introductions and discovery of undesirable species within Sleeping Giant Provincial Park (OMNR, 1973; Momot *et al.*, 1988) and the surrounding area, indicate the importance of baseline data to assess the impact of any future introductions (beneficial to anglers). For many of the same reasons, collections made outside of the Sibley Peninsula are also valuable. Increased timber harvesting in nearby areas suggested that aquatic habitat degradation or angler access via logging roads could disturb the natural distribution of the ichthyofauna before proper documentation is obtained.

Work by Hubbs and Lagler (1949) on Isle Royale suggested that sub-speciation also may be occurring on the Sibley Peninsula. If found, such fishes and the lakes in which they evolved should be protected. The study of such populations would allow for the measurement of the rate of speciation within recently isolated fish populations.

Lakes of Isle Royale presently found at the same height as lakes in the Huron-Porcupine Mountains of Michigan contain more fish species (Hubbs and Lagler, 1949). Due to isostatic rebound, the Isle Royale lakes were isolated at a much later time and therefore were open to invasion by a larger number of species than those of the Huron Mountains, which were isolated much earlier (Hubbs and Lagler, 1949). Isle Royale lakes also contain fewer fish species (31) than does Lake Nipigon (37) (Underhill, 1986), again in part because of the differential rates of isostatic rebound. The fish fauna of the Sibley Peninsula might show similar effects. If Sibley Peninsula lakes were isolated from invasion at a later date than lakes of Isle Royale, more species might occur on the peninsula than Isle Royale. However, the recent advance of the Marquette ice lobe may have confounded this process.

The completion or continuation of major ichthyofaunal surveys in Minnesota (Underhill, 1957; J.C. Underhill, University of Minnesota, pers. comm.), Wisconsin (Becker, 1983; Fago, 1985), Isle Royale (Hubbs and Lagler, 1949), the Quetico region (Crossman, 1976) and parts of eastern Ontario (Scott, 1967; E.J. Crossman, Royal Ontario Museum, pers. comm.) suggests the urgent need for large scale surveys in this area. At present, only fragmentary information exists on the fish distribution in the Thunder Bay area (Hartviksen and Momot, 1989).

MATERIALS AND METHODS

Fish Collection

From May 14, 1989 until October 1, 1990, 210 lakes and streams in the Thunder Bay area were sampled at 325 locations in an attempt to determine the presence or absence of darters and other fish species. The study area extended east to the Jackfish River (49^0 00' N, 88^0 05' W), west to the Kashabowie River (48^0 39' N, 90^0 25' W), north to McKenzie Lake (50^0 17' N, 89^0 05' W) and south to Cloud Lake (48^0 08' N, 89^0 33' W). Its central focus was the Sibley Peninsula and areas adjacent to the City of Thunder Bay. Methods of capture included standard wire minnow traps, gill nets, seine nets, dip nets, plexiglass traps and electroshocking.

Baited wire minnow traps (44.5 cm (centimetres) long, 23.0 cm at largest diameter, 2.5 cm funnels and 6.0 mm (millimetre) square mesh) were used throughout the course of this study. Bait consisted of a piece of dried white bread.

Gill nets were of single strand monofilament in 15.25 m (metre) lengths, 2.5 m deep and of either 19.05, 25.4, 38.1 or 50.8 mm stretched measure mesh. Gangs of at least two nets were set with 19.05 and 38.1 or 25.4 and 50.8 mm always being set together. Except for one lake on the Sibley Peninsula (Pass), gill nets were used solely within the confines of Sleeping Giant Provincial Park during the course of this study.

Seine nets were cotton with 6.35 mm mesh. Straight seines (3.05 x 1.2 m and 6.1 x 1.2 m) were used as well as a 7.6 x 1.8 m bag seine (with 1.8 m bag). Seines were used both actively and passively. Passive seining refers to those situations encountered in streams where seines could not be hauled due to obstructions in the water. In those instances, the seine was secured across the stream and the entire area upstream of the seine was disturbed, usually to a distance of 10 m, in an attempt to force fish into the seine.

Plexiglass (6.35 mm thick) funnel traps, built at Lakehead University, measured 38.0 x 38.0 x 89.0 cm long and had wings of 2.59 m x 38.0 cm fine mesh which attached to each side and aided in directing fish into the traps funnel. The actual trap which contains the fish is 38.0 x 38.0 x 50.8 cm and has a 5.0 cm square opening. Two fine screened holes, measuring 25.4 x 8.9 cm and located at the back and left side of the trap, allow water to pass through. These traps were used successfully during the 1990 field season in both lakes and streams.

Due mainly to problems of access and gear portability, electroshocking was utilized only once as a capture method during this study. A portable Smith Root electroshocker was used in the Nipigon River Lagoon in 1990.

Access to lakes and streams was usually by road, however; in some instances other approaches were necessary e.g. boat.

Some lakes within the boundaries of Sleeping Giant Provincial Park were accessed via helicopter to sample remote lakes that otherwise would not have been sampled at all or sampled as intensively as they were. A large trail system within the park, a remnant of timber harvesting in the 1930's and 40's (OMNR, 1973), enabled the use of two Honda four-wheeled all terrain vehicles (model 300 and 350). Many of the lakes within the park are accessible only by trails that are not large enough to accommodate a motorized vehicle so, in a few cases, all sampling equipment was carried in by foot. In some instances, trails were not present so a compass bearing was needed in order to walk into the lake.

A four man inflatable raft was often used to set gill nets and minnow traps. However; while the helicopter portion of the survey was underway, time and cargo constraints necessitated the use of a one man hard plastic "float tube".

At time of capture, all small specimens were placed in Whirl-pak bags containing ten percent formalin. When time allowed, usually within 1-3 weeks of capture, all specimens were rinsed in cold water and placed in 70% ethanol. All preserved fish were later identified to species and stored at Lakehead University. When large and easily identifiable fishes were captured in gill nets, they were released unharmed whenever possible or discarded due to preservation and storage problems. Most of these larger species were photographed for documentation.

The stomachs of large predator fish, mainly northern pike (*Esox lucius*), were examined whenever these fish failed to survive gill net capture. Several small fish species were collected in this manner.

During fish collecting, numerous measurements or observations were taken including; depth of capture (maximum and minimum), bottom type or habitat, p.H., temperature (both air and water), stream cover, aquatic vegetation and presence of sessile organisms, distance of capture from shore and visibility or transparency of water. On the Sibley Peninsula, total calcium was measured in most locations. Two lakes harbouring johnny (Little Dog Lake 48^0 39'0" N, 89^0 36'0" W) and Iowa (Pickerel Lake 48^0 25'7" N, 88^0 45'2" W) darters were sampled with substrate screens to determine the percentage of substrate size composition. This was performed to see if there were differences in substrate preference between the two species.

Records of fish collected by the Sea Lamprey Control Centre (SLCC) during application of lampricide or operation of electric or check weirs were searched in Sault Ste. Marie. Records of fish stored at the ROM and Lakehead University were also used to compile lists of fish species inhabiting Lake Superior tributaries and lakes on the Sibley Peninsula. Historic, fragmentary survey information available from the Thunder Bay District OMNR and a recently published book (Hartviksen and Momot, 1989) were also used.

Temperature Selection Trials

Trials performed on temperatures selected by both species of darters were conducted in September and December of 1990. Iowa darters were seined August 29, 1990 from Pickerel Lake, Sleeping Giant Provincial Park. Water temperature at this site was 22.5°C. The sample of 43 fish consisted of both males and females ranging in length from 31 to 64 mm TL (total length).

Fourteen johnny darters were seined from Little Dog Lake on September 8, 1990. These fish ranged from 30 to 69 mm TL. Sex could not be determined with certainty for this sample of fish. Water temperature at this site was 20°C.

After capture, fish were transferred to holding aquaria where the temperature was adjusted to match the temperature found at the capture site. In autumn, warm days and cool nights characterize the shallow water areas inhabited by these two species. In order to mimic naturally fluctuating temperatures, aquarium heaters were lowered by approximately 2°C each evening. Varying the temperatures in the holding aquaria prevented the darters from acclimating to the daytime holding temperature (21°C). Lighting followed a normal seasonal photoperiod (14L, 10D).

Due to their benthic habits, only a horizontal gradient needed to be considered. Trial tanks were constructed of "2 x 4" studs (38.0 x 88.0 mm). These were covered with plastic sheeting forming a large trough. Trials were run in 2.4 m long troughs, 40.0 cm wide. Water depth averaged 7.0 cm.

Temperature gradients were achieved through the use of 150 watt aquarium heaters and freezer packs. Heaters, although not engaged, were placed at the cool end of the tank so as not to influence darters that may have simply attempted to seek cover in non-preferred temperatures. Ice packs placed under the plastic sheeting assured that cover was not provided to the darters. Ice was occasionally added near the ice packs to help maintain the gradient. The temperature gradient was held between 19 (+/- 1^0) and 28^0C. Water was oxygenated by a Whisper 800 air pump with a single air stone placed at each end of the trough.

In each trial, darters were introduced to the gradient "tanks" at the same temperatures found in the holding aquaria. Trials were run on: single fish; single species groups; mixed species pairs; and mixed groups. Fish position was noted every minute for the first 30, every 5 minutes for the next 60 and every 15 minutes there after. Means were calculated and compared by the standard "t" test. No fish were tested more than once.

During the trials, lighting was either 100% on or off. Darters were fed live food daily to simulate daily food consumption in wild fish.

Two Iowa and five johnny darters were tested for temperature preference after 90 days of captivity. During this entire period, the temperature was held constant at 21^0C and lighting was maintained as 14L and 10D. Darters were fed live food at least every second day during this period. These darters were tested using the methods described above.

Meristic Data

Both *Etheostoma exile* and *E. nigrum* populations were examined to determine if any geographic variation in meristic characters existed within or near the study area. Characters examined were: number of lateral line scales (both pored and unpored when possible (counted on the right side of the fish); number of spines in first dorsal fin; number of rays in second dorsal fin; number of spines and rays in anal fin (*Etheostoma exile* only); number of preoperculomandibular (POP) pores (left and right sides), number of pores in the infraorbital canal (left and right sides; anterior and posterior for *E. nigrum*) and the extent of scaling on the opercle, nape, breast and cheek (*E. nigrum* only).

Besides those fish collected during the survey, additional material was borrowed from the ROM, the University of Michigan Museum of Zoology (UMMZ), the University of Minnesota Bell Museum of Natural History (BMNH), collections made by the Thunder Bay OMNR and area collections housed at Lakehead University (Tables 1 and 2). All counts of scales, rays and spines were made following Hubbs and Lagler (1983). Infraorbital and POP pore counts were made following Page (1983).

Principal component analysis (PCA) was performed on the above mentioned meristic characters. In total, 567 johnny darters and 301 Iowa darters were analyzed using this method. Principal component analysis calculates new variables (principal component factors) from the original variables (meristic counts) (Johnson and Wichern, 1988). PCA has the advantage of compressing and explaining the total amount of variation present in the original data set (the variables) by reducing the number of original variables into a lesser number of "principal" factors. The first few factors typically explain the largest amount of variance present within a set of variables. The "weighting" of variables within each computed factor allows for the identification of those meristic characters which can be used to best differentiate populations by showing where the greatest amount of variation among populations exists. PCA therefore enables one to focus attention on the most important or informative meristic characters.

After computation of heavily weighted variables using PCA, these variables were used in a discriminant analysis to group populations by geographic location. Populations which grouped together due to similarity of variables could be suspected of having a similar origin.

Table 1: Collection date and capture site of 567 *Etheostoma nigrum* specimens examined for meristic counts.

Capture Site	Collection Date	Number Examined	Origin
Quetico[1]	1967	54	ROM 25629
Flatrock Lake	1968	23	ROM 35561
Boulevard Lake	1958	14	ROM 19886
	1989-90	11	LU-LST-29 LU-ICHTHY
Wolf River[2]	8/15/89	8	LU-LST-52
Portage Creek[2]	6/21/89	1	LU-BB-4
Joe Boy Creek[2]	8/23/90	7	LU-90-115
Moose Bay[2]	7/25/89	1	LU-LST-28A
McVicars Creek	9/11/89	4	LU-LST-84
	1990	13	LU-OMNR
Neebing-McIntyre	1990	149	LU-OMNR
Little Dog Lake	1989-90	45	LU-LST-73 LU-90-124
Nipigon River	9/6/90	110	LU-90-123
Kaministiquia River	1976-89	51	LU-ICHTHY
Sucker River	6/27/84	6	BMNH 24293
Temperance River	7/18/41	5	BMNH 12140
Cloquet River	1942	17	BMNH 14620
St. Louis River	8/29/41	48	BMNH 12481

[1] A "compilation" collection from several nearby lakes.
[2] Grouped as "Sibley" in analyses due to proximity.

Table 2: Collection date and capture site of 301 *Etheostoma exile* specimens examined for meristic counts.

Capture Site	Date	Number Examined	Origin
Isle Royale	1929	14	UMMZ-100065
Dell Lake	1968	20	ROM 26353
Wicksteed Lake	1969	32	ROM 26848
Nipigon River	9/6/90	78	LU-90-123
Pickerel Lake	1989-90	79	LU-3-T LU-90-122
Twinpine Lake	1989/90	13	LU-18-A LU-90-28
Holt Lake[1]	5/25/89	1	LU-4-H
Walkinshaw Lake[2]	8/16/89	16	LU-LST-53
Kingfisher Lake[2]	8/16/89	3	LU-LST-54
Timmus Lake[2]	8/10/89	4	LU-LST-32
Whitelily Lake[2]	8/10/89	3	LU-LST-40
Magone Lake #1[2]	8/26/89 8/31/89	16	LU-LST-77 LU-LST-79
Cascade River	8/6/41	9	BMNH 12200
Elbow Creek	9/14/83	5	BMNH 24608
Mistletoe Creek	9/7/83	8	BMNH 24615

[1] Included with Twinpine Lake in analyses due to proximity.
[2] Grouped as "Armstrong" in analyses due to proximity.

All statistical analyses were performed using the SPSS program (SPSS, 1988).

Jaccard's Analysis of Rivers

A Jaccard's coefficient of similarity (Legendre and Legendre, 1983) was performed on twenty Lake Superior tributaries in the Thunder Bay area. The Jaccard's similarity index was chosen as it takes into account only those species present and therefore does not penalize an area for not possessing a certain species. The Jaccard's method has recently been used by Crossman and McAllister (1986) and Underhill (1986) to cluster rivers and lakes based on ichthyofaunal resemblance. The single and complete linkage methods (Johnson and Wichern, 1988) were then utilized to construct dendrograms to cluster rivers by ichthyofaunal resemblance. The single linkage method bases its grouping of objects on the minimum distance between neighbours. The complete linkage method groups objects that are most similar, but utilizes the greatest distance between the two objects. Data on species present in each river was collected from ROM, Lakehead University collections, SLCC, Thunder Bay OMNR files, OMNR (1990), Moore and Braem (1965), Hartviksen and Momot (1989) and samples collected during the 1989-90 survey.

Species not included in the analyses were those making only seasonal use of certain portions of the rivers. These would be subject to capture only during specific times of the year (e.g. migrating salmonids). Some species, such as lampreys, not susceptible to most standard sampling gears (gillnets and seines) and often underrepresented in sampled rivers, were therefore also excluded from the analysis. All species introduced to Lake Superior were also excluded from the Jaccard's analysis due to differential colonization rates and seasonal appearance in these tributaries. Some records, mainly those from the OMNR but also some from the SLCC, were not used because of the possibility of original misidentifications. Some records from Hartviksen and Momot (1989) were similarly discounted as some of their material is based on these OMNR records.

Only those species collected between Lake Superior and the first lake in the river system were included in calculations. Fish captured only in tributaries to the main river are noted in table 3 as are any extremely rare collections (one specimen only).

Elevation of Lakes and Isostatic Rebound

To determine the effects of isostatic rebound on the distribution of fishes, distributional records from the Sibley Peninsula survey and information from previous surveys (e.g. Hubbs and Lagler, 1949) were used to compare several areas. By plotting the fish species present at various lake elevations above Lake Superior and then comparing these with the suspected height of these same lakes above the Lake Minong water plane, it may be possible to determine the post glacial arrival time for some species into these areas. Fish species could then be labelled as late or early migrants. Additionally, the influence of isostatic rebound on the rate of colonization of fish can be measured.

Table 3. Fish species collected from 20 rivers within the Thunder Bay area*.

River	Pigeon	Pine	Cloud	Kaministiquia	Neebing	McIntyre	Current	Wildgoose	MacKenzie	Blende	Sibley	Demer's	Pickerel	Joe Boy	Portage	Pearl	Wolf	Black Sturgeon	Nipigon	Jackfish
Species																				
Acipenser fulvescens	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-
Coregonus artedii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-
Coregonus clupeaformis	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-
Prosopium cylindraceum	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-
Salvelinus fontinalis	-	X	-	X	X	X	X	X	X	X	X	-	X	-	X	X	X	X	X	X
Salvelinus namaycush	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Umbra limi	-	X	-	X	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-
Esox lucius	X	-	-	X	X	X	X	-	-	-	X	-	-	-	-	-	X	X	X	-
Couesius plumbeus	X	X	-	X[1,2]	X	X	X	X	X	-	-	X	-	X	X	-	X	-	X	X
Notemigonus crysoleucas	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-
Notropis atherinoides	-	X	X	X	-	X	-	X	-	-	X	-	-	X	-	-	-	-	X	X
Notropis cornutus	X	-	X	X	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Notropis heterolepis	-	-	-	X	-	-	-	-	-	-	X	-	-	X	-	X	-	X	-	-
Notropis hudsonius	-	X	X	X	-	X	X	-	-	-	X	X	-	X	-	-	-	X	X	X
Notropis volucellus	X[1,2]	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoxinus eos	-	X	-	X	X	X	X	-	X	X	-	-	-	X	X	X	X	-	-	-
Phoxinus neogaeus	X	X	X	X	X	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-
Pimephales promelas	-	X	X	X	X	X	-	X	-	X	-	-	X	X	X	-	-	-	-	-
Pimephales notatus	X[1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhinichthys atratulus	X	-	-	X	X	X	X	-	X	-	-	-	-	-	X	-	X	-	X	-
Rhinichthys cataractae	X	X	X	X	X	X	X	X	X	-	X	X	-	X	X	X	X	X	-	X
Semotilus atromaculatus	-	-	X	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Semotilus margarita	-	-	-	X	X	X	-	-	X	X	-	X	X	X	X	-	-	-	-	-
Catostomus catostomus	X	-	X	X	X	X	-	X	-	-	-	X	X	X	X	-	X	X	X	X
Catostomus commersoni	X	X	X	X	X	X	X	X	X	X	X	X	-	X	X	X	X	X	X	-
Moxostoma anisurum	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Moxostoma macrolepidotum	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Percopsis omiscomaycus	X	X	X	X	X	X	X	-	-	-	-	X	-	-	-	-	X	X	X	X
Lota lota	-	X	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	X	X	-
Culaea inconstans	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-
Pungitius pungitius	-	-	X	X	-	X	-	-	-	-	-	-	-	X	-	-	-	X	X	-
Ambloplites rupestris	X	X	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micropterus dolomieui[3]	-	-	X	X	X	-	-	-	-	-	X	-	-	-	-	X	-	X	-	-
Pomoxis nigromaculatus	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Percina caprodes	-	-	-	X	X	X	X	-	-	-	X	-	-	X	X	-	X	-	X	-
Etheostoma exile	-	-	-	-	-	-	-	-	X[1,2]	-	X	-	X	X	X	-	-	-	X	-
Etheostoma microperca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X[2]	-
Etheostoma nigrum	X[1,2]	-	-	X	X	X	X	-	-	-	-	-	-	X	X[2]	-	X	X	X	X
Perca flavescens	X	-	X	X	-	X	X	-	-	-	X	-	-	X	-	X	X	X	X	X
Stizostedion vitreum	X	X	-	X	X	X	-	-	-	-	X[2]	-	-	-	-	-	-	X	X	X
Cottus bairdi	-	-	X	X	X	X	-	X	X	-	-	X	X	X	X	-	X	X	X	X
Cottus cognatus	-	-	X	X	-	X	-	X	-	X	-	X	X	X	-	-	X	-	X	-
Cottus ricei[4]	-	-	-	-	-	X[2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ichthyomyzon fossor[4]	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
Ichthyomyzon unicuspis[4]	-	-	-	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
Lampetra appendix[4]	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-
Petromyzon marinus[4]	X	X	X	X	X	X	X	-	X	X	X	-	-	X	-	X	X	X	X	-
Alosa pseudoharengus[4]	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X
Oncorhynchus gorbuscha[4]	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	X	-
Oncorhynchus kisutch[4]	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X	-
Oncorhynchus tshawytcha[4]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-
Oncorhynchus mykiss[4]	-	X	X	X	X	X	-	X	X	X	X	-	-	X	X	-	X	X	X	-
Salmo trutta[4]	-	-		X[2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osmerus mordax[4]	-	X	X	X	-	X	-	X	-	-	-	-	-	X	-	-	-	X	X	-
Anguilla rostrata[4]	-	-	-	X[2]	-	-	X[2]	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinus carpio[4]	-	-	X	X	-	-	-	-	-	-	-	-	-	X	-	-	-	-	X	-
Apeltes quadracus[4]	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of species	18	18	21	45	25	32	17	14	14	11	18	11	9	25	15	11	18	25	33	13
Number of collections	?[1]	17	4+	140+	17+	12+	14+	4+	7+	5+	6+	3	4	10+	10+	5+	16+	?[2]	?[2]	3+

* See text for sources of data.

1 Only collected in tributaries of the main river system.

2 Represented by only one specimen.

3 May be present in some areas due to introduction but not out of native range.

4 Not included in Jaccard's analysis.

?[1] Number of collections unknown but likely low.

?[2] Number of collections unknown but likely high.

RESULTS

Fish Collection

During 1989-90, a total of 40 fish species (representing 13 families and 26 genera) were captured both on (32 species) and off (37 species) the Sibley Peninsula. Depending on the existing records examined, three to six species (some introduced) thought previously to inhabit the Sibley Peninsula were not captured. However; some new species were added to the list of the peninsula's fishes. A complete list of fishes once known to inhabit the Sibley Peninsula, including those captured during this survey, is presented in table 4 with distributional maps in Appendix A. Appendix B lists species by lake elevation.

Iowa darters are much more prevalent than johnny darters throughout the entire study area. They occur at 37 locations (Fig. 4 and Table 5). In comparison, johnny darters are only found at 16 locations within the 210 collection sites visited (Fig. 5 and Table 6). The only location visited in which Iowa and johnny darters occur sympatrically is the Nipigon River.

Johnny darters were captured on three occasions in Sibley Peninsula streams. In all cases, these fish were only taken at or very near the stream's confluence with Black Bay (Fig. 5). Johnny darters were not collected in any Sibley Peninsula lakes. Iowa darters were captured at 20 locations on the Sibley Peninsula. However, they were never collected in Black Bay (Fig. 4; Table 5). Johnny darters were collected only in the lower reaches of the Wolf River (below Wolf Lake) which drains into the north end of Black Bay. Iowa darters were the only darter collected in the upper reaches of the Wolf River.

Johnny darters were captured in Boulevard Lake, a man made impoundment of the lower Current River located in the north end of the City of Thunder Bay. Headwater lakes (Timmus, Whitelily, Kingfisher, Lone Island) draining into the

Table 4: List of fish species known to occur on the Sibley Peninsula, Ontario based on historic records and 1989-90 survey data.

Historic Records	1989-90 Collection
Petromyzon marinus	
Ichthyomyzon unicuspis	
Ichthyomyzon fossor	
Lampetra appendix	
Acipenser fulvescens[1]	
Oncorhynchus mykiss[2]	*
Salmo trutta[3]	
Salvelinus fontinalis[2,4]	*
Coregonus artedii	*
Thymallus arcticus	Introduced 1959: now extirpated
Osmerus mordax[2]	* 1st capture in 1990
Umbra limi	*
Esox lucius	*
Phoxinus eos	*
Phoxinus neogaeus	*
Couesius plumbeus	*
Cyprinus carpio	* 1st sighted in 1989
Notemigonus crysoleucas	*
Notropis atherinoides	*
Notropis heterolepis	*
Notropis hudsonius	*
Pimephales promelas	*
Rhinichthys atratulus	* 1st capture in 1989
Rhinichthys cataractae	*
Semotilus margarita	*
Catostomus catostomus	*
Catostomus commersoni	*
Culaea inconstans	*
Pungitius pungitius	* 1st capture in 1989
Percopsis omiscomaycus	*
Pomoxis nigromaculatus[2]	Introduced 1949: now extirpated
Micropterus dolomieui[2]	*
Micropterus salmoides[2]	*
Perca flavescens	*
Stizostedion vitreum[2]	
Etheostoma exile	*
Etheostoma nigrum	* 1st capture in 1989
Percina caprodes	*
Cottus bairdi	*
Cottus cognatus	*

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1 May have been present but no authentic records.
2 Species introduced to peninsula.
3 Represents a single, unauthenticated specimen.
4 May have been native to some lakes but not authenticated.

Figure 4: Iowa darter (*Etheostoma exile*) populations determined during 1989-90.

Table 5: Location, date and method of capture of Iowa darters (*Etheostoma exile*) collected during the 1989-90 field seasons.

Location	Long / Lat		Date	Method of Capture
Gardner Creek*	48°24'	88°42'	6/2/89	Minnow trap
Kashabowie River	48°38'	90°25'	10/1/90	Seine
MacKenzie Creek	48°32'	88°58'	8/29/89	Seine
Nipigon River	49°00'	88°15'	9/6/90	Electroshocker
Otter Creek*	48°24'	88°46'	6/2/89	Minnow Trap
Pickerel Creek*	48°24'	88°42'	6/4/89	Minnow Trap
Portage Creek*	48°32'	88°43'	8/9/90	Dip Net
Sand Creek*	48°28'	88°46'	8/15/89	Minnow Trap
Scum Creek*	48°22'	88°49'	5/30/89	Minnow Trap
Unnamed Creek	48°53'	89°02'	8/11/89	Minnow Trap
Wolf River (Upper)	48°55'	88°47'	7/6/90	Minnow Trap
Addison Lake*	48°26'	88°46'	7/11/90	Seine
Anders Lake	49°00'	88°54'	7/6/90	Minnow Trap
D'Arcy Lake*	48°36'	88°39'	8/23/90	Minnow Trap
Gardner Lake*	48°25'	88°47'	6/19/89	Minnow Trap
Goldengate Lake	48°53'	88°41'	7/4/90	Seine
Holt Lake #1*	48°27'	88°47'	5/25/89	Minnow Trap
Kingfisher Lake	48°39'	89°04'	8/16/89	Seine
Lizard Lake*	48°28'	88°45'	7/12/89	Minnow Trap
Lone Island Lake	48°45'	89°02'	8/26/89	Seine
Magone Lake #1	48°36'	89°04'	8/26/89	Seine
Marie Louise Lake*	48°23'	88°48'	6/6/89	Minnow Trap
McLeish Lake	48°47'	89°06'	8/16/89	Seine
Otter Lake*	48°25'	88°46'	6/4/89	Minnow Trap
Pesheau Lake	49°15'	89°23'	8/29/90	Seine
Pickerel Lake*	48°25'	88°45'	5/10/89	Seine
Pounsford Lake*	48°29'	88°46'	6/12/90	Seine
Rita Lake*	48°27'	88°44'	7/11/89	Minnow Trap
Shebandowan Lake	48°37'	90°15'	10/1/90	Seine
Smiley Lake	48°58'	89°17'	7/23/90	Seine
Surprise Lake*	48°20'	88°49'	9/18/89	Seine
Timmus Lake	48°40'	89°05'	8/10/89	Seine
Twinpine Lake*	48°25'	88°49'	6/2/89	Minnow Trap
Twinpine Lake #1*	48°25'	88°49'	5/7/90	Minnow Trap
Walkinshaw Lake	48°37'	89°04'	8/16/89	Seine
Whitelily Lake	48°40'	89°05'	8/10/89	Seine
Wiswell Lake*	48°30'	88°45'	7/13/89	Minnow Trap

* Denotes waterbodies on the Sibley Peninsula.

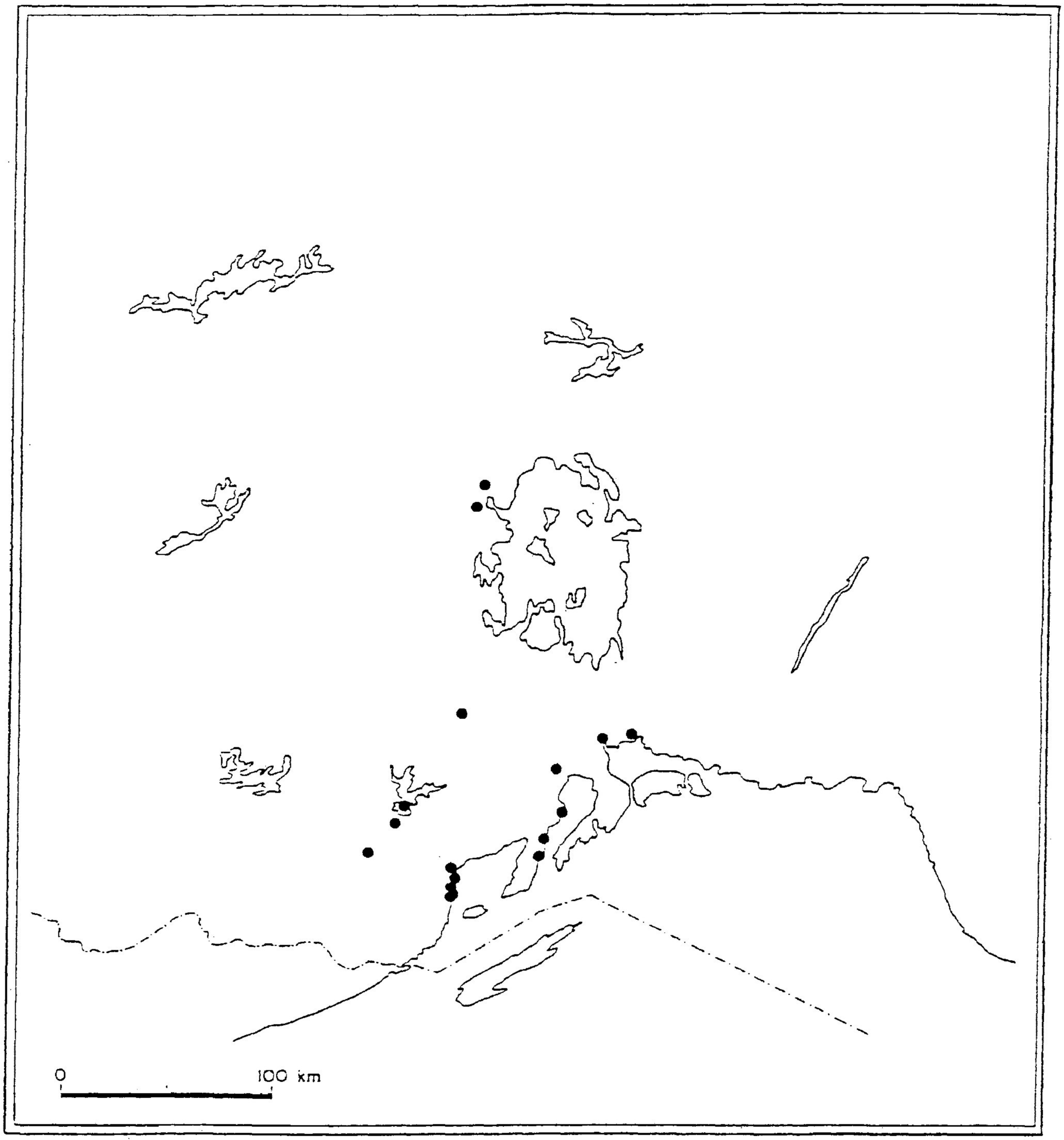

Figure 5: Johnny darter (*Etheostoma nigrum*) populations determined during 1989-90.

Table 6: Location, date and method of capture of johnny darters (*Etheostoma nigrum*) collected during the 1989-90 field seasons.

Location	Long / Lat		Date	Method of Capture
Jackfish River	$49^{0}00'$	$88^{0}05'$	8/15/89	Seine
Joe Boy Creek†	$48^{0}28'$	$88^{0}42'$	8/23/90	Plexiglass Trap
Kopka River	$51^{0}51'$	$89^{0}07'$	7/25/98	Dip Net
McIntyre River	$48^{0}25'$	$89^{0}16'$	9/1/89	Seine
McVicars Creek	$48^{0}26'$	$89^{0}12'$	9/11/89	Seine
Neebing River	$48^{0}22'$	$89^{0}20'$	9/1/89	Seine
Nipigon River	$49^{0}00'$	$88^{0}15'$	9/6/90	Electroshocker
Portage Creek†	$48^{0}32'$	$88^{0}43'$	6/23/89	Minnow Trap
Sunshine Creek	$48^{0}32'$	$89^{0}41'$	10/1/90	Seine
Wolf River (Lower)	$48^{0}49'$	$88^{0}31'$	8/15/89	Seine
Boulevard Lake	$48^{0}28'$	$89^{0}12'$	8/9/89	Seine
Dog Lake	$48^{0}46'$	$89^{0}32'$	8/24/89	Seine
Little Dog Lake	$48^{0}39'$	$89^{0}36'$	8/18/89	Seine
Moose Bay (Black Bay)	$48^{0}40'$	$88^{0}32'$	7/25/89	Seine
Starnes Lake	$49^{0}05'$	$89^{0}15'$	7/23/90	Seine
Waweig Lake	$50^{0}08'$	$89^{0}05'$	7/25/90	Dip Net

† Denotes waterbodies on the Sibley Peninsula.

eastern portion of the twin branches of the Current River also harboured Iowa darters. However, darters were not collected in any riverine portions of the main stem of the Current River nor in the lakes that drain the western portion of the Current River watershed.

Johnny darters were collected in the Neebing and McIntyre rivers as well as just slightly upstream from the mouth of McVicars Creek. All of these locations are within the City of Thunder Bay and are here considered to be part of the broader Kaministiquia basin. Johnny darters were also collected in Dog and Little Dog Lakes. Both of these drain into the Kaministiquia River. Iowa darters were absent from all these areas.

Only a single Iowa darter was collected in those streams located between the City of Thunder Bay and the Sibley Peninsula. This fish came from a small tributary stream flowing into the MacKenzie River. Iowa darters were collected from a first order stream which eventually flows into the Black Sturgeon River and then into Black Bay. Iowa darters were also collected in two headwater lakes tributary to the MacKenzie River. Both of these lakes occur near those headwater lakes of the Current River system that harbour Iowa darters.

Figure 4 shows the location of Iowa darters found to the north and east of Thunder Bay. Johnny darters are mainly absent in this area (Fig. 5). Both species are seemingly absent from Canadian Lake Superior tributaries south of the Kaministiquia basin (*Etheostoma nigrum* now known from Arrow River, tributary to the Pigeon River (W. Momot, Lakehead University, pers. comm.) (Table 3)).

Most darters were collected by seining (53% of all collections). The remainder were collected by minnow traps (36%), dip nets (6%) electroshocking (4%) or in plexiglass traps (2%) (Tables 5 and 6). In all but two cases, darters collected by seine were either captured in the first haul or found to be included with other fish collected in the first successful haul. Often, when employing minnow traps at a given location, darters were only one of two or three of the total species collected (43% of all minnow trap captures).

Fifteen lakes on the Sibley Peninsula visited in 1989-90 were devoid of fishes. Lakes and streams on the peninsula that were sampled but devoid of fish are shown in Fig. 6. All areas sampled on the peninsula in 1989-90 are shown in Fig. 7 (see Appendix C for lake and stream names on the peninsula).

Temperature Selection Trials

The location of johnny and Iowa darters within temperature gradients were summarized by averaging their positions over five hours. In all, 19 fish (two sets of four and two single johnny darters; one set of four, one set of two and three single Iowa darters) were tested during trials of five hour duration.

Darters, introduced to the test tanks when the gradient was not operational, moved freely about the tank. However, when illuminated, some darters sought cover at the tank's edge. Tests were therefore run in total darkness. Darter position was determined by quickly illuminating the tank with a flashlight. This type of illumination appears to have little effect on the behaviour of the fish (Emery, 1973).

Smaller fish (< 36 mm TL) of both species generally sought out warmer temperatures than larger conspecifics ($p < .05$).

Without acclimatization, Iowa darters selected significantly cooler temperatures than did johnny darters ($p < .05$). Iowa darters also selected a narrower range of temperatures than did johnny darters. Although initially both species sought out warmer temperatures immediately following introduction, johnny darters consistently sought out much warmer areas even when introduced at cooler temperatures (Fig. 8).

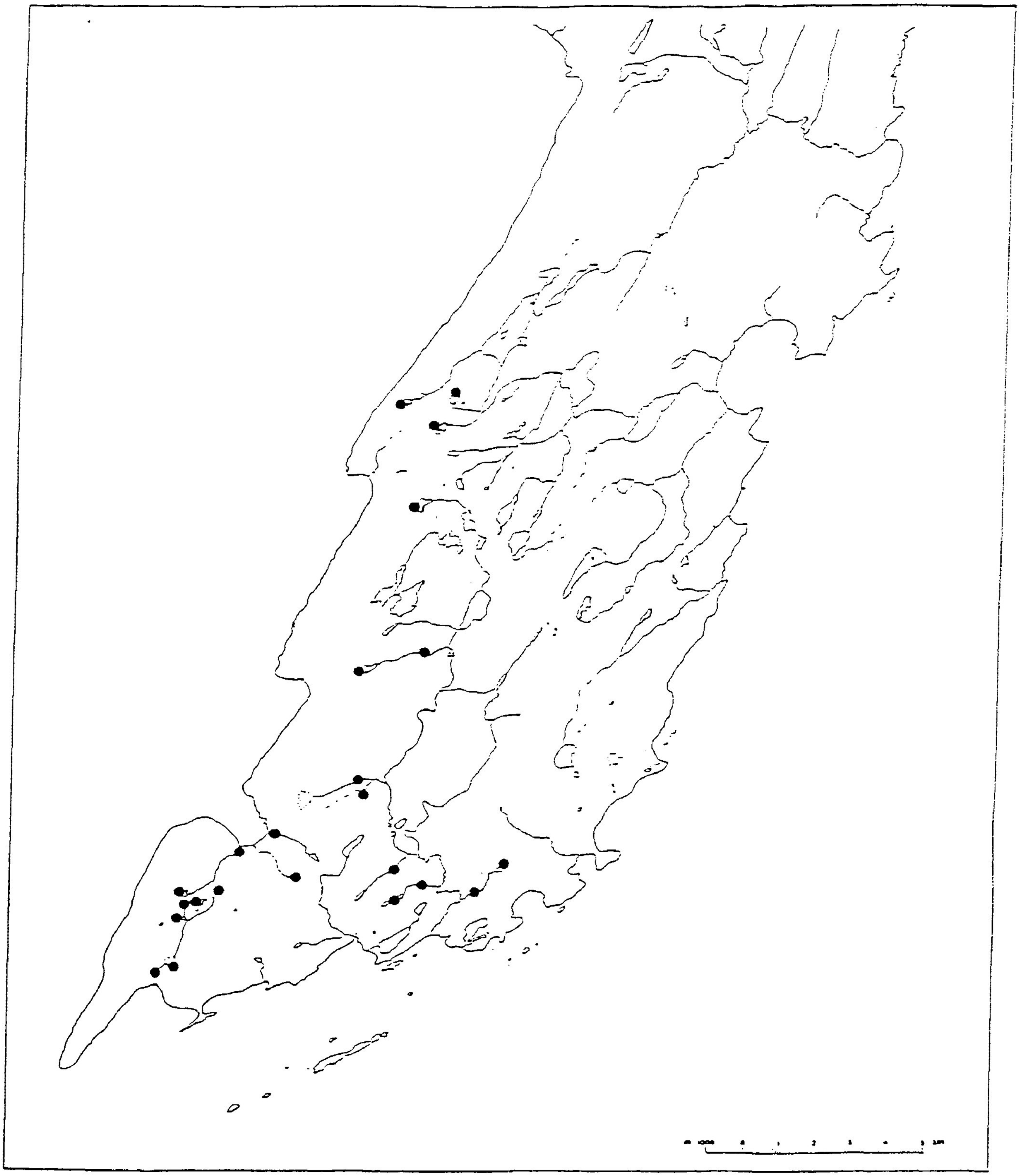

Figure 6: Sampled areas of the Sibley Peninsula devoid of fish.

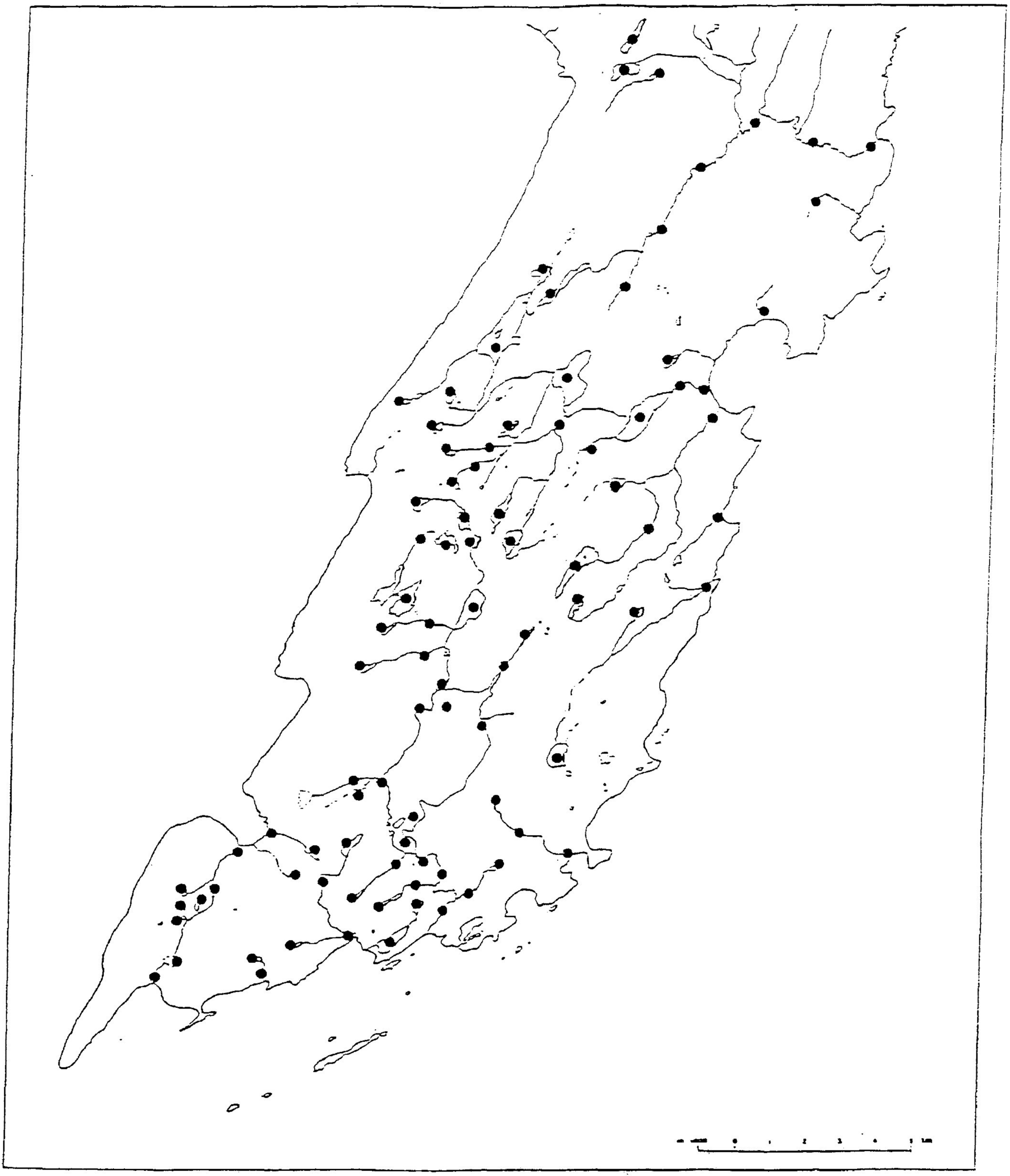

Figure 7: Localities sampled on the Sibley Peninsula during the 1989-90 survey.

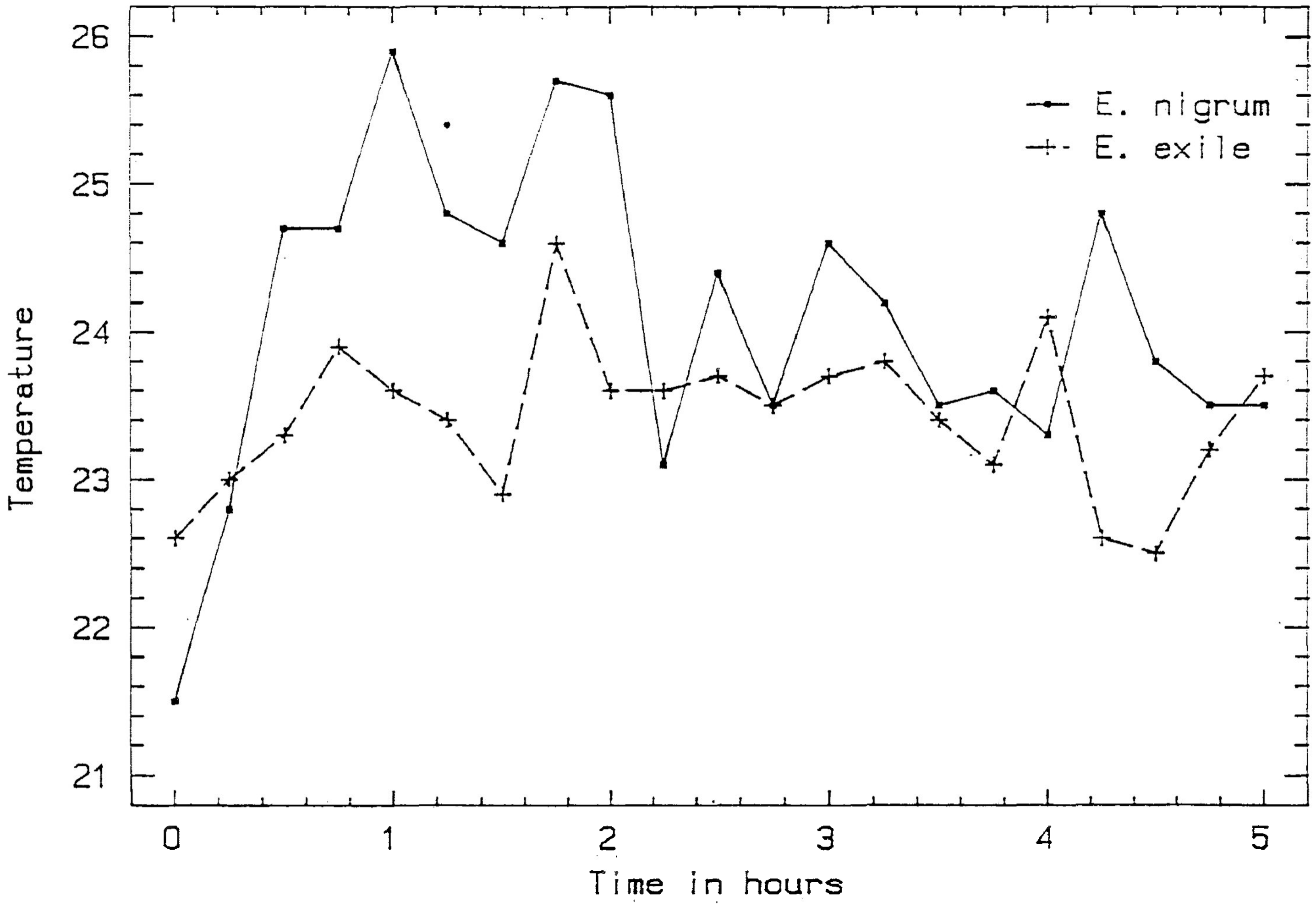

Figure 8: Average temperature selected by nine Iowa darters (*Etheostoma exile*) and ten johnny darters (*E. nigrum*) over a five hour period.

After acclimatization for 90 days at 21^0C, two Iowa and five johnny darters were tested again for temperature preference. Small darters again sought out warmer temperatures than did large darters. However, the small sample size necessitates replication of this test to obtain conclusive results.

Meristic Data

Tables 7 and 8 summarize meristic data from both darters. Johnny darter populations residing in the Kaministiquia basin have a higher number of POP pores and a higher percentage of scaled napes, cheeks and breasts than other populations examined. The association of squamation patterns for these fish is presented in table 9. Few populations, with the exception of the Sucker River, Minnesota, had individuals with such a high percentage of these five characters. Using PCA, these same characters weight most heavily within the first factor (Table 10). Since these characters provide the most efficient means of discriminating populations, they are used in the discriminant function analysis (DFA). Figure 9 shows that most Kaministiquia basin, as well as Sucker River fish, are confined to one area of the scatterplot.

No obvious "best" meristic characters were revealed for Iowa darters. PCA suggests that the number of pores in the infraorbital canal is among the best discriminators as it was the most heavily weighted variable in the first factor (Table 11). Trials of DFA suggested that when the first three factors are employed, some discrimination of populations occurs. However, several attempts to produce informative scatterplots failed.

Jaccard's Analysis of Rivers

The data matrix calculated from the Jaccard's analysis is presented in table 12. The results of this matrix are presented in the dendrograms in Figs. 10 and 11. The species list used to create this dendrogram is given in table

Table 7: Frequency and percent (in parentheses) of meristic counts made on 13 populations of johnny darters (*Etheostoma nigrum*) in northwestern Ontario and northern Minnesota.

	Number of pores in the right preoperculomandibular canal										
	5	6	7	8	9	10	11	12	Mean	N	SD
McVicars Creek	-	3(17.6)	-	4(23.5)	3(17.6)	4(23.5)	1(5.9)	2(11.8)	8.94	17	1.886
Neebing/McIntyre	1(0.7)	32(21.5)	17(11.4)	25(16.8)	32(21.5)	29(19.5)	11(7.4)	2(1.3)	8.32	149	1.681
Kaministiquia River	-	6(11.8)	-	6(11.8)	18(35.3)	21(41.2)	-	-	8.94	51	1.271
Boulevard Lake	2(8.0)	21(84.0)	1(4.0)	1(4.0)	-	-	-	-	6.20	25	1.041
Little Dog Lake	-	25(55.6)	2(4.4)	4(8.9)	13(28.9)	1(2.2)	-	-	7.18	45	1.419
Quetico	1(1.9)	50(92.6)	1(1.9)	2(3.7)	-	-	-	-	6.07	54	0.428
Flatrock Lake	-	22(95.7)	-	-	1(4.3)	-	-	-	6.13	23	0.626
Nipigon River	-	94(85.5)	9(8.2)	4(3.6)	1(0.9)	1(0.9)	1(0.9)	-	6.26	110	0.786
Sibley Peninsula	-	10(58.8)	1(5.9)	4(23.5)	1(5.9)	1(5.9)	-	-	6.94	17	1.298
Sucker River, MN	-	-	-	1(16.7)	5(83.3)	-	-	-	8.83	6	0.408
Temperance River, MN	-	1(20.0)	-	2(40.0)	2(40.0)	-	-	-	8.00	5	1.225
Cloquet River, MN	-	11(64.7)	1(5.9)	1(5.9)	2(11.8)	2(11.8)	-	-	7.00	17	1.541
St. Louis River, MN	-	36(75.0)	2(4.2)	6(12.5)	2(4.2)	1(2.1)	1(2.1)	-	6.60	48	1.198

	Number of pores in the left preoperculomandibular canal									
	5	6	7	8	9	10	11	Mean	N	SD
McVicars Creek	-	3(17.6)	1(5.9)	2(11.8)	1(5.9)	5(29.4)	5(29.4)	9.118	17	1.900
Neebing/McIntyre	-	34(22.8)	17(11.4)	26(17.4)	38(25.5)	30(20.1)	4(2.7)	8.168	149	1.522
Kaministiquia River	1(2.0)	5(9.8)	4(7.8)	11(21.6)	20(39.2)	10(19.6)	-	8.451	51	1.286
Boulevard Lake	-	21(84.0)	2(8.0)	1(4.0)	1(4.0)	-	-	6.280	25	0.737
Little Dog Lake	1(2.2)	23(51.1)	4(8.9)	1(2.2)	14(31.1)	2(4.4)	-	7.222	45	1.506
Quetico	1(1.9)	49(90.7)	3(5.6)	1(1.9)	-	-	-	6.074	54	0.381
Flatrock Lake	-	17(73.9)	2(8.7)	4(17.4)	-	-	-	6.435	23	0.788
Nipigon River	4(3.6)	87(79.1)	11(10.0)	7(6.4)	1(0.9)	-	-	6.218	110	0.655
Sibley Peninsula	-	12(70.6)	1(5.9)	1(5.9)	2(11.8)	1(5.9)	-	6.765	17	1.348
Sucker River, MN	-	-	-	3(50.0)	1(16.7)	2(33.3)	-	8.833	6	0.983
Temperance River, MN	-	2(40.0)	-	2(40.0)	1(20.0)	-	-	7.400	5	1.342
Cloquet River, MN	1(5.9)	6(35.3)	1(5.9)	4(23.5)	4(23.5)	1(5.9)	-	7.412	17	1.502
St. Louis River, MN	-	37(77.1)	3(6.3)	6(12.5)	1(2.1)	1(2.1)	-	6.458	48	0.944

Table 7: Contd.

Number of dorsal spines

	7	8	9	10	N	Mean	SD
McVicars Creek	-	1(5.9)	10(58.8)	6(35.3)	17	9.294	0.588
Neebing/McIntyre	1(0.7)	26(17.4)	104(69.8)	18(12.1)	149	8.933	0.565
Kaministiquia River	-	7(13.7)	43(84.3)	1(2.0)	51	8.882	0.382
Boulevard Lake	1(4.0)	14(56.0)	7(28.0)	3(12.0)	25	8.480	0.770
Little Dog Lake	-	3(6.7)	32(71.1)	10(22.2)	45	9.156	0.520
Quetico	1(1.9)	18(33.3)	34(63.0)	1(1.9)	54	8.648	0.555
Flatrock Lake	-	-	18(78.3)	5(21.7)	23	9.217	0.422
Nipigon River	1(0.9)	3(2.7)	66(60.0)	40(36.4)	110	9.318	0.574
Sibley Peninsula	2(11.8)	2(11.8)	10(58.8)	3(17.6)	17	8.824	0.883
Sucker River, MN	-	-	6(100.0)	-	6	9.000	0.000
Temperance River, MN	-	-	5(100.0)	-	5	9.000	0.000
Cloquet River, MN	-	8(47.1)	9(52.9)	-	17	8.529	0.514
St. Louis River, MN	2(4.2)	17(35.4)	28(58.3)	1(2.1)	48	8.583	0.613

Number of dorsal rays

	10	11	12	13	N	Mean	SD
McVicars Creek	-	2(11.8)	5(29.4)	10(58.8)	17	12.471	0.717
Neebing/McIntyre	-	11(7.4)	94(63.1)	44(29.5)	149	12.221	0.568
Kaministiquia River	-	17(33.3)	33(64.7)	1(2.0)	51	11.686	0.510
Boulevard Lake	-	11(44.0)	13(52.0)	1(4.0)	25	11.600	0.577
Little Dog Lake	-	12(26.7)	25(55.6)	8(17.8)	45	11.911	0.668
Quetico	-	4(7.4)	46(85.2)	4(7.4)	54	12.000	0.389
Flatrock Lake	-	-	23(100.)	-	23	12.000	0.000
Nipigon River	3(2.7)	38(34.5)	58(52.7)	11(10.0)	110	11.700	0.685
Sibley Peninsula	-	10(58.8)	6(35.3)	1(5.9)	17	11.471	0.624
Sucker River, MN	-	4(66.7)	2(33.3)	-	6	11.333	0.516
Temperance River, MN	-	-	3(60.0)	2(40.0)	5	12.400	0.548
Cloquet River, MN	-	4(23.5)	13(76.5)	-	17	11.765	0.514
St. Louis River, MN		7(14.6)	41(85.4)	-	48	11.854	0.357

Table 7: Contd.

Number of pores in the right anterior infraorbital canal

	2	3	4	5	N	Mean	SD
McVicars Creek	-	-	15(88.2)	2(11.8)	17	4.118	0.332
Neebing/McIntyre	-	6(4.0)	135(90.6)	8(5.4)	149	4.013	0.307
Kaministiquia River	-	1(2.0)	48(94.1)	2(3.9)	51	4.020	0.244
Boulevard Lake	1(4.0)	1(4.0)	23(92.0)	-	25	3.880	0.440
Little Dog Lake	-	2(4.4)	41(91.1)	2(4.4)	45	4.000	0.302
Quetico	-	3(5.6)	51(94.4)	-	54	3.944	0.231
Flatrock Lake	-	1(4.3)	21(91.3)	1(4.3)	23	4.000	0.302
Nipigon River	-	3(2.7)	105(95.5)	2(1.8)	110	3.991	0.214
Sibley Peninsula	-	2(11.8)	15(88.2)	-	17	3.882	0.332
Sucker River, MN	-	-	6(100.0)	-	6	4.000	0.000
Temperance River, MN	-	-	5(100.0)	-	5	4.000	0.000
Cloquet River, MN	-	-	16(94.1)	1(5.9)	17	4.059	0.243
St. Louis River, MN	-	2(4.2)	45(93.8)	1(2.1)	48	3.979	0.252

Number of pores in the left anterior infraorbital canal

	2	3	4	5	N	Mean	SD
McVicars Creek	-	-	16(94.1)	1(5.9)	17	4.059	0.243
Neebing/McIntyre	1(0.7)	4(2.7)	135(90.6)	9(6.0)	149	4.020	0.338
Kaministiquia River	1(2.0)	2(3.9)	44(86.3)	4(7.8)	51	4.000	0.447
Boulevard Lake	1(4.0)	1(4.0)	22(88.0)	1(4.0)	17	3.920	0.493
Little Dog Lake	-	2(4.4)	38(84.4)	5(11.1)	45	4.067	0.393
Quetico	-	1(1.9)	53(98.1)	-	54	3.981	0.136
Flatrock Lake	-	1(4.3)	21(91.3)	1(4.3)	23	4.000	0.302
Nipigon River	-	3(2.7)	107(97.3)	-	110	3.973	0.164
Sibley Peninsula	-	1(5.9)	15(88.2)	1(5.9)	17	4.000	0.354
Sucker River, MN	-	-	6(100.0)	-	6	4.000	0.000
Temperance River, MN	-	-	5(100.0)	-	5	4.000	0.000
Cloquet River, MN	-	-	16(94.1)	1(5.9)	17	4.059	0.243
St. Louis River, MN	-	1(2.1)	47(97.9)	-	48	3.979	0.144

Table 7: Contd.

Percent of population exhibiting scaling on the opercle, breast, nape and cheek

	Opercle	Breast	Nape	Cheek	N
McVicars Creek	100	70.6	58.8	64.7	17
Neebing/McIntyre	100	56.4	36.9	49.0	149
Kaministiquia River	100	27.5	27.5	5.9	51
Boulevard Lake	100	-	4.0	-	25
Little Dog Lake	100	-	-	-	45
Quetico	100	-	-	-	54
Flatrock Lake	100	-	-	-	23
Nipigon River	100	-	-	-	110
Sibley Peninsula	100	-	5.9	-	17
Sucker River, MN	100	83.3	83.3	33.3	6
Temperance River, MN	100	-	-	-	5
Cloquet River, MN	100	-	-	-	17
St. Louis River, MN	100	-	-	-	48

Number of lateral line scales

	Range	Mean	SD	Mode
McVicars Creek	47 - 55	50.412	2.785	50
Neebing/McIntyre	44 - 57	49.799	2.878	50
Kaministiquia River	45 - 55	50.431	2.427	50
Boulevard Lake	44 - 53	47.920	2.431	46
Little Dog Lake	46 - 56	51.644	2.176	51
Quetico	48 - 59	52.148	2.382	51
Flatrock Lake	47 - 57	51.130	2.418	49
Nipigon River	46 - 57	52.382	2.334	54
Sibley Peninsula	47 - 59	52.059	3.132	51
Sucker River, MN	46 - 50	47.500	1.761	46
Temperance River, MN	50 - 54	52.000	1.414	52
Cloquet River, MN	48 - 54	50.765	1.985	50
St. Louis River, MN	44 - 55	49.083	2.931	49

Table 7: Contd.

Number of posterior infraorbital canal pores on the left and right side

	Left Range	Mean	SD	Mode	Right Range	Mean	SD	Mode	N
McVicars Creek	2 - 4	2.353	0.606	2	1 - 4	2.235	0.664	2	17
Neebing/McIntyre	1 - 3	2.101	0.324	2	1 - 4	2.134	0.414	2	149
Kaministiquia River	2 - 3	2.275	0.451	2	2 - 3	2.196	0.401	2	51
Boulevard Lake	2	2.00	0.0	2	2	2.00	0.0	2	25
Little Dog Lake	1 - 3	2.067	0.330	2	1 - 3	2.067	0.330	2	45
Quetico	2 - 3	2.019	0.136	2	2 - 3	2.093	0.293	2	54
Flatrock Lake	2 - 3	2.043	0.209	2	2	2.00	0.0	2	23
Nipigon River	2 - 3	2.127	0.335	2	2 - 3	2.109	0.313	2	110
Sibley Peninsula	2	2.000	0.000	2	2	2.000	0.0	2	17
Sucker River, MN	2 - 3	2.667	0.516	3	2 - 3	2.833	0.408	3	6
Temperance River, MN	2 - 3	2.200	0.447	2	2	2.00	0.0	2	5
Cloquet River, MN	2 - 4	2.706	0.588	3	2 - 4	2.706	0.588	3	17
St. Louis River, MN	2 - 3	2.250	0.438	2	2 - 3	2.188	0.394	2	48

Table 8: Frequency and percent (in parentheses) of meristic counts made on 10 populations of Iowa darters (*Etheostoma exile*) near the Thunder Bay area of northwestern Ontario and Lake Superior tributaries of Minnesota and Isle Royale, Michigan.

	Number of anal spines					
	1	2	3	N	Mean	SD
Armstrong	5(11.9)	37(88.1)	-	42	1.880	0.327
Isle Royale	-	14(100.)	-	14	2.000	0.000
Nipigon River	4(5.1)	72(92.3)	2(2.60)	78	1.974	0.277
Pickerel Lake	2(2.5)	77(97.5)	-	79	1.974	0.158
Twinpine-Holt	-	12(85.7)	2(14.3)	14	2.142	0.363
Wicksteed Lake		32(100.)	-	32	2.000	0.000
Dell Lake		20(100.)		20	2.000	0.000
Cascade River, MN		9(100.)		9	2.000	0.000
Elbow Creek, MN		5(100.)		5	2.000	0.000
Mistletoe Creek, MN		8(100.)		8	2.000	0.000

	Number of anal rays						
	6	7	8	9	N	Mean	SD
Armstrong	1(2.4)	21(50.0)	20(47.6)	-	42	7.452	0.550
Isle Royale	-	11(78.6)	3(21.4)	-	14	7.214	0.425
Nipigon River	1(1.3)	33(42.3)	41(52.6)	3(3.8)	78	7.589	0.590
Pickerel Lake	-	30(38.0)	45(57.0)	4(5.1)	79	7.670	0.571
Twinpine-Holt	-	8(57.1)	6(42.9)	-	14	7.428	0.513
Wicksteed Lake	2(6.3)	27(84.4)	3(9.40)		32	7.031	0.400
Dell Lake	-	14(70.0)	6(30.0)		20	7.300	0.470
Cascade River, MN	1(11.1)	8(88.9)	-		9	6.889	0.333
Elbow Creek, MN	-	1(20.0)	4(80.0)		5	7.800	0.447
Mistletoe Creek, MN	-	7(87.5)	1(12.5)		8	7.125	0.354

	Number of dorsal spines							
	7	8	9	10	11	N	Mean	SD
Armstrong	-	3(7.1)	21(50.0)	18(42.9)	-	42	9.357	0.617
Isle Royale	2(14.3)	8(57.1)	4(28.6)	-		14	8.142	0.662
Nipigon River	4(5.1)	37(47.4)	35(44.9)	2(2.60)	-	78	8.448	0.637
Pickerel Lake	-	15(19.0)	55(69.6)	8(10.1)	1(1.3)	79	8.936	0.584
Twinpine-Holt	-	1(7.1)	10(71.4)	3(21.4)	-	14	9.142	0.534
Wicksteed Lake		5(15.6)	16(50.0)	11(34.4)		32	9.187	0.692
Dell Lake	-	1(5.00)	16(80.0)	3(15.0)	-	20	9.100	0.447
Cascade River, MN	2(22.2)	6(66.7)	-	-	1(11.1)	9	8.111	1.167
Elbow Creek, MN	-	3(60.0)	2(40.0)	-	-	5	8.400	0.548
Mistletoe Creek, MN		3(37.5)	4(50.0)	1(12.5)		8	8.750	0.707

Table 8: Contd.

	Number of dorsal rays						
	9	10	11	12	N	Mean	SD
Armstrong	21(50.0)	21(50.0)	-		42	9.500	0.506
Isle Royale	2(14.3)	10(71.4)	2(14.3)		14	10.000	0.554
Nipigon River	-	51(65.4)	27(34.6)	-	78	10.346	0.478
Pickerel Lake	1(1.3)	45(57.0)	32(40.5)	1(1.30)	79	10.417	0.545
Twinpine-Holt	1(7.1)	5(35.7)	7(50.0)	1(7.10)	14	10.571	0.755
Wicksteed Lake	1(3.1)	27(84.4)	4(12.5)	-	32	10.093	0.390
Dell Lake	-	18(90.0)	2(10.0)		20	10.100	0.307
Cascade River, MN		8(88.9)	1(11.1)		9	10.111	0.333
Elbow Creek, MN	-	5(100.0)	-		5	10.000	0.000
Mistletoe River, MN	1(12.5)	6(75.0)	1(12.5)		8	10.000	0.535

	Number of lateral line scales				
	Range	Mean	SD	Mode	N
Armstrong	54 - 67	60.310	2.561	60	42
Isle Royale	50 - 59	55.143	2.685	55	14
Nipigon River	50 - 67	56.295	2.754	55	78
Pickerel Lake	47 - 62	56.734	2.411	57	79
Twinpine-Holt	56 - 63	60.000	2.219	59	14
Wicksteed Lake	54 - 63	58.688	2.429	57	32
Dell Lake	51 - 64	57.250	2.789	55	20
Cascade River, MN	55 - 63	58.444	2.555	57	9
Elbow Creek, MN	58 - 63	60.000	2.345	58	5
Mistletoe Creek, MN	56 - 60	58.625	1.302	59	8

	Number of pores in the right and left infraorbital canal								
	Left Range	Mean	SD	Mode	Right Range	Mean	SD	Mode	N
Armstrong	7 - 9	8.071	0.407	8.0	7 - 9	8.167	0.437	8.0	42
Isle Royale	6 - 9	8.000	0.679	8.0	8 - 9	8.214	0.426	8.0	14
Nipigon River	7 - 10	8.077	0.553	8.0	7 - 9	8.128	0.632	8.0	78
Pickerel Lake	7 - 10	8.544	0.573	9.0	8 - 10	8.595	0.610	8.0	79
Twinpine-Holt	7 - 10	8.214	0.699	8.0	7 - 9	8.429	0.646	9.0	14
Wicksteed Lake	7 - 9	8.188	0.535	8.0	7 - 9	8.281	0.523	8.0	32
Dell Lake	8 - 9	8.400	0.503	8.0	7 - 9	8.350	0.587	8.0	20
Cascade River, MN	8 - 10	8.444	0.726	8.0	8 - 9	8.333	0.500	8.0	9
Elbow Creek, MN	8 - 10	8.800	0.837	8.0	8 - 9	8.600	0.548	9.0	5
Mistletoe Creek, MN	8 - 11	8.750	1.035	8.0	8 - 9	8.375	0.518	8.0	8

Table 8: Contd.

	Number of pores in the right and left preoperculomandibular canal								
	Left Range	Mean	SD	Mode	Right Range	Mean	SD	Mode	N
Armstrong	9 - 12	10.000	0.442	10.0	9 - 11	10.048	0.309	10.0	42
Isle Royale	10	10.000	0.000	10.0	10	10.000	0.000	10.0	14
Nipigon River	9 - 11	10.026	0.226	10.0	9 - 14	10.103	0.549	10.0	78
Pickerel Lake	9 - 12	10.228	0.530	10.0	10 - 12	10.139	0.383	10.0	79
Twinpine-Holt	10	10.000	0.000	10.0	9 - 11	9.929	0.475	10.0	14
Wicksteed Lake	9 - 11	10.031	0.400	10.0	9 - 13	10.188	0.738	10.0	32
Dell Lake	10	10.000	0.000	10.0	10 - 11	10.050	0.224	10.0	20
Cascade River, MN	9 - 11	10.000	0.500	10.0	10 - 12	10.222	0.667	10.0	9
Elbow Creek, MN	10	10.000	0.000	10.0	10	10.000	0.000	10.0	5
Mistletoe Creek, MN	10	10.000	0.000	10.0	10	10.000	0.000	10.0	8

Table 9: Distribution of squamational patterns among 127 johnny darters (*Etheostoma nigrum*) collected from McVicars Creek, the Kaministiquia River and the Neebing-McIntyre rivers.

Location of Squamation	Cheek and Breast	Cheek and Nape	Breast and Nape	Breast, Cheek, Nape	Cheek Only	Breast Only	Nape Only
Number of fish with pattern	18	3	14	57	9	5	21
Percent of Sample	14.2	2.36	11.0	44.9	7.1	3.9	16.5

Table 10: Loadings of 12 characters on the first two principal components obtained from a sample of 567 johnny darters (*Etheostoma nigrum*) from 13 locations in northwestern Ontario and northern Minnesota. Highest loadings in bold.

Character	Principal Component	
	First	Second
Number of dorsal spines	-.00594	.00944
Number of dorsal rays	.31998	-.31116
Right preoperculomandibular pores	**.77674**	.13072
Left preoperculomandibular pores	**.79742**	.13686
Right posterior pores of infraorbital canal	.15219	**.73948**
Left posterior pores of infraorbital canal	.13834	**.79421**
Right anterior pores of infraorbital canal	.17898	.22537
Left anterior pores of infraorbital canal	.16991	.27647
Number of scale in lateral line	-.08299	.16418
Presence of scaling on cheek	**.80917**	-.19790
Presence of scaling on breast	**.82431**	-.17276
Presence of scaling on nape	**.82333**	-.12704

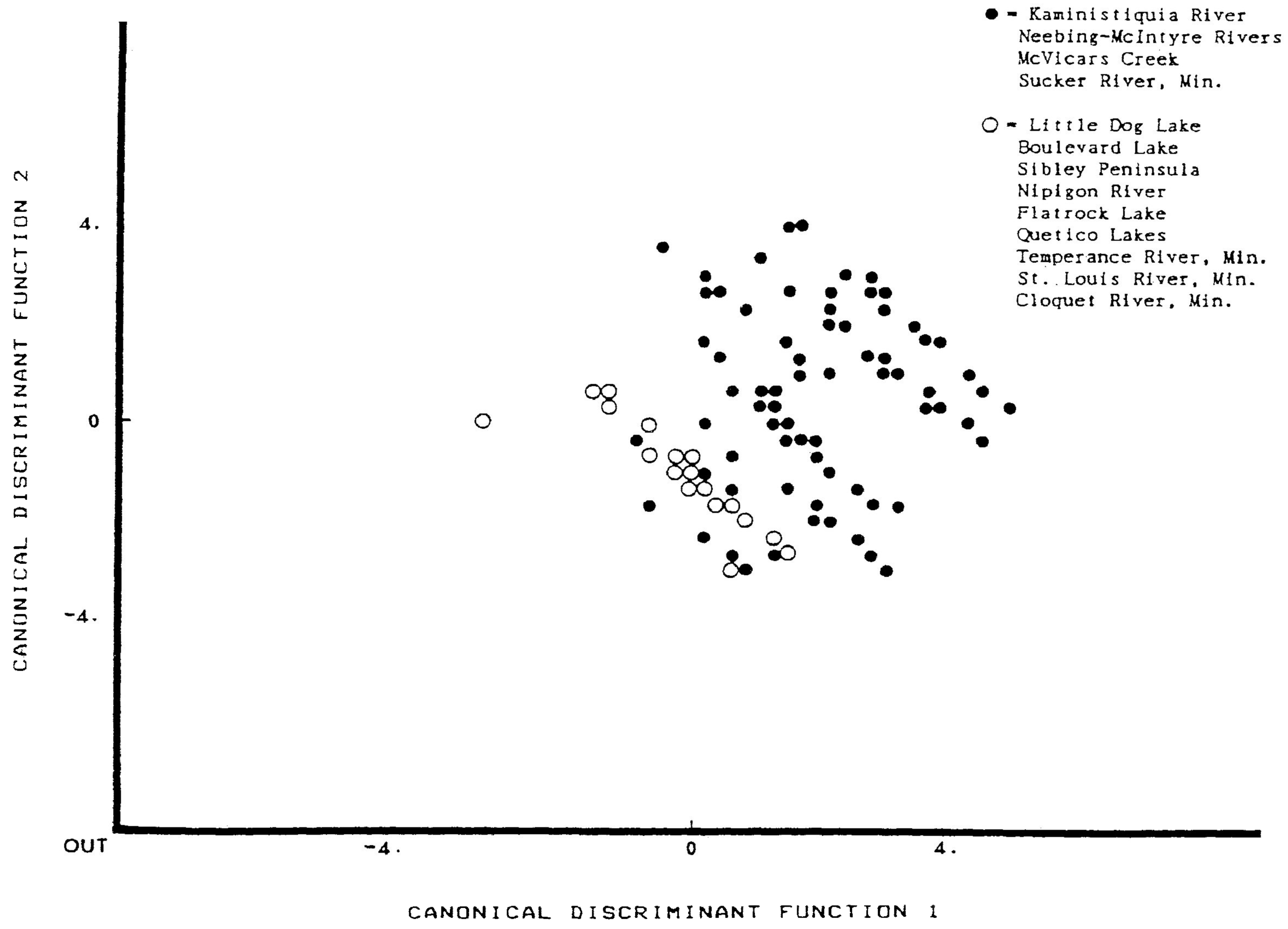

Figure 9: Scatterplot of the first and second discriminant functions based on meristic counts made on 567 johnny darters (*Etheostoma nigrum*). Characters utilized are those identified by the first principal component factor.

Table 11: Loadings of 9 characters on the first two principal components obtained from a sample of 301 Iowa darters (*Etheostoma exile*) from 10 locations in northwestern Ontario, northern Minnesota and Isle Royale, Michigan. Highest loadings in bold.

Character	Principal Component	
	First	Second
Number of anal rays	.47236	.06973
Number of dorsal spines	.15475	**.62940**
Number of dorsal rays	.28909	**-.64439**
Number of scales in lateral line	.08287	**.65980**
Number of anal spines	-.12237	-.32088
Right preoperculomandibular pores	.32449	-.09945
Left preoperculomandibular pores	.50081	.03499
Number of right infraorbital pores	**.67164**	-.05127
Number of left infraorbital pores	**.62961**	.01778

Table 12: Similarity coefficients among twenty rivers in the Thunder Bay area based on native fish taxa*.

RIVER		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1/ Pigeon	**1.00**																			
2/ Pine	.348	**1.00**																		
3/ Cloud	.375	.391	**1.00**																	
4/ Kaministiquia	.395	.405	.459	**1.00**																
5/ Neebing	.500	.458	.423	.541	**1.00**															
6/ McIntyre	.519	.481	.615	.676	.731	**1.00**														
7/ Current	.476	.429	.333	.405	.590	.600	**1.00**													
8/ Wildgoose	.227	.444	.400	.297	.348	.385	.238	**1.00**												
9/ MacKenzie	.286	.300	.217	.263	.409	.384	.368	.375	**1.00**											
10/ Blende	.143	.353	.250	.216	.333	.320	.278	.357	.357	**1.00**										
11/ Sibley	.250	.318	.292	.308	.308	.345	.381	.250	.250	.158	**1.00**									
12/ Demer's	.286	.368	.400	.297	.348	.385	.300	.467	.375	.267	.190	**1.00**								
13/ Pickerel	.087	.200	.238	.211	.261	.259	.091	.429	.333	.417	.150	.429	**1.00**							
14/ Joe Boy	.286	.346	.423	.500	.429	.607	.400	.409	.409	.273	.360	.476	.381	**1.00**						
15/ Portage	.304	.318	.240	.342	.619	.500	.450	.471	.666	.375	.273	.389	.438	.619	**1.00**					
16/ Pearl	.200	.278	.250	.216	.273	.222	.353	.267	.357	.333	.467	.188	.133	.273	.294	**1.00**				
17/ Wolf	.476	.304	.333	.405	.591	.600	.666	.444	.444	.278	.318	.444	.263	.522	.610	.353	**1.00**			
18/ Black Sturgeon	.333	.296	.370	.500	.379	.406	.346	.292	.192	.120	.417	.292	.160	.333	.259	.333	.400	**1.00**		
19/ Nipigon	.290	.300	.323	.525	.333	.485	.345	.346	.206	.143	.357	.296	.222	.419	.310	.143	.444	.571	**1.00**	
20/ Jackfish	.333	.350	.318	.324	.333	.423	.350	.353	.211	.056	.300	.353	.167	.333	.300	.176	.421	.391	.385	**1.00**

* See Table 3 for species list.

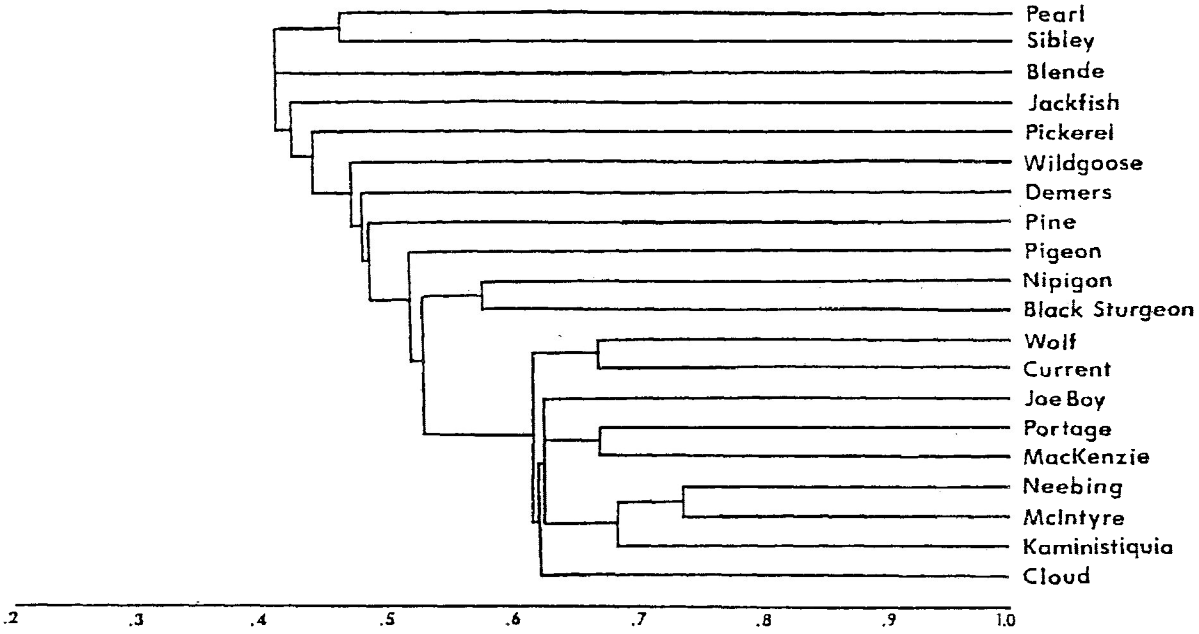

Figure 10: Dendrogram of ichthyofaunal resemblance of 20 rivers in the Thunder Bay area based on a Jaccard's analysis and the single linkage method.

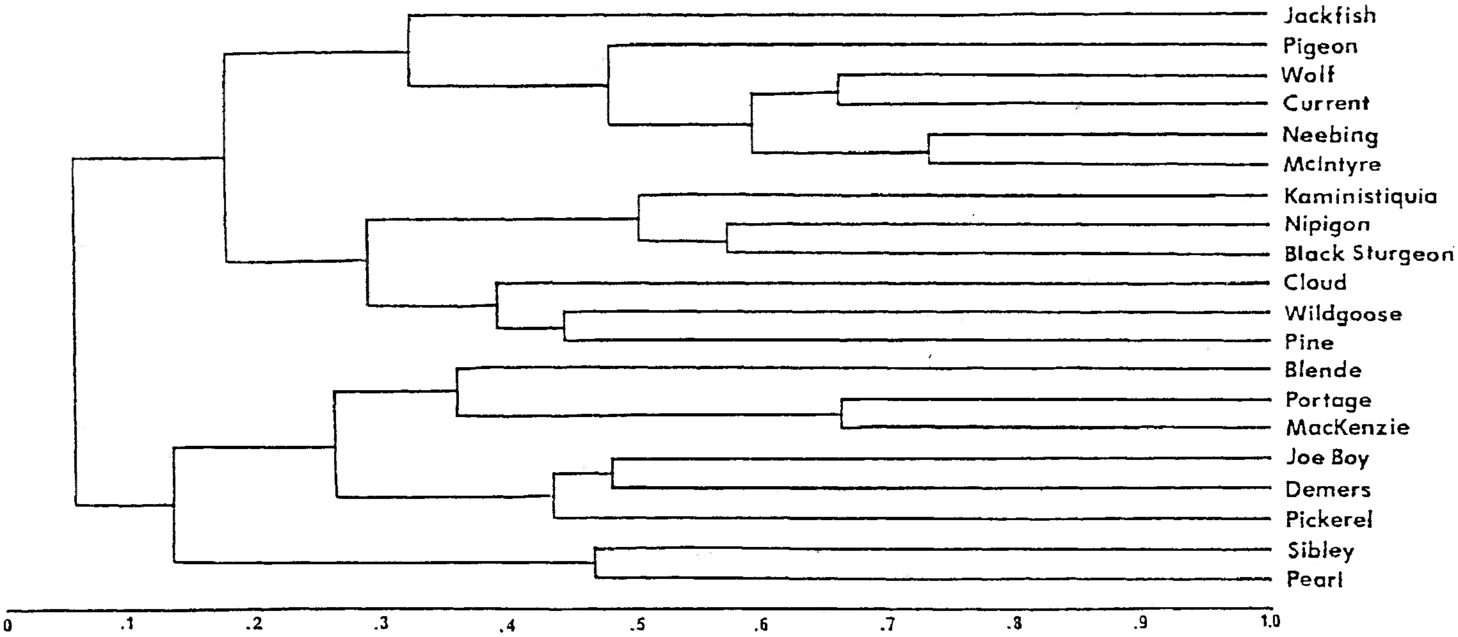

Figure 11: Dendrogram of ichthyofaunal resemblance of 20 rivers in the Thunder Bay area based on a Jaccard's analysis and the complete linkage method.

3. Since there has been a disproportionate amount of sampling on many of these rivers (Table 3), all results are considered tentative.

The single linkage method clustered three rivers within the Kaministiquia basin (Kaministiquia, Neebing and McIntyre) and the Cloud (Fig. 10). The two largest and nearest rivers draining from the north were linked (Nipigon and Black Sturgeon). As well, two of the other southward draining rivers (Current and Wolf) were linked. Two Sibley Peninsula rivers (Portage and Joe Boy) linked with the MacKenzie River draining from the north. Most other linkages seemed to occur whenever additional species were added to rivers.

Complete linkage (Fig. 11) created three broad clusters: large rivers; Sibley rivers; and one miscellaneous grouping. The large river grouping including the Kaministiquia, Nipigon and Black Sturgeon, also included some rather small rivers with depauperate faunas (Pine, Cloud and Wildgoose). The Sibley river grouping (Sibley and Pearl; and Demer's, Pickerel and Joe Boy) also includes two Sibley Peninsula rivers (Blende and Portage) as well as one draining from the north (MacKenzie). The final grouping contains the two most distant rivers (Pigeon and Jackfish), two from the Kaministiquia basin (Neebing and McIntyre) and two draining from the north (Current and Wolf).

Elevation of Lakes and Isostatic Rebound

Table 13 lists the species present in selected lakes of: the Huron and Porcupine Mountains (Hubbs and Lagler, 1949; Doug Nelson, Curator of Ichthyology, UMMZ, pers. comm.); those on Isle Royale (Hubbs and Lagler, 1949); and the Sibley Peninsula. It also includes the estimated heights of these lakes above or below the Minong water plane and their present elevation above Lake Superior. Lakes of the Huron and Porcupine Mountains have fewer species than those of Isle Royale and the Sibley Peninsula. Most of the Huron-Porcupine lakes containing fish have

Table 13: Comparison of fish present on the Sibley Peninsula, Isle Royale and the Huron and Porcupine Mountains.[1]

	Sibley Peninsula			Isle Royale			Huron Mts.		Porcupine Mts.	
Present elevation of lakes above Lake Superior in metres.	19 lakes 4-60.	11 lakes 61-80.	6 lakes 81-109.	26 lakes 3-60.	Desor 72.	Lily 122.	Ives 46.	others 71.-75.	Carp 153.	Little Carp 290.
Estimated elevation above Lake Minong Beach in metres.	-10 - -63	-10 - +14	+14 - +42	-43 - +18	+37	+92	+53	+77-80	+177	+314
Acipenser fulvescens	?	-	-	-	-	-	-	-	-	-
Coregonus artedii[2]	X	X	-	X	X	-	X	X	-	X
Coregonus clupeaformis	-	-		X	X		-	-	-	-
Salvelinus fontinalis[2]	-	?		X	X		X	X	-	X
Salvelinus namaycush	-	-	-	X	-		X	X	-	-
Catostomus commersoni	X	X	X	X	X		-	-	X	X
Catostomus catostomus	-	-	-	-	-		X	X	-	-
Semotilus atromaculatus	-	-	-	X	-		-	-	X	X
Semotilus margarita[2]	X	X	X	X	X		-	-	X	?
Couesius plumbeus	-	X	-	-	X		X	X	-	?
Rhinichthys atratulus		-	-	-	-		-	-	X	X
Rhinichthys cataractae	-	-	-	-		-	-	-	-	-
Phoxinus neogaeus	X	X	X	X		X			X	-
Phoxinus eos	X	X	X	X		-			-	X
Notemigonus crysoleucas	X	-	X	X		-			-	-
Notropis atherinoides	-	-	-	X					-	-
Notropis cornutus	-	-		-					-	?
Notropis hudsonius	X	X		X					X	-
Notopis volucellus	-	-	-	X					-	-
Notropis heterolepis[2]	X	X	X	X					X	
Stizostedion vitreum	-	-	-	X[3]				-	-	-
Pimephales notatus	-	-	-	-		-		X	-	-
Pimephales promelas[2]	X	X	X	X		X		-	X	X
Esox lucius	X	X	X	X		-		-	-	-
Umbra limi	X	-	-	-		-			-	-
Lota lota	-	-	-	X	-			-	-	
Percopsis omiscomaycus	X	X	-	X	X		-	-	X	
Perca flavescens	X	X	X	X	-		X	X	X	
Percina caprodes	X	-	-	X	-		-	-	-	
Etheostoma exile	X	X	X	X	-		-	-	-	-
Lepomis gibbosus	-	-	-	X	-	-		-		-
Culaea inconstans	X	X	X	X	X	X		X		X
Pungitius pungitius	-	-	-	X	X	-		-		X
Cottus cognatus	X	X	-	X	X	-		-		-
Cottus bairdi	-	-		X	-					-
Cottus ricei	-	-	-	X	X	-	-	-	-	-
Total number of species	17-18	15-16	11	27-28	11	3	6	8	10	9-12

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[1] Includes only native species found in lakes.

[2] Includes possible subspecies.

[3] Possible introduction but not out of native range.

? May have been present but reports are unconfirmed and therefore questionable.

a high percentage of what typically constitutes a coldwater fauna. This coldwater fauna is represented by both large and small species (e.g. *Coregonus artedii, Catostomus catostomus, Couesius plumbeus, Pungitius pungitius*). Lower elevation Isle Royale lakes (less than 60.0 m above Lake Superior) have more species (27 -28) than do lakes located at similar heights on the Sibley Peninsula (17 - 18). Isle Royale and the Sibley Peninsula have many species in common (17 - 18). Both areas also contain a few endemic species (Isle Royale = 10 - 11, Sibley Peninsula = 1 - 2) (Discrepancies in numbers due to unverified species reports (Table 13)).

Isle Royale lakes have many large, open water species (e.g. *Salvelinus namaycush, Coregonus clupeaformis, Lota lota*) compared to lakes on the Sibley Peninsula (Table 13). Isle Royale also contains several small coldwater (*Cottus ricei* and *Pungitius pungitius*) and warmwater species (*Lepomis gibbosus* and *Semotilus atromaculatus*) not found on the Sibley Peninsula. This becomes apparent when comparing the species composition of two lakes, one from Isle Royale and the Sibley Peninsula, which are presently found at approximately the same elevation above Lake Superior (72.0 m) (Table 14). Both Pounsford and Desor Lake are relatively deep lakes (+11.0 m) with large surface areas. Pounsford Lake is suspected of lying only 6.0 m above the Lake Minong water plane while Desor is thought to have been over 36.0 m above this same lake level (Hubbs and Lagler, 1949: P. Fralick, Dept. of Geology, Lakehead University, pers. comm.). Desor Lake, on Isle Royale, has a high percentage of large and small coldwater species. Pounsford Lake lacks many of these species and instead possesses several species commonly associated with near shore areas (e.g. *Etheostoma exile*). Isostatic rebound (Farrand and Drexler, 1985) and the lowering of lake levels have since resulted in both lakes being approximately the same elevation

Table 14: Comparison of fish present in Pounsford Lake (Sibley Peninsula) and Desor Lake (Isle Royale).[1]

	Sibley Peninsula	**Isle Royale**
Present elevation of lakes above Lake Superior in metres.	Pounsford 72.7	Desor 72.0
Estimated elevation above Lake Minong Beach in metres.	6.0	36.6
Coregonus artedii	-	X
Coregonus clupeaformis	-	X
Salvelinus fontinalis	-	X
Catostomus commersoni	X	X
Semotilus margarita	-	X
Couesius plumbeus	X	X
Notropis hudsonius	X	-
Notropis heterolepis	X	-
Esox lucius	X	-
Percopsis omiscomaycus	-	X
Perca flavescens	X	-
Etheostoma exile	X	-
Culaea inconstans	X	X
Pungitius pungitius	-	X
Cottus cognatus	X	X
Cottus ricei	-	X
Total number of species	9	11

[1] Includes only native species.

above Lake Superior.

Data of fish collected from Loch Lomond (48^0 15' N, 89^0 20' W) near the City of Thunder Bay (Hartviksen and Momot, 1989; this survey) were used to compare fish distribution among locations found at various heights above Lake Superior. Loch Lomond, a large, oligotrophic lake, has several large, open water species and many smaller fish typically considered coldwater species (e.g. *Pungitius pungitius*, *Couesius plumbeus*) (Table 15). Four species are shared between Loch Lomond and lakes of high elevation on the Sibley Peninsula while twelve species are unique to only one of the two locations. The similarity between Loch Lomond and lakes in the Huron and Porcupine Mountains appears to be mainly due to the presence of coldwater species such as *Salvelinus namaycush* and *Couesius plumbeus*. The present occurrence of these species may be more dependent on the physical shape of the lake basin providing suitable, stable habitat rather than their former accessibility to colonization (although accessibility was initially important).

Table 15: Comparison of fish present on the Sibley Peninsula, Loch Lomond, Isle Royale and the Huron and Porcupine Mountains.[1]

	Sibley	**Loch Lomond**	**Isle Royale**	**Huron Mts.**		**Porcupine Mts.**	
Present elevation of lakes above Lake Superior in metres.	(6 lakes) 81-109.	102.	Lily 122.	Ives 46.	others 71-75.	Carp 153.	Little Carp 290.
Estimated elevation above Lake Minong Beach in metres.	+14-42	+40	+92	+53	+77-80	+177	+314
Salvelinus fontinalis[2]	-	-	-	X	X	-	X
Salvelinus namaycush	-	X	-	X	X	-	-
Coregonus clupeaformis	-	X		-	-	-	-
Coregonus artedii[2]	-	-		X	X	-	X
Catostomus commersoni	X	X		-	-	X	X
Catostomus catostomus	-	-		X	X	-	-
Semotilus atromaculatus	-	-		-	-	X	X
Semotilus margarita	X	-		-	-	X	?
Couesius plumbeus	-	X	-	X	X	-	?
Rhinichthys atratulus	-	-	-	-	-	X	X
Phoxinus neogaeus	X	X	X	-	-	X	-
Phoxinus eos	X	X	-			-	X
Notemigonus crysoleucas	X	-	-			-	-
Notropis cornutus	-	-				-	?
Notropis hudsonius	-					X	-
Notropis heterolepis	X		-		-	X	-
Pimephales notatus	-		-		X	-	-
Pimephales promelas	X	-	X		-	X	X
Esox lucius	X	-	-			-	-
Lota lota	-	X	-			-	-
Percopsis omiscomaycus	-	-		-	-	X	
Perca flavescens	X	-	-	X	X	X	-
Etheostoma exile	X	-	-	-	-	-	-
Culaea inconstans	X	X	X	-	X	-	X
Pungitius pungitius	-	X	-	-	-	-	X
Total number of species	11	9	3	6	8	10	9-12

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[1] Includes only native species found in lakes.

[2] Includes possible subspecies.

? May have been present but reports are unconfirmed and therefore questionable.

DISCUSSION

Distribution of Thunder Bay Area Fishes

Species other than Iowa and johnny darters collected in 1989-90, also revealed peculiarities in distribution. Golden shiners (*Notemigonus crysoleucas*) were collected only on the Sibley Peninsula. Rock bass (*Ambloplites rupestris*), common shiner (*Notropis cornutus*) and creek chub (*Semotilus atromaculatus*) were mainly confined to the Kaministiquia basin and nearby areas. These four species are common in the west, in the Hudson Bay catchment, and areas to the south (Scott and Crossman, 1973). Either currently operative physical or physiological factors or, more likely, a larger historic event influencing distribution (*sensu* Mayden, 1987; 1988), halted the expansion of these four species in the Thunder Bay area and has similarly affected Iowa and johnny darter distribution.

1/ General Distribution of Darters

Previous to this study, it was believed that the presence or absence of darters in the Thunder Bay area could help explain possible recolonization routes. Johnny darters occurred in or near the Kaministiquia basin (Fig. 5). Iowa darters were concentrated on the Sibley Peninsula but were not present in the Kaministiquia basin (Fig. 4). Many lakes immediately north of Thunder Bay also harboured Iowa darters. Both darters were seemingly absent from rivers south of the City of Thunder Bay over a distance of more than 100.0 km (Steven Persons, Minnesota DNR, pers. comm.). Why did darters bypass all these potential habitats if their sole invasion route into this area was from the south?

Except for the Kaministiquia basin, *Etheostoma nigrum* is rarely found in Thunder Bay area Lake Superior tributaries (Hartviksen and Momot, 1989). Previous to this study, johnny darters were not known south or north of the Kaministiquia River mouth marshes (Mission, McKellar and Neebing) except for populations in Boulevard Lake (ROM 19886) and the Current River (ROM 19896) located immediately below it. One johnny darter record within the City of Thunder Bay was not considered (McIntyre River - ROM 16584) due to lack of data on the collection site. Johnny darters were, however, collected here in 1989.

The Current River was temporarily impounded in 1901. In 1909, this impoundment (Boulevard Lake) became a permanent water storage reservoir and local beach (Schlereth, 1980). During winter, Boulevard Lake is subject to complete drawdowns (personal observation). The Boulevard Lake population of johnny darters presently exists at approximately 27.0 m ALS (above Lake Superior) and is separated from Lake Superior by a large set of rapids. It was initially hypothesized that this population of johnny darters arrived when Lake Superior levels were much higher, providing easy access. Johnny darters were expected to be present at lower elevations in three Lake Superior tributaries (McVicars Creek, McIntyre and Neebing rivers) between Boulevard Lake and the Kaministiquia River. Johnny darters were collected in the Neebing River but are not in its headwater lakes (Momot, 1978). The McIntyre River harbours johnny darters but they are absent from its headwaters lakes. In McVicars Creek, johnny darters occurred only near the mouth.

Their presence in Boulevard Lake suggested that johnny darters might be found east of the Current River in lakes or rivers at similar elevations including those on or near the Sibley Peninsula. This was not so. Johnny darters were not captured in any Lake Superior tributary north or east of the Current River. Their first occurrence was on the east side of the Sibley Peninsula. One johnny darter was collected at the mouth of the Portage River and one in Moose Bay on Black Bay. Seven johnny darters were also collected at the mouth of Joe Boy Creek in 1990. Johnny darters were collected in considerable numbers in the lower Wolf River which drains into the north end of Black Bay. Johnny darters were, however, not collected in any lakes or streams above Wolf Lake. Johnny darters are also thought to occur in the lower Black Sturgeon River (B. Hamilton, Thunder Bay OMNR, pers. comm.) draining into Black Bay.

Although johnny darters were collected in Boulevard Lake, these darters were not collected in either branch (east or west) of the Current River that empties into the lake. A single OMNR record exists for a small headwater lake in the western branch of the Current River. It was initially hypothesized that the series of falls that exist in the Current River just north of Boulevard Lake prevented upstream colonization by johnny darters. However, since johnny darters were not collected between Boulevard Lake and this lake, these johnny darters may have arrived in the headwater lake via an alternative route, then moving downstream to Boulevard Lake. Additionally, populations of Iowa darters were collected in headwater lakes of the eastern branches of the Current River. Neither species, however, were collected in the mainstream of the Current River.

Iowa darters were collected from fourteen lakes and six streams on the Sibley Peninsula and are known to occur in at least one other lake (Joe Boy) (Appendix A). Iowa darters were captured in headwater lakes of the two eastern Current River branches (4 lakes in total) and two headwater lakes and a stream draining into the MacKenzie River system. Iowa darters were also collected in one lake that enters Dog Lake (north of the City of Thunder Bay) and in one first order stream draining into the Black Sturgeon River. Records from the ROM show Iowa darters present in two headwater lakes that drain from the west into the Kaministiquia River (ROM 25536 and 16529). These two lakes, Echo and Strange, are near the height of land bordering the Hudson Bay watershed (Winnipeg System).

Iowa darters have reportedly been collected in a large number of lakes west of the City of Thunder Bay, near the height of land bordering the Quetico area (Hartviksen and Momot, 1989). The presence of *Etheostoma exile* in many of these lakes bordering the Winnipeg-English systems could be due to the effects of stream capture or local flooding (discussed below).

The johnny darter is apparently less demanding of specific habitat than other darters (Scott and Crossman, 1973). It has been termed a "pioneer species" quickly establishing itself in disturbed areas (Becker, 1983). Glaciation could render an area suitable for colonization by any "pioneering" species present. The absence of the johnny darter, and other species, from lakes on the Sibley Peninsula, suggests that some species found near the Thunder Bay area are not present on the Peninsula because they could not reach the area immediately following, or since, deglaciation.

2/ Distribution and Consideration of Other Species

I Golden shiner (*Notemigonus crysoleucas*)

One species in the Thunder Bay area known only from the Sibley Peninsula is the golden shiner (Hartviksen and Momot, 1989). Golden shiners were captured in five lakes on the Sibley Peninsula in 1989-90 (Appendix A) and are known only from one other lake in the general area. Crescent Lake (50^0 28' N, 88^0 20' W) is north of and drains into Lake Nipigon via the Little Jackfish River (ROM B). Due to the 1943 Ogoki Diversion (MacKay, 1963), golden shiners may have been introduced into this Lake Nipigon tributary from the Hudson Bay watershed as they were not previously known from this area (Dymond 1926; Scott and Crossman, 1973). Approximately 8,463.0 km^2 of drainage area was diverted to create the Ogoki diversion (Energy, Mines and Resources Canada, 1974). Portions of the diverted area abut the English River catchment; a small part of the Nelson River catchment draining into Hudson Bay. Golden shiners are known from or near the English River system (Lee *et al.*, 1980) but were not captured by Ryder *et al.* (1964) in the Albany River system. Golden shiners may be native to the Albany system but simply not collected by Ryder *et al.* (1964), as was the case with common shiners (see below). Since they are a bait fish (Scott and Crossman, 1973; Schmidt, 1986), fly-in fishermen could introduce them. Such an introduction could not, however, occur on the Sibley Peninsula. The park is closed to aircraft and most lakes are too small for landings by fixed wing aircraft.

Golden shiners are found in the Quetico region (Crossman, 1976). They also occur in lakes west of the City of Thunder Bay near the height of land in the Hudson Bay watershed (Scott and Crossman, 1973; Lee *et al.*, 1980) and reach their northernmost distribution limit in Lake Winnipeg, Manitoba (Keleher, 1956).

Golden shiners on the Sibley Peninsula are known from lakes currently found up to 87.8 m ALS. Hubbs and Lagler (1949) suggested that the presence of golden shiners in ten lakes of low elevation (< 30.8 m ALS) on Isle Royale indicates that they were late colonists to that island. Isobases of isostatic rebound (Farrand and Drexler, 1985) imply that the difference in elevation between former beaches of pro-glacial Lake Minong on both Isle Royale and the Sibley Peninsula should be 30.0 m. The almost 30.0 m difference in elevation between lakes of the Sibley Peninsula and Isle Royale harbouring golden shiners suggests three possibilities: (1) the isobases shown by Farrand and Drexler (1985) are in error by 30.0 m, (2) golden shiners accessed lakes lying 30.0 m above the water plane at their time of arrival to the Sibley Peninsula; or, (3) golden shiners found their way to the Sibley Peninsula long before accessing the lakes of Isle Royale. This could make them late colonists on Isle Royale but earlier colonists on the Sibley Peninsula. The last two possibilities are most likely and I shall return to them later.

II Rock bass (*Ambloplites rupestris*)

Rock bass do not occur on the Sibley Peninsula, in Lake Nipigon (Scott and Crossman, 1973) or in lakes on Isle Royale (Hubbs and Lagler, 1949). Rock bass are, however, very common in the Kaministiquia River (Stephenson, 1989) and Quetico Park (Crossman, 1976). ROM Records show the capture of a single rock bass (ROM 57588) from Loganberry Lake (49^0 22' N, 90^0 10' W), tributary to Lake Nipigon. This record, in a headwater lake tributary to Lake Nipigon, suggests either natural movement, due to the lakes nearness to the height of land, or introduction by man. Rock bass were captured in the Neebing River and some lakes near the Kaministiquia basin in 1989. Maps of rock bass distribution (Lee *et al.*, 1980) suggest rock bass are absent from the area between the McIntyre River in Thunder Bay and the Nipigon River.

Rock bass occur at least as far north as central Lake Winnipeg in Manitoba (Scott and Crossman, 1973). A single rock bass was taken in Lake St. Joseph, the headwaters of the Albany River in Ontario by Ryder *et al.* (1964). The Lake St. Joseph occurrence was suggested as being due to stream capture but could also represent introduction by man. Since 1964, only one other rock bass has been collected in the Albany River drainage (ROM 56868 - Pashkokogan River, 50^0 50' N, 90^0 05' W). The absence of rock bass in distant northern Ontario areas suggests that they may be nearing their limit of physiological (likely thermal) tolerance.

III Creek chub (*Semotilus atromaculatus*)

Contrary to OMNR reports, creek chub have never been captured on or near the Sibley Peninsula but are quite common in the Kaministiquia River (Stephenson, 1989). Creek chub are absent from Lake Nipigon (Scott and Crossman, 1973) and are unknown from Quetico Park (Crossman, 1976). *Semotilus atromaculatus* occur only in Hatchet Lake, Isle Royale which drains northeast into Lake Superior (Hubbs and Lagler, 1949). Hatchet Lake stands 45.0 m ALS. In 1989, large numbers of creek chubs were captured in the east branch of the Current River. Creek chub are common in the Neebing and McIntyre rivers (Hartviksen and Momot, 1989). Distributional maps (Lee *et al.*, 1980) suggest creek chub range at least as far north as central Lake Winnipeg in Manitoba. Keleher (1956) suggested that they reach their northernmost point in North America in that province. Records from ROM and Hartviksen and Momot (1989) suggest creek chub are restricted to the western end of the Thunder Bay region and areas to the south.

IV Common shiner (*Notropis cornutus*)

The common shiner (*Notropis cornutus*) apparently also reaches its' distributional limit in the Thunder Bay area. This species was collected only once in 1989-90 in a Kaministiquia River tributary. The common shiner is somewhat rare in the Kaministiquia River (Stephenson, 1989). Hartviksen and Momot (1989) suggest that common shiner are limited in distribution and are found mainly in Kaministiquia River tributaries and areas to the south of Thunder Bay. Common shiners are "widely distributed" in the Quetico region (Crossman, 1976), absent from Isle Royale (Hubbs and Lagler, 1949) and were not collected in or north of the Albany River by Ryder *et al.* (1964). Since 1964, ROM records show the occurrence of *Notropis cornutus* in both the Albany (ROM 35571 and 39536) and Ogoki (ROM 43516) river drainages. Distributional maps by Lee *et al.* (1980) reveal common shiners to be absent from almost all of the Lake Superior north shore. Common shiner frequently occur in the Red River system in Manitoba (Lee *et al.*, 1980).

V Blacknose dace (*Rhinichthys atratulus*)

In 1989 a single blacknose dace (*Rhinichthys atratulus*) was captured, for the first time, on the Sibley Peninsula in the mouth of the Portage River. Several others were collected at the mouth of Joe Boy Creek in 1990. This species is absent from Lake Nipigon (Scott and Crossman, 1973) and Isle Royale (Hubbs and Lagler, 1949). Records from the ROM show two blacknose dace captured just below Lake Nipigon in the Nipigon River in 1921 (ROM 8154). *Rhinichthys atratulus* is present mainly in the southern portions of Quetico Provincial Park (Crossman, 1976). Blacknose dace are present in the Kaministiquia River (Stephenson, 1989) and were taken in the east branch of the Current River, McVicars Creek and the Neebing and McIntyre rivers in 1989. Blacknose dace are common in streams and rivers south of Thunder Bay (Hartviksen and Momot, 1989). This species was noticeably absent in the area between the Portage and Current rivers except for one capture in MacKenzie Creek.

VI Pumpkinseed (*Lepomis gibbosus*)

Pumpkinseed (*Lepomis gibbosus*) present one of the strangest problems regarding the recolonization of the Lake Superior basin. Pumpkinseed are present in two lakes (Mason and Richie) draining to the southeast at the northeastern end of Isle Royale (Hubbs and Lagler, 1949). Although extremely scarce within the study area (Hartviksen and Momot, 1989), pumpkinseed are somewhat common in the Quetico region (Crossman, 1976). Moore and Braem (1965) suggest that pumpkinseed are limited to south shore Lake Superior tributaries.

3/ Summary of Species Distributions

Since the above species are found in more northerly latitudes than Thunder Bay, factors such as temperature or the number of frost free days likely do not completely govern their distribution within this area. If ecological factors, e.g. competition, physiological tolerances, do not control distribution, then former historic events provide a likely explanation.

The present distribution of the above fishes suggests the idea that all of them colonized the Lake Superior basin from the south and have since moved north. The limited extent to which rock bass, common shiner and creek chub have recolonized this area suggests they are relatively recent arrivals. The capture of blacknose dace on the east side of the Sibley Peninsula and in the Nipigon River suggests arrival to this area at an earlier date. Blacknose dace likely had a greater opportunity for colonization and a greater tolerance to the conditions encountered between Lake Superior tributaries. The concentrated presence of rock bass, common shiner, creek chub and johnny darters in and near the Kaministiquia basin suggests entry into southern Lake Superior at a later time than many other species and, perhaps, some difficulty with colonization.

Stream Capture and Other Methods of Transport

Stream capture is a possible means (especially in headwater areas) as a method of assisting fish recolonization (Burr and Page, 1986). However, this event has never been documented in the Thunder Bay area compared to elsewhere (see Underhill (1957) for an interesting example). While stream capture is occasionally witnessed in other areas, it has likely been an infrequent event in the Thunder Bay area during the past 9000 years.

While stream capture may be the primary means by which upland fishes cross barriers into other watersheds, stream capture, by the standard definitions (Burr and Page, 1986; Conner and Suttkus, 1986), does not seem applicable for this area. Localized flooding provides a better means for interconnecting the low lying areas between most northern Ontario rivers and lakes. Flooding could result in transfers of fish between drainages flowing in either the same or opposite directions. Beaver are widely distributed in the Thunder Bay area and through their activities provide ideal conditions necessary for such events to occur.

Anyone who has lived in areas inhabited by beaver has likely witnessed the, sometimes drastic, changes that can occur when dams are constructed. At least four of the five "lakes" on the "Sleeping Giant" formation found on the Sibley Peninsula are the direct result of the actions by beavers. One lake in the headwaters of Walkinshaw Creek was created solely by the construction of a very large, solid dam. One can easily visualize how a dam, if constructed by chance in the right place, easily backs up a considerable amount of water. This water could flow over a small height of land into another waterbody, thus indirectly aiding in the distribution of fish. Severe spring rains or rapid thawing might also contribute to stream capture by local flooding (Hubbs and Lagler, 1983). However, fortuitously placed beaver dams greatly improve this possibility.

Several lakes now supporting populations of Iowa darters are in the headwaters. Stream capture or flooding provides one means for explaining the distribution of Iowa darter populations in adjacent headwater areas. The preference of Iowa darters for clear, cool water, noted by several authors (Trautman, 1957; Scott and Crossman, 1973), can be met in most headwater areas.

The proximity of the Hudson Bay watershed to Lake Superior tributary border lakes such as Echo and Strange, headwater lakes of the Whitefish River, both of which harbour Iowa darters, suggest the possibility that these populations are the result of stream capture. The same is probably true for the many lakes containing Iowa darters that are found west of the City of Thunder Bay, near the height of land in the Shebandowan area (Hartviksen and Momot, 1989).

A comparison of species present in the small headwater lakes of both the east branch of the Current River and the Walkinshaw Creek (tributary to the MacKenzie River) systems reveals that 7 of 8 species, including the Iowa darter, are common to both. The only species not occurring in both is the northern redbelly dace (*Phoxinus eos*) which, thus far, is found only in the Current River system. While this is not positive proof of stream capture, it suggests that these two systems may have at one time been connected or at least received their present fish fauna at the same time. The presence of the longnose sucker (*Catostomus catostomus*) in both watersheds further adds credence to this theory. The longnose sucker is relatively rare in the Thunder Bay area but is found in large, cool lakes. The low topography of this area could allow for transfers between Kingfisher Lake and a small unnamed lake just north of Walkinshaw Lake at 48^0 39' N, 89^0 04' W.

Darter distribution in the Current and MacKenzie river systems immediately north of Thunder Bay proper may be explained in a variety of ways. One explanation is that Iowa darters travelling north from the St. Croix, bypassed all of the Kaministiquia basin rivers, as well as many rivers to the south, but then gained access into headwater areas of the MacKenzie and/or the east branch of the Current River. This is possible but unlikely. The general low topography of the entire area north of the City of Thunder Bay suggests that many areas were interconnected through localized flooding with areas now draining into the Wolf or Black Sturgeon rivers that hold Iowa darters. The earliest overflows from Lake Agassiz are suspected of entering the Lake Superior basin via the Wolf, Wolfpup and Black Sturgeon spillways (Teller and Thorleifson, 1983) (Fig.3).

Darters on the U.S. side of the north shore of Lake Superior are mostly found in headwater areas (S. Persons, Minnesota DNR, pers. comm.). This suggests the possibility of stream capture from known areas of higher darter concentration. Stream capture is, however, not necessary to explain darter distribution in that area of Lake Superior. The high gradient of many of these streams (Waters, 1977) may restrict darters mainly to headwater areas. Darters may have also arrived in these headwater areas when Lake Superior levels were much higher.

Another man made possibility, hard to qualify at this time, is the construction of many small dams to assist loggers in floating logs out of the bush. The history of logging in the Thunder Bay area goes back to before the turn of the century. Temporary, and generally, unrecorded dams would have been as effective as beaver dams in flooding low lying areas. Remains of these dams still persist in some areas (e.g. Sibley Peninsula) although most have now disintegrated. In heavily logged portions of northwestern Ontario, hundreds of these structures were likely built. After logging, these dams could have persisted for decades in transferring fish before their disintegration.

The possibility of intentional or unintentional introductions of fishes into various waterbodies is one that can in many cases be discounted. The remoteness of most lakes on the Sibley Peninsula, as well as low sport fishing pressure, likely assured "purity" of samples in that area. However, those lakes containing camps and/or alongside roads may be more susceptible to introductions from the release of bait fish by anglers. One such lake is Howcum (48^0 39' N, 89^0 17' W). Howcum Lake is a small lake (8.3 ha) with approximately six camps on it. According to OMNR records (R. Ryder, Thunder Bay OMNR, pers. comm.) a single johnny darter was collected here in 1983. Extensive seining and minnow trapping of this lake in 1989-90 produced only a single young-of-the-year white sucker. Further, another lake (High) of about the same size which drains into

Howcum was also extensively seined and no fish were captured in it. In the case of Howcum Lake, it is possible that some camp owner has tried to "stock" fish with whatever was caught in a minnow trap set in some other lake or released fish from a bait bucket after a days angling. This may have led to the introduction of this darter. However, as darters are seldom used as bait, a more interesting and likely possibility is that Howcum Lake contains (contained?) a relic population of johnny darters. These fish may be present due either to spillover from Dog Lake or from flooding by glacial Lake Kaministikwia. This could also explain how johnny darters arrived in Boulevard Lake in the lower Current River. Rather then moving into only the western branch of the Current River, johnny darters may have instead migrated downstream. In the discriminant analysis (Fig. 9), Boulevard Lake darters more closely resembled those from the western areas (e.g. Little Dog Lake, Quetico) than any from the Kaministiquia basin.

If this record of johnny darters represents a natural population, it becomes notable for two reasons. The first is that it is unlikely johnny darters could overcome the falls in the lower Current River to move upstream. If johnny darters did surmount the falls, why were they not found in both the eastern and western branches of the river? Secondly, the capture of johnny darters in a western, but not an eastern, Current River headwater lake suggests that the Iowa darter populations found in eastern branch headwater areas likely gained access during flooding (stream capture) of nearby areas rather than by upstream migration into only a single branch of the Current River. The presence of johnny darters in Howcum Lake is likely a result of former connection with, or flooding from, Dog Lake which currently holds johnny darters. This explains the occurrence of johnny darters in Boulevard Lake as a result of downstream movement and may further suggest more migrational tendencies than Iowa darters (depending on time of arrival by both species to their present locations).

Factors Controlling the Distribution of Thunder Bay Area Fishes

Thunder Bay and other nearby Lake Superior tributaries provide a diverse array of habitats for a large number of fish species. Large rivers offer more potential habitats for both migratory and resident fish species of all sizes than do smaller rivers. Both large and small rivers in the Thunder Bay area provide habitat that may be suitable, at least seasonally, for migratory, spawning fishes such as rainbow trout (*Oncorhynchus mykiss*), rainbow smelt or carp (*Cyprinus carpio*). Some of these migratory species may utilize these rivers year round for feeding excursions. An examination of the available habitat in these rivers might suggest if this is a limiting factor to fish distribution.

1/ Rivers, Lakes and Available Habitat

At least 25 rivers or streams capable of providing potential habitat for a variety of fishes are found in the area between the mouth of the Portage River on the east side of the Sibley Peninsula and the mouth of the Current River at the north end of the City of Thunder Bay. Compared with other streams or rivers within the city of Thunder Bay (the Neebing, McIntyre, and Current), at least seven of these drainages are similar in terms of available depths, widths or flow rate. Wildgoose, MacKenzie and Blende all drain into Thunder Bay proper while Demer's, Pickerel and Joe Boy drain eastward from the Sibley Peninsula into Black Bay. Sibley Creek drains south from the peninsula directly into Lake Superior. Although some were not intensively sampled in 1989-90, fish were captured in all of these rivers. They ranged from a low of 4 to a high of 19 species per stream (mean=8.7). Several species known to inhabit these rivers were not captured in 1989-90 (Hartviksen and Momot, 1989; SLCC and ROM records) which, if included, increases the mean number of species known to seasonally inhabit these rivers to 13. The remaining 18 streams provide at least temporary habitat for fishes and many are roughly equal in width and flow to McVicars Creek located in the City of Thunder Bay. During 1989, fish were captured in 13 of these 18 streams ranging from a low of 1 to a high of 5 species captured per stream (mean=2.9). Since some species were not collected in the previously mentioned rivers, it is equally likely some species were not captured in these smaller streams during 1989. If so, this could therefore raise the mean number of species inhabiting these smaller streams to approximately 4.

The wide variety of rivers and streams located between the Portage and Current Rivers would seem to provide habitat for darters in at least several locations. Wiley (1981) noted how most species are not found in every locality within their range and suggested that this absence could be due to historical factors or simply that through chance dispersal, they had somehow missed habitats. It is possible for a species to undergo contraction from a larger range but such an event seems very doubtful for either of these darter species.

Page (1983) lists substrate as being among the most important factors controlling darter distribution. Substrates found in the 25 streams and rivers between the Portage and the Current ranged from bedrock to organic muck. Cover ranged from heavily vegetated to total absence. Currents varied from swift to almost standing water and overhead cover varied from dense to minimal which would aid in the development of a variety of thermal regimes. Many of the species normally associated with johnny darters were collected in some of these streams.

Quite possibly some physical or physiological barrier might be keeping darters and some other species from colonizing some of these streams. This supposition is primarily based on the assumption that if fish could move from the site of the present St. Louis River up to Thunder Bay, something must have prevented their movement beyond this area especially when one considers both the time available to accomplish such movement as well as the relatively short distances involved.

Barrier falls of sufficient height to prevent small fish migration presently exist only on the lower reaches of the MacKenzie River and one Sibley Peninsula stream (in which no fish were captured). There is little reason to believe that falls have acted as major barriers. Any fish arriving in this area during higher water levels could have easily surmounted such falls. The presence of johnny darters at the mouths of two Sibley Peninsula streams (Portage and Joe Boy) suggests that johnny darters do move along suitable near shore areas between some rivers. Lower stretches of the remaining six rivers (Pickerel, Demer's, Sibley, Blende, MacKenzie, Wildgoose), many of the smaller streams and areas between them, seem habitable. The possibility of some recent physical or physiological barrier acting to prevent further colonization seems untenable.

2/ The Role of Ecological Factors in Regulating Distribution

I Darters

Darter distribution in the Thunder Bay area provides a clue to their ecological preferences and suggests reasons for segregation prior to and after deglaciation. Almost two-thirds (63%) of the johnny darters captured in 1989-90 occurred in lotic waters. Preferred substrates were mainly sand or sand-rubble. All lotic waters observed were often quite turbid. Johnny darters were not necessarily associated with any kind of aquatic vegetation.

The most common species collected in association with johnny darters were: white sucker (*Catostomus commersoni*) (62%), longnose dace (*Rhinichthys cataractae*) (50%) and mottled sculpin (*Cottus bairdi*) and blacknose dace (*Rhinichthys atratulus*) (both at 38%). As most of the 29 species collected with johnny darters are commonly associated with lotic waters (Scott and Crossman, 1973), this type of association is not unexpected.

Approximately 70% of all Iowa darters captured were taken in lakes during 1989-90. Substrates were usually a mud or mud-sand mixture. Rooted vegetation and/or fallen timber was often present. Water was usually clear although in a few locations darkly stained but never turbid.

The most common species associated with Iowa darters during 1989-90 were yellow perch (*Perca flavescens*) (67%), brook stickleback (*Culaea inconstans*) (49%), blacknose shiner (*Notropis heterolepis*) (40%) and northern pike and white sucker at 35%. The other 26 species captured with Iowa darters occurred at only 30% of the collection sites. Many were found at only 4% of the sites. The common species associated with Iowa darters are lentic and can be found in weedy, slow water areas favoured by Iowa darters (Scott and Crossman, 1973).

Scott and Crossman (1973) reported that Iowa darters might not frequent areas containing northern pike. However, northern pike were collected, or are known to occur, in most lakes or rivers that held Iowa darters (25 out of 37 locations). In several instances, pike had consumed Iowa darters. It does not appear that northern pike regulate the occurrence of Iowa darter populations.

Capture site habitat for both darter species approximates individual species accounts in Scott and Crossman (1973) and Page (1983) among others. The occurrence of these two species was most often associated with their spawning habitat in 1989-90 (Page, 1983) most likely because most darters were captured in early spring, prior to spawning.

Substrate size within two lakes (Pickerel and Little Dog) that produced large numbers of Iowa or johnny darters was measured. Using Attenberg's classification of soil particles (Royce, 1984), both substrates would be classified as fine and coarse sand or silt but Pickerel Lake had a higher percentage of pebbles and cobble. Iowa darter habitat was often, but not always, associated with vegetation and/or woody debris. Johnny darters were often collected over barren sandy areas with little, if any vegetation. In a few instances, johnny darters were collected in rivers containing a rubble substrate. However, as both species were collected in the Nipigon River Lagoon, and both species do occur sympatrically to the west (Crossman, 1976) and south (Becker, 1983) in a variety of habitats, any darter gaining access to an area will likely survive. Similarly, competition between the two species is an unlikely cause for explaining their present disjunct distribution in the Thunder Bay area due to their sympatry in many areas.

Page (1983) noted that darter populations are often clumped. Likely substrate and current preferences play a role, perhaps, a need to stay close to conspecifics is also important. Clumping was noted during the 1989-90 survey. While seining, movement several metres in any direction sometimes resulted in a large increase or decrease in the number of darters captured. This clumping characteristic could be a possible reason for failure to detect darter populations, however I do not feel it is valid because: (1) darters were usually the first species included in any successful seine haul (95% of all seine captures); and (2) darters were usually among the most common species captured in minnow traps (43% of all minnow trap captures). Field experience was sufficient to detect likely darter habitat on sight. All darters in this study were taken at depths less than 1.0 m. The greatest depth of johnny darter capture is recorded as 64.0 m while Iowa darters have not been taken at such depths (Becker, 1983). Present depths around Isle Royale exceed 184.0 m. If clumping is a valid trait, why would a clumped population of darters travel into the depths of Lake Superior to Isle Royale? Neither current, substrate preferences, food availability or a host of other needs and preferences would be satisfied by beginning such a movement. A near shore movement between suitable stream mouths (north or south) is a much more likely method of long distance dispersal.

II Consideration of Other Species

Any species entering the Lake Superior basin by moving north from the St. Croix River, should not display the disjunct distribution noted for several species in this area. Although many lakes or streams were not suitable for a great number of species at the time of their entry into this area, and may remain hostile to them today, some species seem to have deliberately bypassed suitable areas. There is little explanation as to why these areas have not been recently colonized by these same species. It is possible that some of these areas have only very recently become either suitable and accessible or unsuitable. Local extinctions of small populations or the range reduction of certain species is a very real possibility which can never be proved. However, the possibility that conditions have changed sufficiently since the last glacial retreat to completely eliminate all traces of a species once present seems unlikely except in the most extreme cases (the paddlefish again comes to mind, but of course it was never completely eliminated until, perhaps, just recently (Parker, 1988)). Late arriving species to the Thunder Bay area were likely prevented from entering some areas by isostatic rebound and/or falling lake levels. However, the presence of many species in uplifted areas (e.g. golden shiners, Iowa darters), suggests that favourable conditions have existed since their arrival. Their arrival in this area may have been relatively early in the recolonization process.

By examining the elevation of the lakes on the Sibley Peninsula and the species within these lakes, it may be possible to determine if their arrival to the peninsula was late or early in the recolonization process. Any species initially gaining access to high elevation lakes should be present providing that conditions for their physiological maintenance have remained constant. Six lakes on the Sibley Peninsula are currently over 80.0 m ALS (Appendix B). These lakes contain eleven species: *Esox lucius* (two lakes), *Phoxinus eos* (three lakes), *Phoxinus neogaeus* (two lakes), *Notemigonus crysoleucas* (one lake), *Notropis heterolepis* (one lake), *Pimephales promelas* (two lakes), *Semotilus margarita* (two lakes), *Catostomus commersoni* (three lakes), *Culaea inconstans* (five lakes), *Perca flavescens* (one lake) and *Etheostoma exile* (two lakes). These species also occur in lakes of lower elevation. Excluding the possibility of colonization of these lakes long after deglaciation, these species suggest early colonization of the peninsula.

Five species first appear in the ten lakes between 80.0 and 60.0 m ALS. These are: *Coregonus artedii* (one lake), *Notropis hudsonius* (two lakes), *Couesius plumbeus* (one lake), *Percopsis omiscomaycus* (one lake) and *Cottus cognatus* (one lake). All of these species except *Couesius plumbeus* occur in lower elevation lakes. These species may be relatively late arrivals to the peninsula. Physiological requirements of some of these species may limit their present distribution and may have caused the reduction of their former distribution. This may be the case with *Salvelinus fontinalis* which may have naturally occurred in Pass Lake (Table 13) but which is not included at this time.

Species only inhabiting lakes below 60.0 m ALS suggest very late arrival to the peninsula. These species are *Umbra limi* (five lakes) and *Percina caprodes* (three lakes) (*P. caprodes* also occurs only in low elevation lakes on Isle Royale (Hubbs and Lagler, 1949)). Unconfirmed reports suggest that *Acipenser fulvescens* may have inhabited Surprise Lake until only very recently. Surprise Lake is the lowest lake on the peninsula. *Osmerus mordax* may be the most recent colonist of the peninsula but, may have been introduced by man into Surprise Lake. Those fish found only in the peninsula's rivers represent either very late arrivals or are not adapted to life in lakes. Johnny darters fit the previous description.

One fish that may be a relatively recent colonizer to the Thunder Bay area, and therefore worth considering, is the central mudminnow (*Umbra limi*). In this area, the mudminnow is confined mainly to streams and is found in only a very few lakes. The mudminnow is common in lower elevation lakes on the Sibley Peninsula (Appendix A, B). On the Sibley Peninsula, the mudminnow is found in lakes of up to 70.0 m ALS but appears abundant mainly in lakes less than 40.0 m ALS. Although some suggest that the mudminnow has been introduced into the area by anglers or bait dealers (R. Ryder, Thunder Bay OMNR, pers. comm.), the distribution of this fish in some remote areas on the peninsula appears to mimic what would be expected for a naturally invading, but late arriving, species.

The mudminnow does exhibit some disjunct distribution. That is, it appears to be absent from several rivers before being once again captured. However, the small amount of sampling that occurred in the Thunder Bay area prior to their first capture in 1977 (Hartviksen and Momot, 1989) suggests that mudminnows were simply not captured due to lack of effort. Increased sampling effort in some areas will probably show the mudminnow to be more common than once thought. The mudminnow may be the closest example we have of a native species attempting to colonize a new area.

Although the power of dispersal of the mudminnow is certainly greater than that of the johnny darter, there is some similarity evident in the distribution of both species on the Sibley Peninsula. Both species are confined to areas of relatively low elevation. The johnny darter is not as widely distributed as the mudminnow on the peninsula and this is likely due to the darter's more limited power of dispersal. The mudminnow, however, appears to be colonizing the Thunder Bay area from the south whereas the johnny darter, at least on the Sibley Peninsula, appears to be reinvading from the north.

Distribution on Isle Royale

The problem of how a "pond" fish like the pumpkinseed, as well as creek chub and Iowa darter, reached Isle Royale has prompted suggestions of how they may have been brought there. Hubbs and Lagler (1949) stated that they felt none of these fish had been introduced by man to the island which means that natural processes alone would have been responsible. Present depths around the northern and western edges of Isle Royale generally exceed 184.0 m at some point between the island and the mainland. Lake levels at the time immediately following deglaciation may have been much lower making for a much shorter distance and shallower depth for fish to navigate. A lower lake level would allow for more complete funnelling of initial Agassiz overflows arriving from Lake Nipigon into Black Bay and direct it towards Isle Royale. However, even those reduced depths encountered by fish lacking an air bladder and considered to be inhabitants of slow or sluggish water, would still seem prohibitive. A warming trend likely would have had little effect in the depths of Lake Superior. However, as Hubbs and Lagler (1949) pointed out, temperatures encountered within Lake Superior are no worse than those encountered in any other area in which the water freezes during winter. Possibly the creek chub and pumpkinseed arrived while Lake Superior surface temperatures were somewhat warmer. It is hard to visualize (though not impossible) a school of pumpkinseed finding their way across 25.0

km (or more, depending on point of origin) of open water to just one Isle Royale lake. It is harder to imagine a congregation of darters finding their way to that same island while moving along the bottom. However, it becomes somewhat easier to visualize this type of movement if in fact these fish were first given an "assist" i.e. carried by passive transport in the direction of Isle Royale.

It is important to recall the general area in which these unusual fish are found. Without exception, all of the unique inhabitants of Isle Royale are found in only one or two lakes on the northeast end of the island which lies directly south of Black Bay. The possibility exists that some fishes may have been transported to Isle Royale by one of the gigantic surges of water that reportedly escaped from Lake Agassiz approximately 9,500 BP (Farrand and Drexler, 1985). Initial Agassiz discharge is postulated to have been in excess of 100,000 m^3/s over a period of months (Farrand and Drexler, 1985). The Mississippi River, for comparison, has an average discharge of about 20,000 m^3/s (Robison, 1986). In contrast, peak discharge from Lake Missoula, which formed the Channelled Scablands of Washington, is postulated to have been 21,000,000 m^3/s over a period of several hours (Baker, 1983).

The possibility exists of some other western route (Pigeon River area) (Crossman, 1976) providing another source for the origin of some Isle Royale inhabitants. Evidence of large spillways exist in several areas near the Pigeon River at the International border (Zoltai, 1963). However, use of a Pigeon River spillway would likely not deposit fish on the northeast end of Isle Royale unless overflows from that area were also catastrophic.

Lagler and Goldman (1982) commented on the problem of origin of some of the Isle Royale fishes. Several are generally absent from Lake Superior tributaries. Pumpkinseed, and creek chub could have swum the entire distance to Isle Royale. It is possible, although highly improbable, that the Iowa darter population of the island is a result of a rafting event. As Iowa darters usually lay eggs on vegetation (Page, 1983), it is possible that some of this vegetation, with viable eggs attached, floated to Isle Royale although point of origin is still a problem. Problems with point of origin still persist in the case of pumpkinseed and creek chub since they do not lay eggs on vegetation. Both of the Isle Royale lakes (Mason and Richie) harbouring pumpkinseed have elevations less than 30.8 m ALS. Hubbs and Lagler (1949) felt that the elevation of these two lakes suggested that they were among the last to be colonized.

Why are the pumpkinseed and creek chub not found in the area north of Black Bay and the Sibley Peninsula today? Presence is more readily proven than absence and as most of the area north of Black Bay and west of Lake Nipigon is very inaccessible and unsurveyed, perhaps pumpkinseed and creek chub may still be found to exist in isolated pockets. The recent (1973) discovery of black bullheads (*Ictalurus melas*) in the Lake Nipigon area (Hartviksen and Momot, 1989), as well as reported occurrences in other nearby lakes (C. Hartviksen, Lakehead University, pers. comm.), gives some credence to the theory that many species utilized the Agassiz to Superior connection. At this time, however, there is insufficient evidence to suggest the utilization of this route by pumpkinseed and creek chub. One possible explanation for pumpkinseed distribution on Isle Royale is that they simply swam over from the mainland during a later, warmer period (Hubbs and Lagler, 1949). Determining a possible point of origin is difficult as pumpkinseed are uncommon in U.S. Lake Superior tributaries (Hubbs and Lagler, 1949; Moore and Braem, 1965; Lee *et al.*, 1980). However, the larger size of the pumpkinseed does give it greater powers of dispersal than that of the darters and cyprinids. At present, it may be more plausible to suggest pumpkinseed utilized a Pigeon River spillway.

The two Isle Royale lakes inhabited by Iowa darters are less than 30.8 m ALS. This elevation may indicate these fish were also late arrivals to the island. Both of these lakes drain northeast into the same outlet. Creek chub live in one Isle Royale lake approximately 45.0 m ALS. This lake also drains northeast. Its height suggests colonization by creek chub came at an earlier time than colonization by Iowa darters or pumpkinseed. It could also mean that creek chub successfully colonized a lake that remained inaccessible to Iowa darters and pumpkinseed. The second possibility seems more plausible since Underhill (1957) considered both creek chub and Iowa darters to be early colonists of nearby Minnesota. Creek chub may have reached Isle Royale from some Minnesota north shore stream. This, however, seems less likely for Iowa darters and pumpkinseed. The closest Iowa darters to Isle Royale would appear to be those on the Sibley Peninsula while the closest creek chub populations may be those in the Pigeon River. Perhaps creek chub, like pumpkinseed, arrived on Isle Royale while transported down a glacial Pigeon River spillway that flowed towards the island.

The most perplexing question remaining is why small fish (e.g. Iowa darters and golden shiners) took so long to reach Isle Royale since all of them are considered early colonists to Minnesota (Underhill, 1957) and appear to be early colonists of the Sibley Peninsula. Furthermore, what forces might have caused these species, and perhaps pumpkinseed, to arrive on Isle Royale at approximately the same time so as to occur only in low elevation lakes? The most likely possibility is overflow from Lake Agassiz (via Lake Nipigon or, perhaps, the Pigeon River) assisting their transport to the island.

The absence of several species from the Sibley Peninsula suggests that several factors may be operating to prevent access for those fish. These factors, by necessity, can be of only two kinds, ecological or geological. Geological forces have acted mainly in the past and therefore are only presently acting in that some fish recently arriving can not gain access to high elevation lakes either because of barrier falls or steep gradients in the streams draining these lakes. Ecological or physiological factors therefore must presently limit the range expansion of any species. However; as fishes not found on the Sibley Peninsula are, at least presently, located within close proximity, physiological tolerances alone should not be responsible for affecting distribution. The lack of suitable habitat (i.e. streams) between the Blende River and Sibley Creek is a possible but, again, not a likely explanation. Fish colonizing Lake Superior from the south certainly migrated much further on many other occasions to reach the next suitable stream. The absence of some species from the Sibley Peninsula because of their low powers of dispersal or their slow rate of colonization is also not, on its own, an entirely plausible explanation.

The "Agassiz Connection": Effects on Distribution North of Superior

The most widely held theory of recolonization suggests that some fish moved through from Lake Superior into Lake Agassiz. Therefore fishes found in Lake Nipigon and its tributaries are there due to this northwest movement from Lake Superior (Stewart and Lindsey, 1983). Fish postulated to have moved into Lake Superior from Lake Agassiz should be found, in both the Atlantic and Hudson Bay watersheds, in the area west of and including Lake Nipigon. Fish not utilizing this route should be absent in Lake Nipigon and its tributaries. However, fishes that moved from south to north, through the Lake Nipigon connection, would be expected to be found in all Lake Superior tributaries, with minor "leapfrogging" allowed for insufficient habitat, from the southern area of dispersal (St. Croix) to the Black Bay and/or Nipigon Bay areas.

If this theory is incorrect, then fish moving via Lake Agassiz into Lake Superior, from north to south, should be found north of their centres of highest population density with possible (large) gaps between populations. These gaps would be due to populations arriving from the south failing to meet up with those northern populations arriving in Lake Superior. Conversely, late arriving southern fish might be at the limit of their range. Some fishes in the Thunder Bay area have distributions that best reflect this latter example (e.g. rock bass, creek chub).

The question of timing is also of great interest when determining possible recolonization routes. Although the last connection of Lake Agassiz with a drainage into the Mississippi River is postulated to have occurred just prior to the time that outlets to the Nipigon basin were opened (Clayton, 1983; Teller, 1985), exchange of fish fauna has likely occurred between the Mississippi and Hudson Bay drainages since that time (Underhill, 1957; Burr and Page, 1986). Southern outlets from Lake Superior to the Mississippi basin (the Portage and Brule) were likely severed prior to the overflows from Lake Agassiz and may have functioned for the last time during the Marquette re-advance around 9700 BP (Clayton, 1983). The Agassiz overflow into Lake Superior left the basin via the present day St. Mary's river and other nearby channels (Farrand and Drexler, 1985). This suggests that most fishes following the Lake Superior shore from the south must have been or arrived in the Superior basin just before overflows from Agassiz occurred and while the Marquette ice lobes were beginning their retreat. Possibly some fish arrived via the St. Mary's River or earlier outlets in the eastern Superior basin. Therefore, only recent exotics have had less than 9500 years to colonize all areas.

Fishes failing to move through the "Agassiz Connection" may be present in the Hudson Bay watershed, but in general, should be found only south and not immediately westward of Lake Nipigon except for areas to the far west, e.g. Manitoba (Nelson River system). Many species, not found in Lake Nipigon or on the Sibley Peninsula and, at or near their limit of distribution near the City of Thunder Bay, exhibit this pattern (rock bass, creek chub, common shiner) (Keleher, 1956; Scott and Crossman, 1973; Lee *et al.*, 1980). This is a likely result of northward movement towards Thunder Bay from the St. Croix area as well as movement into Lake Agassiz during one of its later stages shortly before it overflowed into Lake Nipigon cutting off its outlet to the Mississippi. If these species were in Lake Agassiz during the time of overflow into the Nipigon basin, they were probably limited to the southern most end of Agassiz which was shallow and possibly very warm (Radforth, 1944; Teller, 1985) and therefore would have provided suitable habitat for their ecological and physiological needs. These species would all be considered "very late colonists" because they missed utilizing the "Agassiz Connection" and do not occur, "naturally", or, have a very limited occurrence, in the Albany, Attiwapiskat, Winisk or Severn drainages of northern Ontario (Ryder *et al.*, 1964; ROM records). Species considered "late colonists" to northwestern Ontario would be found in all or some of the above Ontario rivers but would not be present in Lake Nipigon tributaries due to the establishment of the height of land before their arrival in that area.

The height of land, separating the Hudson Bay and Atlantic watersheds north and west of the Lake Nipigon area, was formed in part by isostatic rebound after removal of the ice dams that permitted Lake Agassiz to flow into lakes Nipigon and Superior. This height of land prevented further entry of fishes or water into the Lake Nipigon basin (Farrand and Drexler, 1985) but allowed Lake Agassiz water flowing eastward to meet with glacial Lake Ojibway (Teller, 1985; Farrand and Drexler, 1985). Species that are suspected of using this route to move further east include the river darter (*Percina shumardi*), the goldeye (*Hiodon alosoides*) (Ryder *et al.*, 1964) and perhaps *Catostomus catostomus* (Crossman and McAllister, 1986). Rock bass may have also utilized this route (Ryder *et al.*, 1964) although this is not necessary to explain their present distribution in northwestern Ontario.

Species moving through Lake Agassiz (Iowa and, at a later time, johnny darters as well as a large number of other species) and into Lake Superior should not exhibit the above pattern. Instead, darters exhibiting disjunctions along the Lake Superior north shore, should be commonly found north of Thunder Bay and the Sibley Peninsula in both Lake Nipigon, its' tributaries and the Hudson Bay watersheds. Many other species suspected of utilizing this "Agassiz Connection" do not exhibit the same disjunctions seen in darter distribution in Lake Superior. This is due to their greater powers of dispersal which has eliminated any initial disjunctions in distribution.

Crossman and McAllister (1986) suggested the possibility of an Agassiz-Barlow-Ojibway connection which they felt explained the eastern and western northern Ontario distribution of several species not present in Lake Superior tributaries. Those fishes, and only those considered to be primary freshwater fish (Brown and Gibson, 1983; Moyle and Cech, 1988), would by my definition be considered "very late colonists" to northern Ontario. Although strong evidence suggests the Agassiz-Barlow-Ojibway connection existed, there is no evidence to suggest that it ever flowed into Lake Superior (Farrand and Drexler, 1985). This explains why some species (such as the river darter) found north of Lake Superior, never entered it. Once the Agassiz connection to Lake Superior closed, late arriving species no longer had access to Lake Superior but could still access areas further north and east. The disjunctions shown by some species in northeastern and northwestern Ontario, e.g. the rock bass, might suggest an arrival from two different areas. The Barlow-Ojibway connection may have nothing to do with their distribution (although the distribution of the goldeye suggests the existence of such a connection). Presumably, the present absence of these species within the area of the Agassiz-Barlow-Ojibway corridor is due to a lack or loss of previous habitat. However, the presence of rock bass in streams tributary to northeastern Lake Superior and in portions of northeastern Ontario suggests the possibility of colonization into these areas via a route which allowed them access to both areas. Rock bass may have achieved their present distribution in the Nipigon Bay area by utilizing a St. Mary's River outlet.

The Role of Physical and Physiological Processes in Recolonization

If Iowa darters, using the Agassiz Connection moved through in advance of johnny darters, what then caused the initial separation of the two species so that only Iowa darters were carried with the initial overflows? Two possibilities, individually or collectively, may have contributed to this initial segregation; physical processes or physiological tolerances.

1/ The Role of Refugia

Perhaps Iowa darters emigrated from a refugium that was not available to johnny darters. The Missouri is postulated as a possible refugium for several cold adapted species including Iowa darters (McPhail and Lindsey, 1970; Crossman and McAllister, 1986). Iowa darters are presently found in the Upper Missouri but johnny darters are absent (Page, 1983). This refugium may have been in contact with developing Lake Agassiz before other refugia came in contact (McPhail and Lindsey, 1970). A Missouri refugium providing early access to Lake

Agassiz would have enabled Iowa darters to reach their present locations in northern Alberta (Page, 1983) before isostatic uplift prevented access to other, later arriving species.

2/ The Role of Temperature

One of the main factors suggested as influencing the present distribution of fishes is temperature (Radforth, 1944: Stauffer *et al.*, 1984). Any temperature preferences or tolerances currently operative must have been equally operative and important during recolonization.

The results of temperature selection trials on both Iowa and johnny darters suggested that Iowa darters prefer cooler temperatures than johnny darters (Fig. 8). The mean temperature selected for johnny darters over a five hour period are higher than the findings of Ingersoll and Claussen (1984). The mean temperature selected by their johnny darters was 22.9^{0}C for summer tests. These fish had been acclimated to 15^{0}C (+/- 1.0^{0}C) for a two to three week period (Ingersoll and Claussen, 1984). In this study, the mean temperature selected for autumn tested johnny darters was 24.2^{0}C after less than a week at 20.0^{0}C (+/- 2.0^{0}C). These differences are likely due to acclimatization. In contrast, the calculated mean temperature selected by Iowa darters in this study was 23.4^{0}C.

In many fish species, younger and smaller individuals exhibit a greater preference or tolerance of higher temperatures (Barans and Tubb, 1973: McCauley and Read, 1973). These findings were upheld in this study. Small individuals of both darter species always sought out temperatures 1-2^{0}C warmer than the larger individuals. The results of temperature trials of small darters were not included in the final analysis.

These tests suggest a preference for cooler temperatures by Iowa darters and could explain early movement into Lake Agassiz.

The Iowa darter has the most northerly distribution of any other darter species (Page, 1983). It has been called a glacial relict (Scott and Crossman, 1973) when found in southern areas. The designation "glacial relict" suggests an affinity for cold water. Such a preference for cooler temperatures would have enabled Iowa darters to follow the retreating ice margins thus gaining early access to far northern regions. Large amounts of silt from glacial runoff may have forced Iowa darters to remain far from the retreating glaciers but yet close enough to be within preferred temperatures. Lake Agassiz was likely becoming quite warm and shallow at its southern most end as it expanded further north (Teller, 1985). An early movement into Lake Agassiz would have allowed Iowa darters to be positioned near the vicinity of the first Agassiz overflows. Additionally, early movement into Lake Agassiz, perhaps to remain within preferred temperatures, would have allowed Iowa darters to reach northerly areas before isostatic rebound halted the northward movement of late arriving species. The removal of ice dams near Lake Nipigon quickly drained much of Lake Agassiz and rapidly increased Lake Superior water levels (Farrand and Drexler, 1985). Such overflows would have carried fish that were quite distant from the site of this initial breach. However, it is mainly those fish in the northern end of the lake that were first carried into Lake Superior. A large influx of warmer water into Lake Superior, still harbouring ice in the eastern basin, likely produced pronounced stratification. The warm water likely helped keep both fish and debris afloat. Fish did not immediately mix and sink into the colder Lake Superior water but were carried upon the top layer. Such an influx of warm water from Lake Agassiz could easily keep darters, and many other species, near the surface until reaching Isle Royale.

A combination of physical location and processes, as well as their physiological tolerances or preferences, likely contributed to earlier access and movement northward into Lake Agassiz by Iowa darters and then, subsequent catastrophic southward movement into Lake Superior.

Meristic Data

1/ Johnny Darters

Underhill (1963) examined variation in squamation among populations of johnny darters in Minnesota and found less than 2% of johnny darters from Lake Superior tributaries were scaled on the nape, breast or cheek. He suggested that this scaly form of johnny darter (then designated *Etheostoma nigrum eulepis*) had not invaded Lake Superior. The highest concentration of this scaly form was collected in the Ottertail River, a tributary of the Red River. The scaly form was absent in the northern border area with Ontario. Underhill (1963) noted that if there was some initial segregation of the two forms, the evidence as to their origin had since been lost. Underhill (1963) suggested that the trinomial designation be dropped as the two forms did not exhibit typical subspecies disjunctions. However, while not advocating the revival of the trinomial, the Kaministiquia basin fish may in fact be the remnant of a once distinct population. The Kaministiquia basin darters do exhibit a distribution that might warrant distinction as a subspecies due to this disjunction. This scaly form may have begun to differentiate during glaciation although the time required for speciation was insufficient. Subsequent mixing of scaled and unscaled populations prevented further continuation of this evolutionary process.

Kott and Humphreys (1978) found only a single specimen from eastern Lake Superior that possessed scaling on the nape. Breast and cheek scaling was totally absent within their Lake Superior sample.

The findings in this study are, in many ways, in direct contrast to most previous findings. Unfortunately, the number of POP pores found on the fish in either study is not available.

Kott and Humphreys (1978) found high lateral line scale counts on the eastern Lake Superior population (mean 50.8), similar to most populations examined in this study. The exceptions to their count are the Nipigon River (mean=54) and Flatrock and Boulevard lakes with mean counts of 49 and 46, respectively (Table 7). Kott and Humphreys (1978) suggested that a character cline exists for lateral line scaling from northwest (high counts) to southwest. However, the counts from Flatrock and Boulevard lakes suggest that their argument for the cline is tenuous.

Kott and Humphreys (1978) give dorsal spine counts (mean=9.0, range 7-10) and dorsal ray counts (mean=11.0, range 10-13) that are in general agreement with values from this study, although the number of dorsal rays in this study is somewhat higher than those of the eastern Lake Superior population (Table 7).

Underhill (1963) did not feel that ecological conditions were responsible for variation in squamation and Lagler and Bailey (1947) demonstrated that the squamation was genetically and not environmentally controlled. If environmental conditions are responsible for the high POP pore counts and scaling on the breast, nape and cheek, it would be expected that at least some portion of the Nipigon, Cloquet or St. Louis River populations would also exhibit these characteristics. The chance expression of some gene controlling these characters is also not a suitable explanation otherwise this phenotype would be expressed in other populations. The high degree of scaling and high POP pores found only in Kaministiquia basin and some Minnesota north shore fish suggests that they form a remnant of a once larger and perhaps more continuous population.

Scott and Crossman (1973) did not consider *Etheostoma nigrum* and *E.*

olmstedi distinct species. Chapleau and Pageau (1985) studied the morphological difference between the two species. Their sample of johnny darters was a compilation of many collections taken from across Canada. They (Chapleau and Pageau, 1985) found a low degree of scaling on the nape and cheek and a mean of 8.22 POP pores in this sample. The amount of squamation seen in Kaministiquia basin darters is much higher than any found by Chapleau and Pageau (1985). The number of POP pores for Kaministiquia basin fish is also higher than their mean. All other populations examined in this study fell far short of this mean (Table 7). Chapleau and Pageau's (1985) data display a bimodal distribution in the number of POP pores with 37.4% of those fish examined having nine pores and 25.5% of those fish examined possessing six pores. The same type of bimodal distribution is exhibited by the fish examined in this study. However, as Chapleau and Pageau (1985) did not break down the characters by region, one can not determine the exact location of those fish possessing a high degree of squamation or a high number of POP pores. It is also impossible to determine if these four characters were found in conjunction as was typical in this study.

2/ Iowa Darters

Few published papers deal with variation in Iowa darters. Gosline's (1949) work is the exception but since the entire sample was derived from only a few parents (the hatchery pond from which the sample was taken had been drained earlier in the year and few of the fish were over 6 months old), this limited the possibility of finding much variation. The number of dorsal rays, dorsal spines and anal rays in Gosline's sample of Michigan fish exceeded all populations examined in this study. The number of scales in the lateral line for all populations examined in this study is higher than those from Michigan. Gosline (1949) suggested fish from coldwater have higher scale counts than those from warmwater. The differences in latitude might explain the differences in high lateral line scale counts of specimens examined in this study.

Character clines (Scott and Crossman, 1973) were not exhibited by any of the Iowa darter populations examined in this study. The central Canada location for this study may make the finding of such clines unlikely.

The inability to create an informative discriminant scatterplot suggests that Iowa darters are not as variable as the johnny darter. However, as DFA did show similarity between those Iowa darters in high elevation lakes on Sibley and areas to the north, and because these populations in turn appeared most similar to those in low elevation lakes on Sibley and those on Isle Royale, it may be that all these populations share a similar origin. Iowa darters from the Nipigon River were most similar to those inhabiting the Quetico region.

Lake Kaministikwia and Possible Western Routes

Fishes entering the Thunder Bay area prior to the Marquette re-advance may have been trapped in the ensuing creation of an impoundment called Lake Kaministikwia. Perhaps some species surviving in this impoundment moved west into Lake Agassiz via this route.

Crossman and McAllister (1986), among others, suggested that fishes moved north and west by utilizing the Agassiz outlet and possibly some other unknown routes. However; there seems to be two major problems with the reasoning that fish used only an east to west Agassiz route. First, the overflow from Agassiz is considered to be catastrophic and, except during the very last stages before flow was cut off, would have been extremely difficult if not impossible for any small fish species to navigate such a flow and overcome the difference in elevation between the two lakes. It is much easier to believe that fish were carried with this overflow rather than swimming against it. Secondly, this theory carries the implication that fishes may have entered the west via this route, but were then extirpated from this northern area due to climatic change. The theory continues that some species utilizing this route now persist only in areas to the south. The assumption that ecological conditions are a primary factor regulating distribution is correct. However; to assume that fish passing through an area following the breach of an ice dam and still very close to retreating glaciers, could now no longer survive in the area (which is likely considerably warmer than it must have been at the time of their arrival) is simply not tenable.

Underhill (1957) originally suggested that the distribution of the finescale dace (*Phoxinus neogaeus*) and the lake chub (*Couesius plumbeus*) was a result of utilization of the Agassiz connection into the west from an eastern refugium although Underhill (1986, 1989) and others (McPhail and Lindsey, 1970; Burr and Page, 1986; Cross *et al.*, 1986) now suggest that refugia for these and other species in the Upper Mississippi or Missouri rivers was a real possibility. Willock (1969) presented evidence for possible areas of movement from a Missouri refugium. The continued acceptance of Upper Mississippi or Missouri refugia allows us to abandon the belief in the use of a Superior to Agassiz connection as a means of explaining the presence of certain species in the west.

That glacial Lake Kaministikwia, or some precursor of it, flowed into Lake Agassiz near the Quetico region is now considered fact (Burwasser, 1977; Farrand and Drexler, 1985). This drainage into Lake Agassiz was caused by the formation or constriction of water between the leading edge of both the Dog and Marks' ice fronts and likely occurred approximately 9,900 BP (Teller and Thorleifson, 1983). As these ice fronts were formed during the Marquette re-advance into the Thunder Bay area, previous to the final overflows from Lake Agassiz, one can assume that, at least for a short time prior to the re-advance, the climate had warmed. During this warm period of glacial retreat, it is possible that some of the "cool water" species now present in this area were present at that time. Some species may have been trapped in Lake Kaministikwia, somehow survived, and moved into Lake Agassiz during this westerly overflow. It is likely that any fish trapped in this lake would have to have been a cold adapted species. It is equally possible, although not as likely, that some species from the Quetico region moved east to find themselves in Lake Kaministikwia. If so, we would expect to find at least some similarity between present day Kaministiquia basin ichthyofauna and that of either the Quetico region or in the Lac des Mille Lac area (site of suspected overflow) if the exchange, in fact, took place. However, there seems to be very little actual similarity between the Kaministiquia basin and areas to the west. The Kaministiquia basin is centrarchid poor (3 compared to Quetico's 8), lacks any ictalurids, the mooneye and both the blackchin shiner (*Notropis heterodon*) and the bluntnose minnow (*Pimephales notatus*) (Crossman, 1976). Lac des Mille Lac does have the bluntnose minnow but lacks most of the centrarchids, the mooneye, the ictalurids and the blackchin shiner (Hartviksen and Momot, 1989). Both Lac des Mille Lac and the Quetico region lack the brook stickleback and although the ninespine stickleback (*Pungitius pungitius*) has been collected in Lac des Mille Lac and is found in the Kaministiquia basin (lower reaches only), ninespine sticklebacks have only recently been collected in the Quetico region (ROM 31166 and this study). This suggests that most of the "unique" fishes found in the Quetico region owe their arrival to the utilization of southern routes via Lake Agassiz or later connections and not to any connection with Lake Kaministikwia. Most of the species common to both areas are suspected of arriving by simultaneous movement into Lake Superior and Lake

Agassiz from the south.

There are few species, due to the ubiquitous distribution of most species in this area, indicating a west to east movement from the Quetico or nearby areas. Presently, only Iowa darters and bluntnose minnows might indicate this type of movement. The bluntnose minnow is common in the Quetico region (Crossman, 1976) and has recently been collected in both Arrow Lake (ROM 30503) and the Arrow River (W. Momot, Lakehead University, pers. comm.) but is otherwise absent in the study area (Lee *et al.*, 1980). Iowa darters are now thought to occur in many of the headwater lakes bordering the Quetico and Lac de Mille Lac region (Hartviksen and Momot, 1989). Crossman (1976) suggested that some fish entered the Quetico area via a route near the Pigeon River. This was suggested by the presence of certain species in only the southeast portion of the park. The Pigeon River route may in fact represent a possible corridor due to the appearance of bluntnose minnows and johnny darters in headwater areas of the Pigeon River (Table 3). This might suggest past routes to the west followed by more recent movement towards the east.

Isostatic Rebound and Species Richness

The elevations of lakes on the Sibley Peninsula are among some of the highest and lowest found in close proximity to Lake Superior. The lake of lowest elevation on the Sibley Peninsula that harbours fish is Surprise Lake. Surprise Lake is less than 4.0 m ALS and less than 150.0 m from Lake Superior and may hold up to 12 species (including Iowa darters). This lake must have recently been separated from Lake Superior and its present ichthyofauna should reflect those species present in the area just prior to, or immediately after, this separation. The collection of rainbow smelt in Surprise Lake in 1990 suggests the possibility of very recent, natural colonization during times of high spring outflow via the single outlet stream.

Norwegian Lake is the highest lake (108.8 m ALS) that holds fish on the Sibley Peninsula and contains at least 5 species (*Catostomus commersoni*, *Esox lucius*, *Culaea inconstans*, *Phoxinus eos* and *Semotilus margarita*). Norwegian Lake is located 9.5 km from the east side of Black Bay and 1.5 km east of Thunder Bay.

Sibley lakes at high elevations would not hold some of the Kaministiquia basin species since these lakes were presumably isolated before colonization of the Kaministiquia basin was completed. However, all lower elevation lakes on the peninsula (e.g. Surprise) as well as the above mentioned rivers or streams (e.g. Wildgoose, Sibley) lacking several of the common Kaministiquia basin species or the Current River species, require an alternative explanation. A wide range of ecological conditions are found in these lakes and streams. As well, many species present on the Sibley Peninsula (e.g. *Pimephales promelas*, *Phoxinus eos*) occur in areas of higher elevations in the Kaministiquia basin and Current River system. The most logical answer is earlier multi-directional arrival of certain species (Iowa darters and golden shiners) to the Sibley Peninsula. Except in the most extreme cases (e.g. barrier falls), barriers operational for some late arriving species have since been removed in most areas.

The absence of both golden shiners and Iowa darters from the Kaministiquia basin suggests that similar factors could have prevented their migration into it. This factor may have been ecological. Judging by their present locations in high elevation lakes on the Sibley Peninsula, access was not a problem. Lake size or depth does not appear to be a factor as both species are found in both the largest and deepest (Marie Louise) as well as one of the smallest and shallowest (Otter) lakes on the peninsula. Both species also occur in riverine habitats on the peninsula. Iowa darters and golden shiners must have arrived when the Sibley Peninsula was free of ice, but likely not yet at its present height above Lake Superior. Lowering of water levels and isostatic rebound (perhaps as much as 50.0 m) have since increased the elevation of these lakes to their present heights. One possibility is that at their time of arrival, the Kaministiquia basin was so turbid from carrying large amounts of runoff from retreating glaciers and increased precipitation, that it was not suitable for either species. The Kaministiquia River becomes very turbid after periods of rain and remains quite turbid, often for up to a week, after a rain storm (personal observation). However, the great variation in riverine habitats available in the Thunder Bay area suggests that ecological factors alone cannot solely control distribution. A physical or some ecological factor is then not a satisfactory solution explaining the absence of Iowa darters from so many Lake Superior tributaries, especially near the City of Thunder Bay.

Since a large number of lakes on Isle Royale contain golden shiners, perhaps these fish were well distributed throughout Lake Superior prior to separation of these lakes from the main body of Lake Superior. Hubbs and Lagler (1949) suggested that their presence in only low elevation lakes suggested a late arrival to the island. Higher elevation lakes on the Sibley Peninsula that hold golden shiners suggest a greater occurrence in certain near-shore areas rather than the open lake. Therefore golden shiners likely arrived on and colonized the Sibley Peninsula long before reaching Isle Royale. When water overflowed from Lake Agassiz, perhaps some golden shiners were transported from this near-shore area. Some of these transported shiners then simply found refuge on Isle Royale.

The small number of lakes on the Sibley Peninsula containing golden shiners, however, suggests that they were never very common in the Thunder Bay area or that their numbers have been greatly reduced since their arrival. The second line of reasoning seems less plausible so we assume that golden shiners colonized only the Sibley Peninsula in the Thunder Bay area. Further survey work in the north may reveal that golden shiners were involved in the Agassiz to Superior connection.

1/ Lakes and Streams Without Fishes on the Sibley Peninsula

In 1989-90, the highest lake on the Sibley Peninsula found to harbour fish was Norwegian Lake with an elevation of 292.0 m ASL (Above Sea Level) or approximately 108.8 m ALS. Lakes which are devoid of fish are perhaps just as interesting as the lakes holding fish. There are several possible explanations for the absence of fish in certain lakes.

Ten of fifteen lakes sampled on the peninsula in 1989-90 found to be devoid of fish lie above Norwegian Lake. Five of these ten lakes are perched on the Sleeping Giant formation at a height exceeding 167.0 m ALS (Appendix C). The remaining five lakes below the height of 108.8 m ALS are probably devoid of fish for a number of reasons. Scum Lake (54.0 m ALS) has been created solely by the building of a beaver dam within a ravine. This "lake" is often drained of water which is suggested by the spring of 1989 washout of the road located below the lake. A 3.0 m barrier falls located above this road regularly prevents fish migration from Marie Louise Lake into Scum Lake. No fish were collected after repeated trapping in the stream above the falls. Temporary and catastrophically altered habitat is the probable reason why only aquatic insects were captured in Scum Lake.

Shale Lake (73.0 m ALS) was slightly over a metre deep June 1, 1989 but was almost dry 3 days later. Only frog larva were captured in this lake and the outlet stream reported to exist was not located.

Ravine Lake (48.0 m ALS) likely suffers anoxia due to insufficient depth and lack of inlets. Only large numbers of amphipods and aquatic beetles were captured. The outlet stream from Ravine Lake was dry in the summer of 1989 and no fish were captured in this stream during 1990 sampling.

Berry Blue Lake (35.0 m ALS) was visited in the fall of 1990 and found to be less than 1.0 m deep. The outlet stream of this lake had dried up. Several attempts to capture fish in this stream in the spring and summer when it was flowing did not result in fish capture.

Verandah Lake (91.0 m ALS) is more puzzling than the other lakes. Depths of up to 2.0 m were encountered and a large food supply (amphipods) exists. It is probable that the depths have not always been sufficient to prevent winter-kill. This was hypothesized by observing the large number of trees that are being submerged at the edge of the lake, perhaps due to the construction of beaver dams. This lake, therefore, likely was once much shallower. Verandah is the largest of these five lakes and has a surface area of 8.1 hectares (OMNR, 1973).

Although it might at first appear that elevation has been the deciding factor as to whether a lake above the elevation of 108.8 m ALS contains fish, it is more likely that in most cases, the physical shape of the lake basin is critical. Without exception, the ten lakes lying above 108.8 m ALS are small (mean=4.0 ha (OMNR, 1973)), relatively shallow (most < 2.0 m average depth), and many are heavily vegetated. Few of these lakes contain inlets which may contribute to low oxygen levels. Fish reportedly have been stocked in some of these lakes although none of these stockings have succeeded (OMNR, Thunder Bay, unpublished reports).

Several of the streams that connect the above mentioned lakes to other lakes containing fish were found to be mere trickles or a series of small unconnected pools by mid July, therefore eliminating the possibility of permanent habitat. Some of these streams also follow steep gradients preventing most upstream movement, even in the spring. Therefore the majority of these lakes are likely to remain devoid of fish.

That fish are not found above 108.8 m ALS is then, disappointing but, not surprising considering the physical characteristics of these lakes. These high elevation Sibley lakes are not directly comparable with those of Isle Royale or the Huron and Porcupine Mountains due to the lack of depths, and corresponding lack of habitat, that accompanies the increase in elevation. Lakes at much higher elevations on Isle Royale contain fish but all of these lakes are much deeper than any on the Sibley Peninsula (see Hubbs and Lagler, 1949, p. 80).

2/ Isostatic Rebound and Basin Morphology

Hubbs and Lagler (1949) suggested that lakes of Isle Royale held more fish due to their being isolated from colonizing fishes much later and less abruptly than lakes in the Huron and Porcupine Mountains. Once the weight of the glaciers had been removed, Isle Royale lakes were slowly elevated as the earth's surface rebounded. Higher lake levels were a function of both increased volumes of water in the Superior basin due to Lake Agassiz overflows and the lower elevation of Isle Royale due to incomplete isostatic rebound at the time of fish colonization. Assuming more fish species were present in the Lake Superior basin during the uplift of Isle Royale meant that there were more potential colonizers available for Isle Royale than were present during colonization of the Huron and Porcupine lakes.

Although the same and even more species might have been available to colonize the Sibley Peninsula, the Marquette advance may have upset this pattern.

Ice may have retreated so fast that uplift occurred quickly. Conversely, ice melt may have been so slow on the peninsula itself that potential colonizers were denied access to some lakes on the peninsula. Another possibility is that the Marquette advance covered the Sibley Peninsula but not all, or perhaps none, of Isle Royale.

Saarnisto (1974) feels that ice marginal features found in the vicinity of Mt. Desor on Isle Royale suggest that at least half of that island was unglaciated and could have been open to colonizing fishes during the Lake Superior Beaver Bay level (pre Minong). Quite possibly, coldwater fish presently found in Desor Lake arrived at this time. This could explain some of the dissimilarity of fauna between Desor Lake and Pounsford Lake on the Sibley Peninsula (Table 13). Eliminating the coldwater forms from Desor Lake results in Pounsford Lake having almost twice as many species. Some warmwater species may have arrived on Isle Royale shortly after glacial retreat by using a Pigeon River spillway which directed them towards Isle Royale.

Comparisons are possible among lakes on the Sibley Peninsula, Isle Royale and nearby Loch Lomond. Loch Lomond (48^0 15' N, 89^0 20' W) is a large, oligotrophic lake located just south of the City of Thunder Bay at an elevation of 102.0 m ALS. Table 14, compares species richness in high elevation lakes of the Sibley Peninsula, Isle Royale, the Huron and Porcupine Mountains and Loch Lomond. Depth of the lake basin is likely the most important factor in determining both the numbers and types of species present. These deep basin lakes are necessary for the continued survival of most of these large, pelagic species.

Eliminating large, open water species and those that are typically cold water species reveals that Isle Royale and the Sibley Peninsula have a more similar number of species in their lower elevation lakes. The low elevation lakes, less than 60.0 m ALS, are represented by 26 lakes on Isle Royale and 19 on the Sibley Peninsula. Removing coldwater species and adjusting for the number of lakes suggests the Sibley Peninsula lakes actually contain more species than Isle Royale. The presence of coldwater species (e.g. lake trout, lake whitefish (*Coregonus clupeaformis*)) on Isle Royale suggests that the lack of deep basins on the Sibley Peninsula has resulted in the extirpation of any previous populations of these fishes from lakes on the peninsula. Removing the coldwater species from lakes in the Huron and Porcupine Mountains and Loch Lomond would almost completely eliminate their ichthyofauna.

Jaccard's Analysis of Rivers

The Jaccard's analysis, using the single linkage method (Fig. 10), suggests a certain affinity exits among rivers within the Kaministiquia basin. This suggests that Kaministiquia basin rivers, and those to the south, resemble each other perhaps because their present inhabitants had a common source. The inclusion of two Sibley rivers and three rivers draining from the north into the grouping of Kaministiquia basin rivers suggests colonization from both the north and south, due in part to the process of stream capture or local flooding. The similarity of the Sibley rivers to the Kaministiquia grouping is mostly because the Sibley list includes some species collected only near their mouths. The similarity of the Nipigon and Black Sturgeon rivers is likely due to their northern drainage and the acquisition of their fauna from a common source. Much of the complete linkage dendrogram appears to join rivers upon removal of species. The last few rivers to link up are among the most depauperate.

The complete linkage method produces two very broad groupings (Fig. 11). One group consists almost entirely of rivers on the Sibley Peninsula and may be interpreted as denoting a common source of origin. The other group can be broken down into two smaller groups. Large rivers join with those on the east side of the Sibley Peninsula. Kaministiquia basin rivers join with those that, at least in the lower reaches, contain some species found in the Kaministiquia basin rivers. Large rivers likely join because they contain diverse habitats and so harbour a large number of species (see Eadie *et al.*, 1986).

Increased sampling effort on some of these rivers (Table 3) will likely increase the number of species present and therefore no doubt change the results of these analyses. These results are therefore tentative. Likewise, including all species known to inhabit a watershed would greatly change the groupings and perhaps create more confusion in interpreting the results. Some rivers (e.g. Wolf, Current) only possess Kaministiquia basin fish (e.g. *Ambloplites rupestris*, *Semotilus atromaculatus*, or *Etheostoma nigrum*) in their lower reaches but then possess "Sibley" type species (e.g. *Etheostoma exile*) in their upper reaches. Probable colonization from both the south and north, as well as possible flooding in many areas, does suggest that mainly it is those rivers in and south of the Kaministiquia basin that will remain clustered.

Some of the species considered in the analysis may not be native to this area of Ontario. Specifically, the smallmouth bass and the black crappie (*Pomoxis nigromaculatus*) were included as, but may in fact not be, native. Dymond (1926) suggested that smallmouth bass were native to the area. Scott and Crossman (1973) suggested that black crappie arrived in Lake Superior due to migration following introduction to a nearby lake. However, the original report (OMNR, Thunder Bay, unpublished) detailing the 1949 black crappie stocking into a Sibley Peninsula lake (see Appendix A), suggests that the likelihood of survival of any of these fish was minimal after their release (e.g. 35 fish released (sex unknown), several died during transport and upon release, truck breakdown, delays at border, October introduction, carried in "buckets" for 2.0 km, none collected or seen during survey the following year). Movement into Lake Superior and successful colonization of that lake is highly doubtful from this stocking. The exclusion of these two species could have altered the final analysis. However, as there seemed to be little proof concerning their introduction in this area, it was decided to include both species as native.

While it is certainly true that some rivers afford varying amounts of habitat to different species, Kaministiquia basin rivers and those to the south often clustered even though they possess many different habitats. This clustering is therefore based on faunal resemblance and not habitat diversity. Similarly, the clustering of Sibley Peninsula rivers seems to be due to faunal similarity, and, perhaps, origin, as many of these rivers offer very diverse habitats.

Possible Theories Explaining Colonization

The present disjunctions in the distribution of the johnny and Iowa darters in the Thunder Bay area is likely due to some factor that has also prevented further colonization. Utilizing available data as well as additional information gathered during 1989-90, I believe the distribution of many species in this and nearby areas can not be solely due to ecological or physiological factors. While some segregation can be attributed to preference for or tolerance of physical and physiological factors, glacial activity is the most overwhelming event shaping present distributions.

While the exact sequence of ice re-advancement and subsequent deglaciation remains conjectural, one of several of the following possibilities may in fact represent the true sequence of these events.

1/ The first possibility is that johnny darters and several other species now limited in distribution, may have recolonized the Thunder Bay area prior to the Marquette re-advance. These species probably came from the south (Mississippi refugium) through the St. Croix drainage, perhaps via the Brule or Portage outlets. The Marquette re-advance forced these fish into the Kaministiquia basin and the advancing ice reached the Marks Moraine. Some fish survived in the impounded water (likely cold hardy species). This might explain why johnny darters are found in the Kaministiquia basin and are largely absent to the south and in Sibley Peninsula lakes. Johnny darters initially invading this area were the scaly form with high POP pore counts. These fish may have been part of a larger population, undergoing speciation during the Wisconsin glaciations and occupying an unknown area near the ice margins. Iowa darters arrived on the Sibley Peninsula through one of the first overflows coming east from Lake Agassiz. These first overflows(?) from Lake Agassiz entered present day Lake Superior near what is now Black Bay by utilizing the Wolf, Wolfpup, Shillabeer and Black Sturgeon spillways (Farrand and Drexler, 1985). These overflows occurred as ice retreated northeast from low lying areas. Water temperatures near this ice dam were cool but, most of the Agassiz influx was warmer. Since Iowa darters prefer clear and tolerate cool water headwater areas, they were one of the first species swept into the area as they occupied northerly portions of Lake Agassiz (compared to many other species). Their preference or tolerance for cooler waters, as indicated in this study, and presence in the Missouri refugium not occupied by johnny darters, assured the initial separation of Iowa from johnny darters. As Iowa darters occupied areas near the retreating ice margin, they were probably deposited on or near the Sibley peninsula during the first Agassiz overflows. The enormous discharge from these Lake Agassiz overflows probably swept Iowa darters past the Sibley Peninsula and directly out to Isle Royale. The introduction of vast quantities of warmer water into Lake Superior, still occupied by retreating ice in the eastern basin, probably resulted in thermal stratification. Many species would have been buoyed by this warmer water. Other species present (e.g. golden shiners) may also have been carried out to Isle Royale at this time. This hypothesis explains the presence of Iowa darters in the general area north of the Sibley Peninsula and their absence in the Kaministiquia basin. Johnny darters were also swept through in this manner, but at a later date. Water levels fell in Lake Superior due to progressively reduced flows coming from Lake Agassiz and the opening of eastern Lake Superior outlets. The accompanying isostatic rebound, then prevented johnny darters from reaching high elevations on the Sibley Peninsula and nearby areas.

2/ The second possibility is similar to the first except in this case re-advancing ice eliminated all fish in the Thunder Bay area except for large, open water species. Recolonizing fish would then have to regain access to the present day Kaministiquia basin while Thunder Bay and part or all of the Sibley Peninsula was ice covered. Most fish species presently found in the Thunder Bay area arrived via a southern route near the site of the present St. Louis River. Iowa darters are suspected of arriving in this area through the previously mentioned Lake Agassiz outlet.

3/ A third possibility finds Iowa darters invading the Thunder Bay area from the south prior to johnny darters. This early invasion gave them access to lakes on the Sibley Peninsula and the headwater lakes of the Current and MacKenzie River systems during higher water stages. Johnny darters, arriving from the south at a much later time, were denied access to the Sibley Peninsula and many headwater areas due to falling water levels. Unfortunately, this hypothesis can not explain why johnny darters are not found in any lakes on the Sibley Peninsula or why Iowa darters are not found in any tributaries to the Kaministiquia River or other drainages in the Kaministiquia basin. While this theory would agree with all reinvasion theories to date, it requires three dramatic events to separate these darters. First, Iowa darters had to move north well in advance of johnny darters in order to gain access to many rivers and lakes. This required initial segregation on the basis of (likely) physiological preferences. Second, Iowa darters must either be denied access to the Kaministiquia River basin area (due to some unknown physical (e.g. turbidity?) or physiological barriers (e.g. temperature)) or be displaced by another means at a later time. Factors such as competition with other species seems unlikely. Third, either johnny darters had to advance into Lake Superior from both the St. Croix and the St. Mary's River, continuing upward to their present locations, or they somehow had to move from the lower Current to the lower Wolf River but fail to establish themselves in any stream or river located between these two points. This again raises even more questions. This hypothesis is least likely unless some unknown ecological factors greatly influenced darter distribution in this area.

4/ This theory suggests that Iowa darters prefer cooler waters than johnny darters and, gaining earlier access to Lake Agassiz, were always found nearer the retreating glaciers. Johnny darters, adapted to more turbid waters (Becker, 1983) but, limited by temperature preference, lagged further behind the advance of the Iowa darters, perhaps occurring only in the southernmost portions of Lake Agassiz. Since Iowa darters do not presently inhabit the St. Louis River (Schram *et al.*, 1986) (perhaps due to recent habitat loss), Iowa darters may have moved mainly into Lake Agassiz rather than the St Croix River. If they were in the area, they may have been prevented from accessing early Lake Superior at this time since flow from the north was from Lake Agassiz rather than through the Brule or Portage outlets of Lake Superior. The more northerly and westerly distribution exhibited by the Iowa darter (Page, 1983) supports this theory. If Iowa darters were early immigrants into Lake Agassiz, they could reach areas not accessible to later arriving species because of isostatic uplift. Advancing Marquette ice likely eliminated all fish in the Thunder Bay area and much of the Superior basin (excluding large, open water fish e.g. lake trout and lake herring). As ice retreated, fish moved into the Thunder Bay area from the south but, since Iowa darters were not in the St. Croix (as they are presently absent), or at best only in limited numbers, they did not colonize the Thunder Bay area from the south. During this earliest invasion of Lake Superior from the south, the scaly form of johnny darter now living in the Kaministiquia basin moved northward (although they may have survived the Marquette advance in Lake Kaministikwia). Overflows from Lake Agassiz carried some of the fish species nearest the northern end of the lake: e.g. Iowa darters. These were then deposited on the Sibley Peninsula and perhaps as far south as Isle Royale. The influx of large amounts of warmer water from a large and shallow Lake Agassiz into a very deep, cold lake still containing ice in the east basin, would have resulted in thermal stratification. Some fish and much debris would have been buoyed up and carried for great distances by this warmer water. Much later subsequent Lake Agassiz overflows likely carried johnny darters (as well as several other warmer water species (black bullheads?)) that originally moved north from their Mississippi refugium. By this time, reduced overflows discharged from Lake Nipigon via, or near, the Nipigon River (Farrand and Drexler, 1985). However, these lesser and later overflows from Lake Agassiz would likely not have introduced johnny darters into Lake Superior at a quick rate. Overflows via the Armstrong or Pikitigushi spillways (Fig. 3) from Agassiz would have to have flowed almost 90.0 km before entering the Nipigon River. Due to the expanding size of Lake Nipigon, the initial surge of these overflows would have been dissipated over a broad area and perhaps not carried items afloat for any length of time. Johnny darters may have had to actively migrate from the north end of Lake Nipigon before reaching access to Lake Superior via the Nipigon River. This event deposited johnny darters far from the Sibley Peninsula. Most lakes on the Sibley Peninsula were, by now, cut off from johnny darter invasion due to isostatic uplift as well as reduced water volumes. The continued absence of johnny darters from the upper Wolf River system is due to their failure to reach the Wolf River spillway while it was operational.

This theory is the most tenable because; 1/ it allows for initial segregation of Iowa and johnny darters on the basis of presently suspected physical refugia and physiological preferences. It explains the presence of only Iowa darters near the area of the first overflows from Lake Agassiz and allows them access to the higher lakes of the Sibley Peninsula; 2/ it explains why both darters are present in some U.S. north shore streams without having to employ stream capture as a mechanism (although stream capture is a possibility); 3/ it explains the presence of both species in Lake Nipigon and northern Ontario; 4/ it suggests how some fish species reached Isle Royale; 5/ it explains that the northern and western distribution of Iowa darters was due to their gaining early access to Lake Agassiz; and 6/ suggests that the scaly form of johnny darter has persisted in the Kaministiquia basin due to that population being relatively free of large immigrations of later arriving, unscaled, johnny darters which therefore prevented gene "swamping".

While not totally discounting the possibility of western movement by some fish (mainly larger species) through Agassiz outlets, many species are now believed to have arrived in the Superior basin via these outlets (Fig. 12). Several species, notably the Iowa and johnny darter, likely used multiple routes to invade Superior. Isle Royale was most likely colonized by the coldwater forms found throughout Lake Superior as well as species introduced to the area by Agassiz overflows through the Nipigon basin and, perhaps, via Pigeon River.

Areas for Further Study

This study has pointed out many areas for further study or concern. They are;

1/ To understand fish distribution in this area, a larger survey effort must be expended to determine exact species locations. Once completed, then we can set about finding why species exist where they do. One particularly promising area lies west of Lake Nipigon, in both the Atlantic and Hudson Bay drainages, where Lake Agassiz overflows are postulated to have occurred. Survey work in this area could certainly help in proving or disproving the theories presented above.

2/ The proportion of survey work allotted to large or "sport" fish greatly exceeds that allotted to smaller or "non sport" species, particularly in the Thunder Bay area. We must include surveys of the more abundant small species (minnows and darters) to determine physical preferences and physiological tolerances if we are to determine what presently limits their distribution. Many questions could be asked pertaining to the distribution of creek chub, rock bass and common shiner. Are these three species at their limit of physiological tolerance so far as temperature (or some other factor) is concerned? I believe the answer is no due to more northern distribution in other areas but, as of this

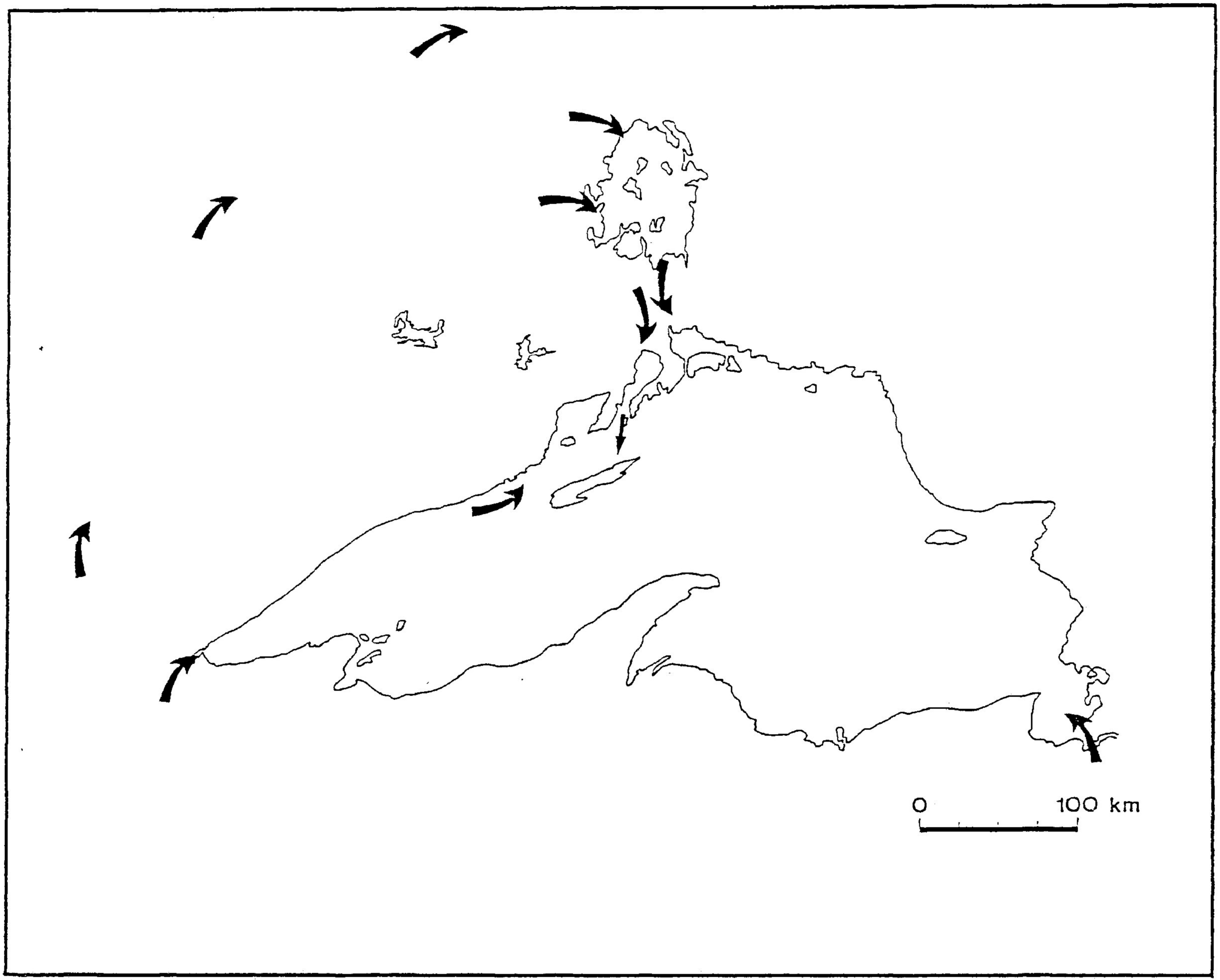

Figure 12: Revised interpretation of routes utilized by fish recolonizing the Lake Superior basin.

time, the answer remains unknown.

3/ Closely coupled with number 2 is the possibility of further study into geographic variation. Do creek chub or rock bass in the Quetico region or in Manitoba differ from those found in the Kaministiquia basin? Do the creek chub of Isle Royale more closely resemble those of the Current River or the Pigeon River? Electrophoresis or mitochondrial DNA studies would be very interesting and could help explain the origin of some of these populations, however; the more traditional meristic techniques (such as utilized in this study) should not be ignored or abandoned.

What of the scaly johnny darter? What is its' total distribution pattern? Does (did) it occur in Manitoba (former Lake Agassiz) or is it limited to areas near Lake Superior and other large lakes? What are the possible reasons for the great variation in the number of preoperculomandibular pores in the johnny darter? Do the clines for Iowa darters really exist?

4/ More geological field work is needed, especially in the Black Bay area. The Bay has many interesting, unexplained hydrologic features. The same is true of the Black Bay Peninsula. Work on both of these areas may shed further light on overflows from Lake Agassiz as well as more information on the Marquette re-advance.

5/ Although fishing is generally the only type of resource extraction permitted within Ontario Provincial Parks, this type of resource can be easily upset by the thoughtless introduction of new species into a waterbody. The fish survey of Sleeping Giant Provincial Park pointed out several populations of fish unique to this area (e.g. golden shiner) and they should be protected from bait bucket introductions. Therefore I propose that a live bait ban be implemented within Provincial Parks to prevent future introductions. Rainbow smelt should be banned as bait as it already has been within Quetico Provincial Park. The occurrence of smelt in two lakes on the Sibley Peninsula (Pass and Surprise) are likely due to introduction by thoughtless anglers or smelt fishermen.

6/ The golden shiner has a very limited distribution in the Thunder Bay area, occurring only within five lakes on the Sibley Peninsula. As it is a rare species, the lakes in which it occurs should not be subjected to the introduction of game fish as they may harm these unique populations. As these populations appear to be the result of natural processes, they should be preserved and protected due to their uniqueness.

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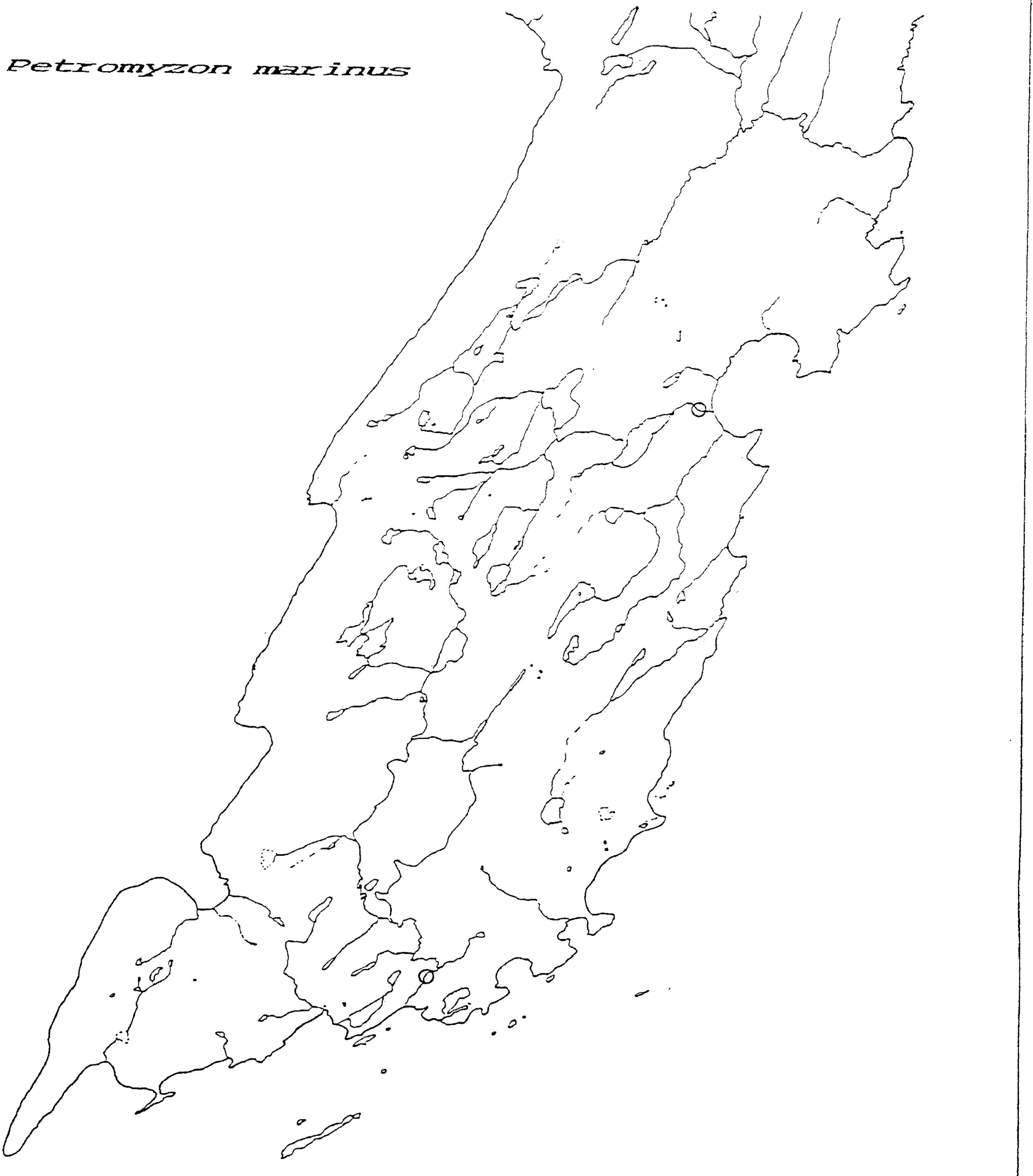
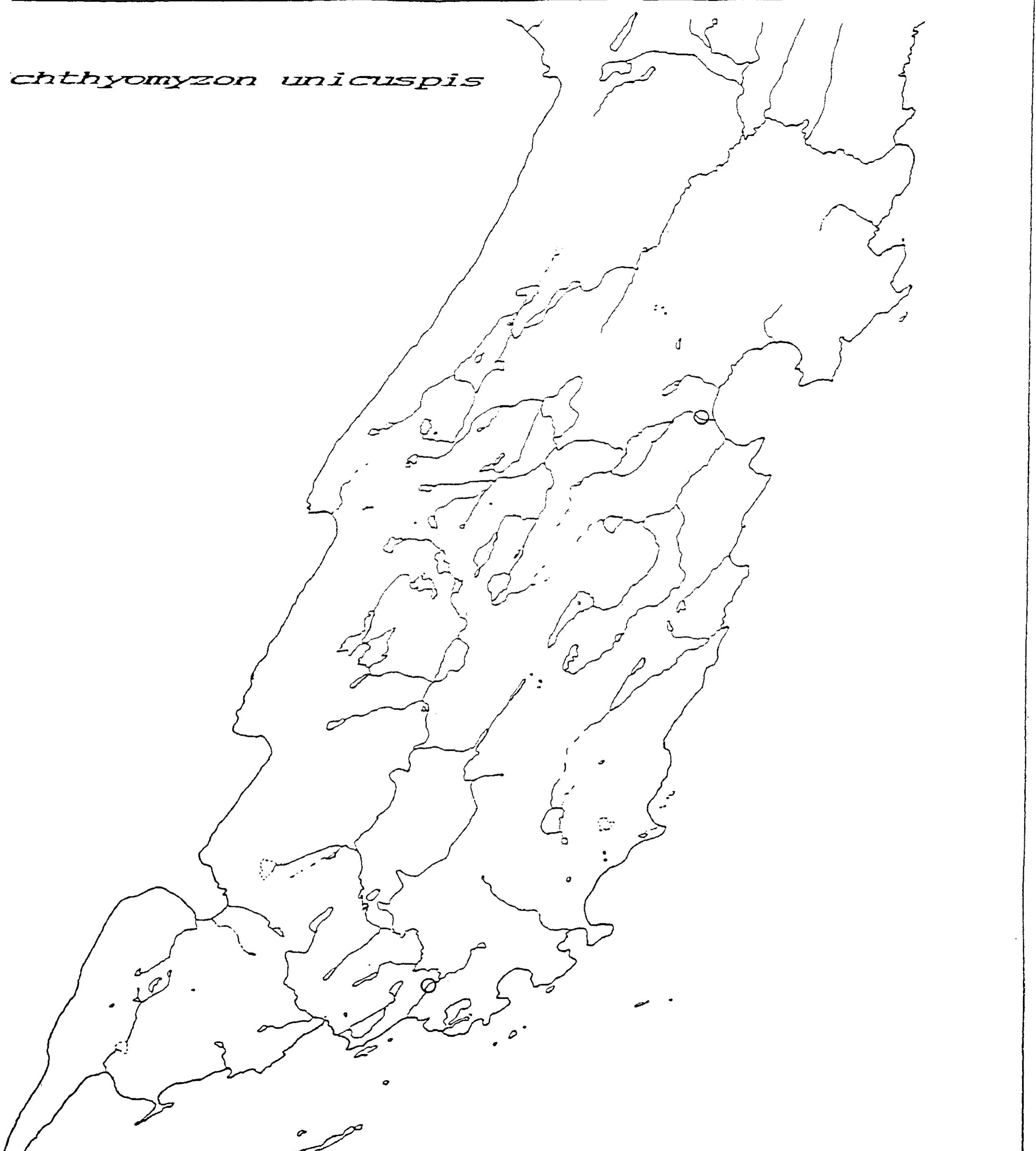
APPENDICES

APPENDIX A

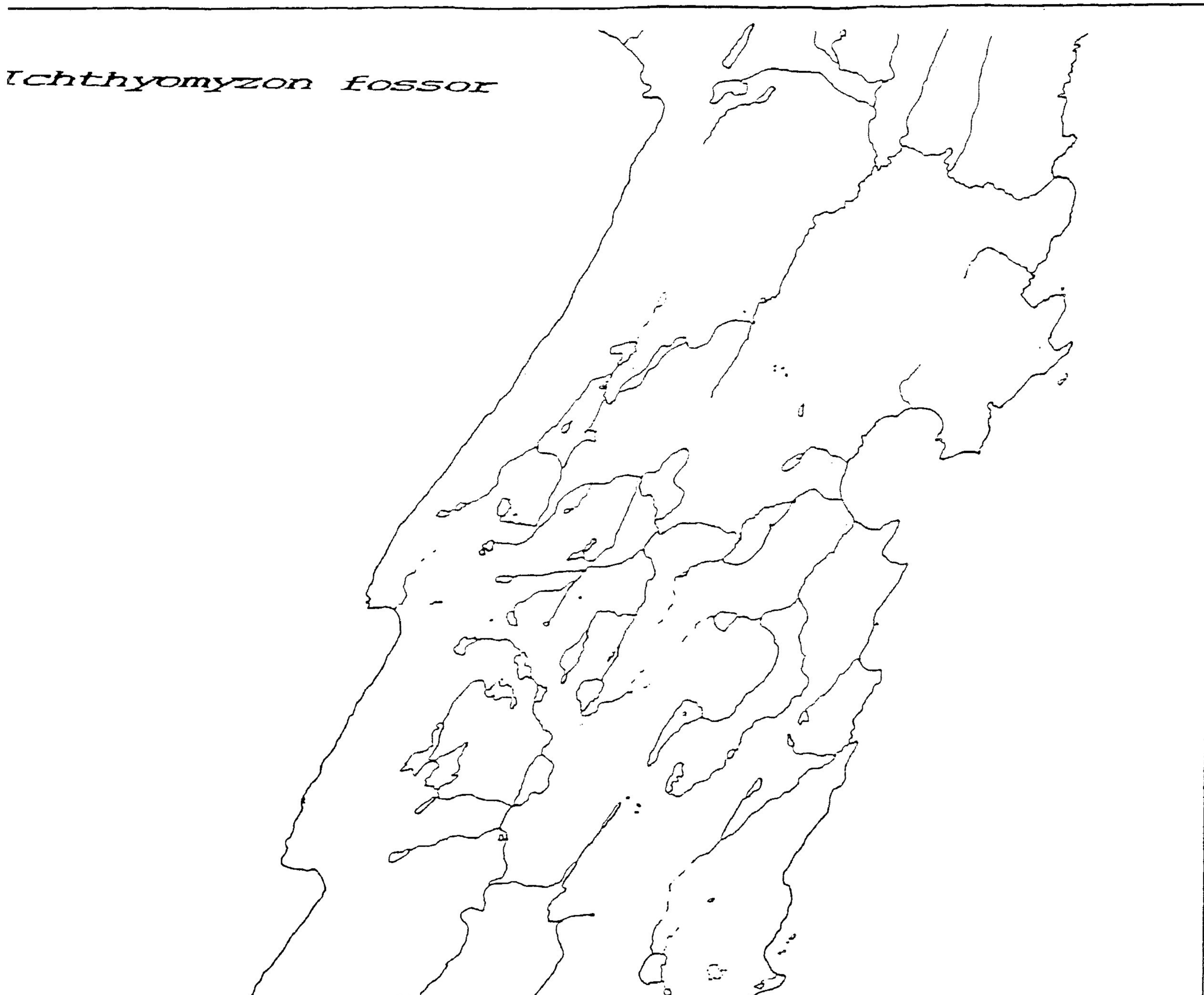
Throughout the distributional maps on the following pages, solid dots denote collections made during 1989-90. These fish are preserved in the Lakehead University collections or have been forwarded to the Royal Ontario Museum (ROM). Hollow dots are historic records and all 1989-90 captures have superceded any previous historic record. Historic records are based on ROM records, other collections housed at Lakehead University, records from the Sea Lamprey Control Centre (SLCC) in Sault Ste. Marie, Ontario, or based on records from surveys and stockings carried out by the Ontario Ministry of Natural Resources (OMNR) (some of which have been ROM verified). Some of the records from SLCC or OMNR may be incorrect and there is no way of verifying them now as the fish were never deposited in any collections. However, I have deleted any grossly conspicuous errors in identification (e.g. creek chub) and ignored identifications that were too ambiguous (e.g. did "bullhead" mean *Ictalurus* sp. or *Cottus* sp.?). Appendix B lists only lake records and, therefore, the origin of stream records shown on the distributional maps is not recorded here.

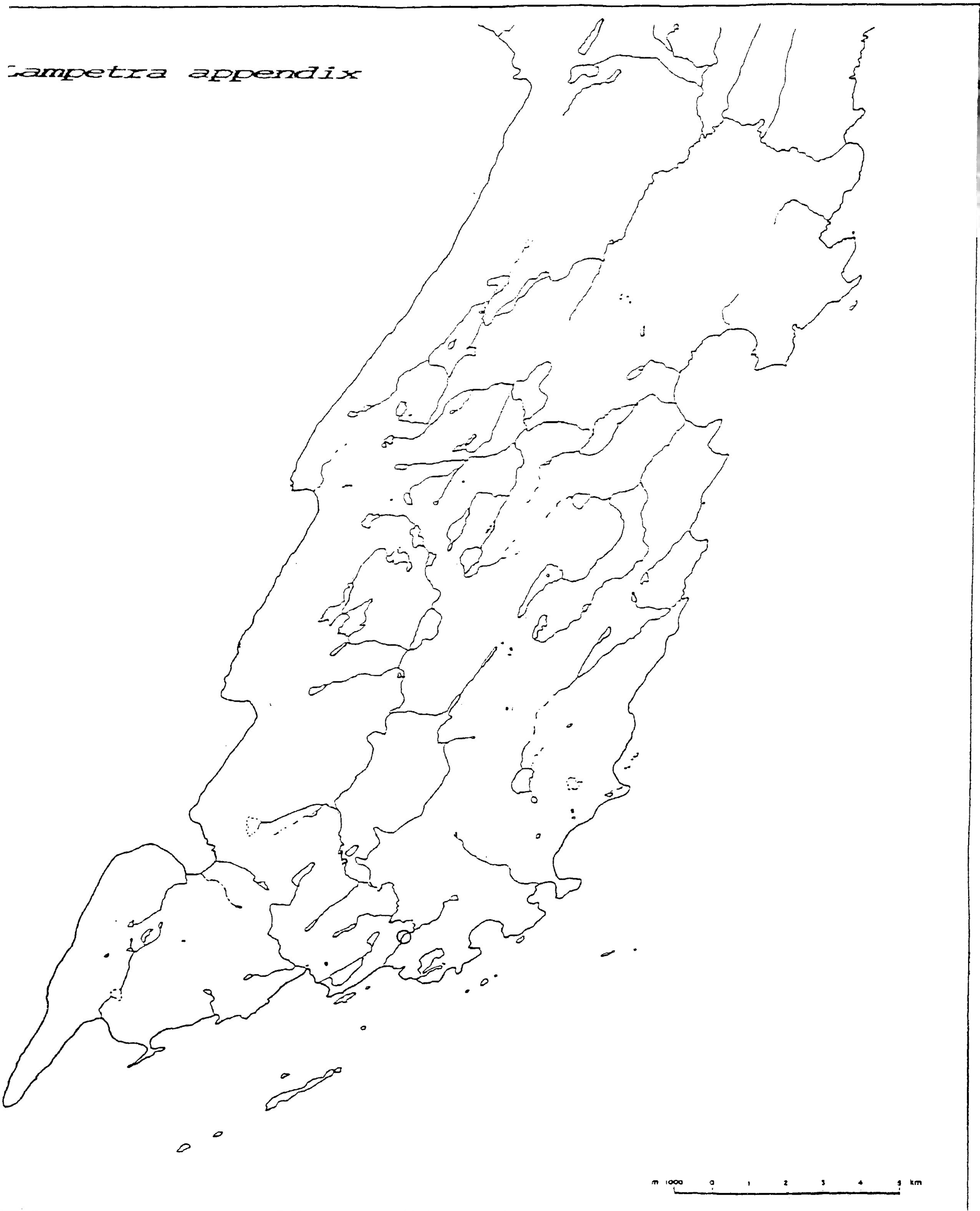
Petromyzon marinus





chthyomyzon unicuspis

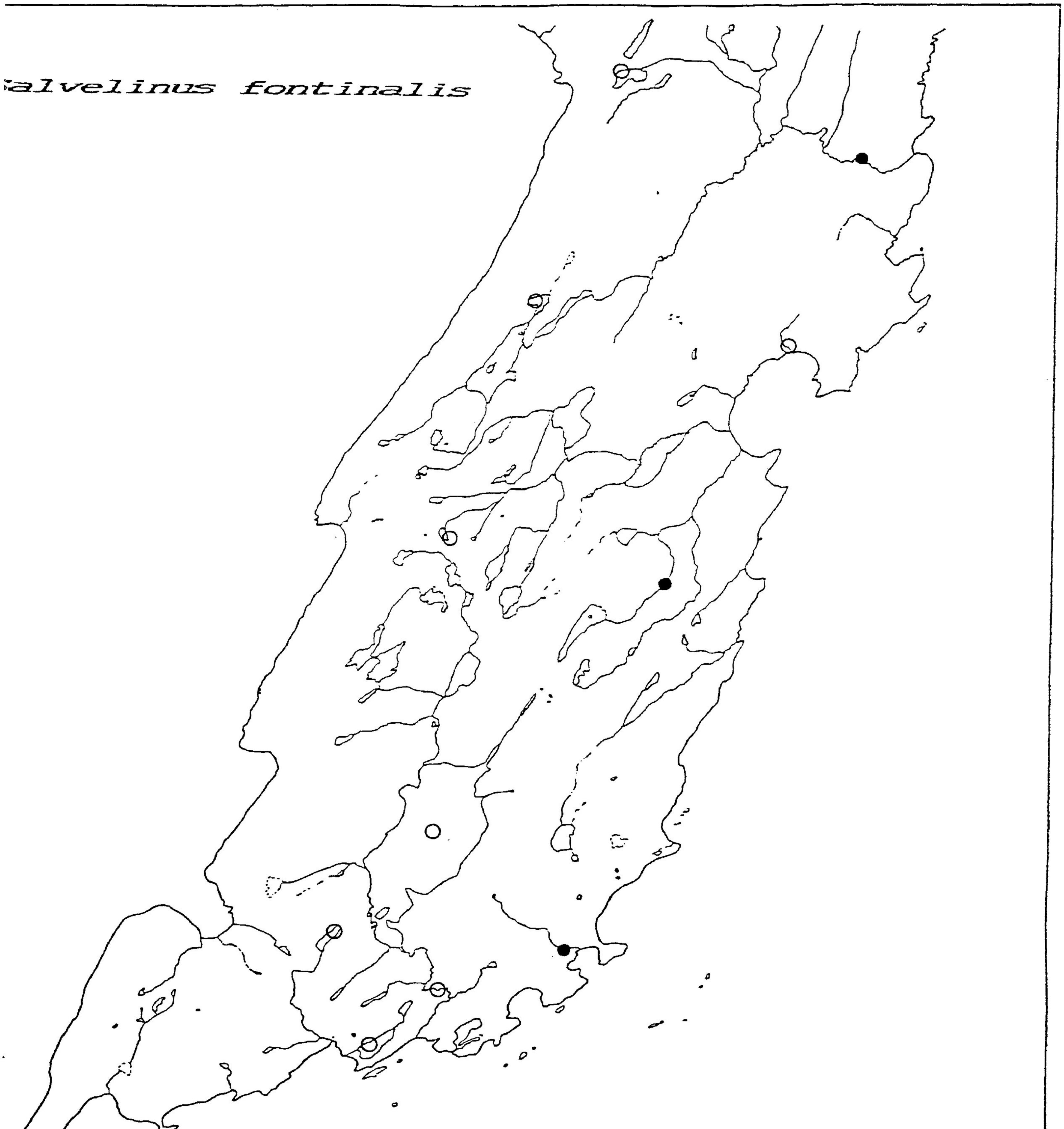

Ichthyomyzon fossor
m 1000 0 1 2 3 4 5 km


Lampetra appendix
m 1000
0
1
2
3
4
5 km

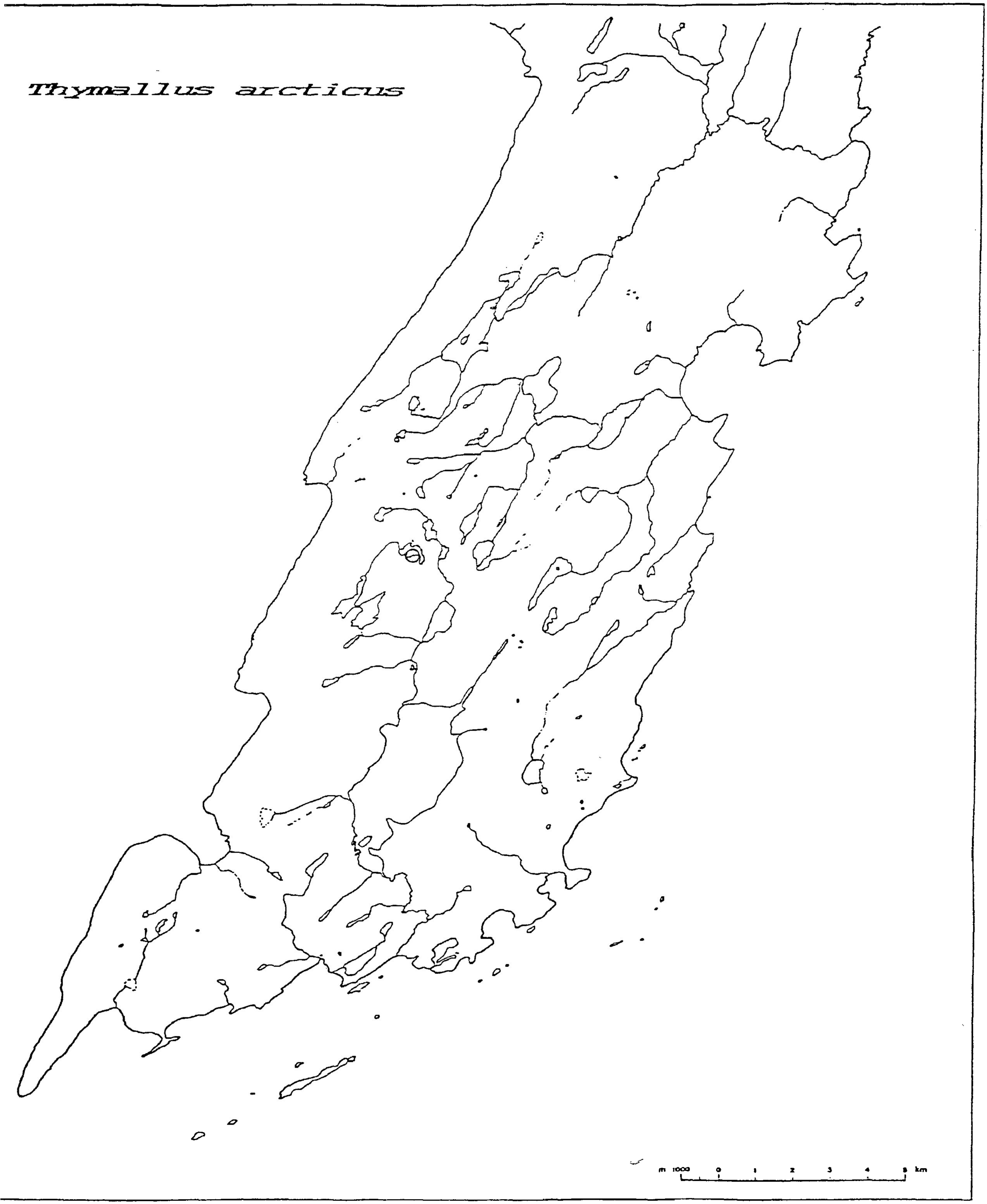
Acipenser fulvescens

Oncorhynchus mykiss

Salmo trutta


alvelinus fontinalis
m 1000 0 1 2 3 4 5 km

Coregonus artedii



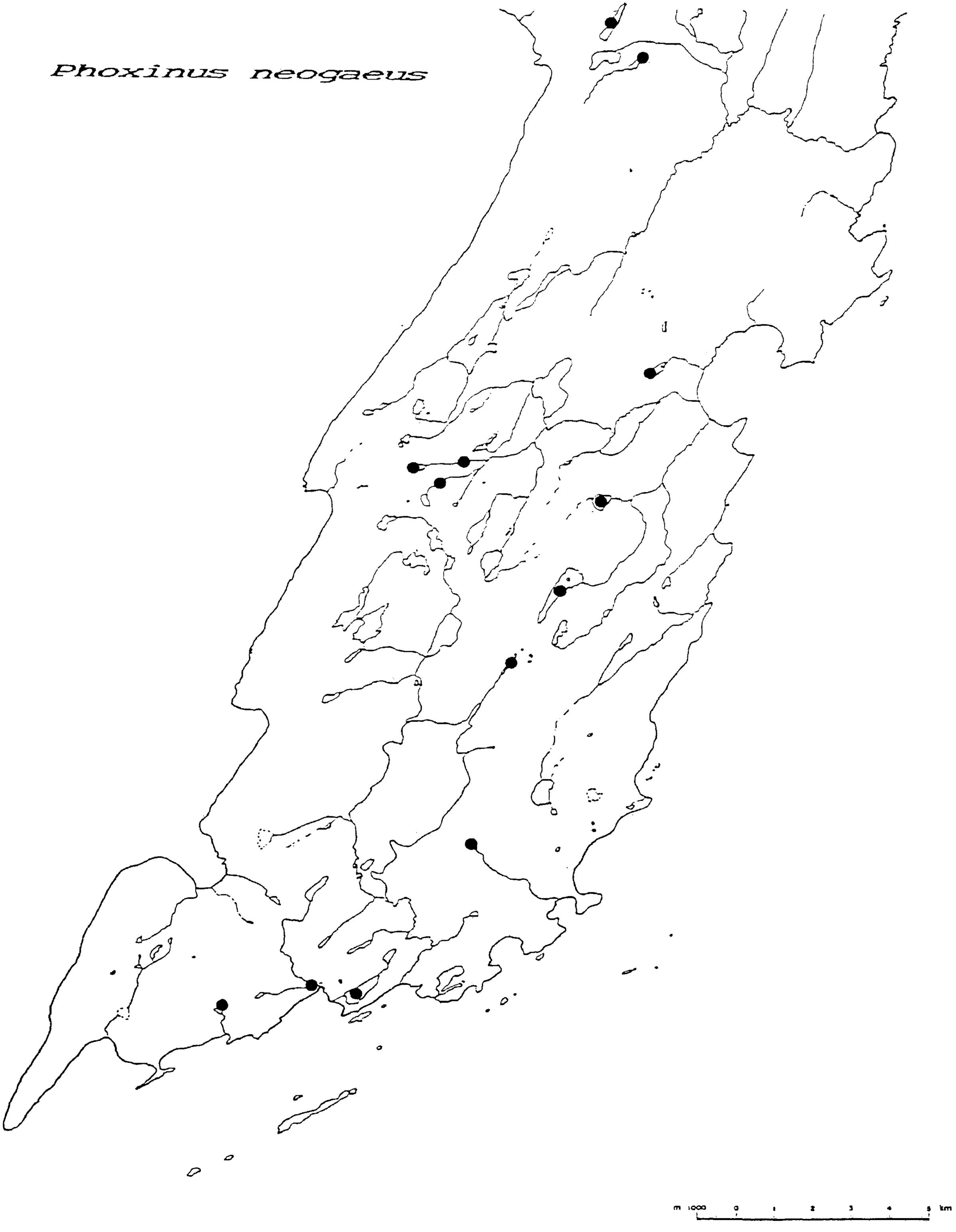
Thymallus arcticus

Osmerus mordax


Umbra limi
m 1000
0
1
2
3
4
5 km

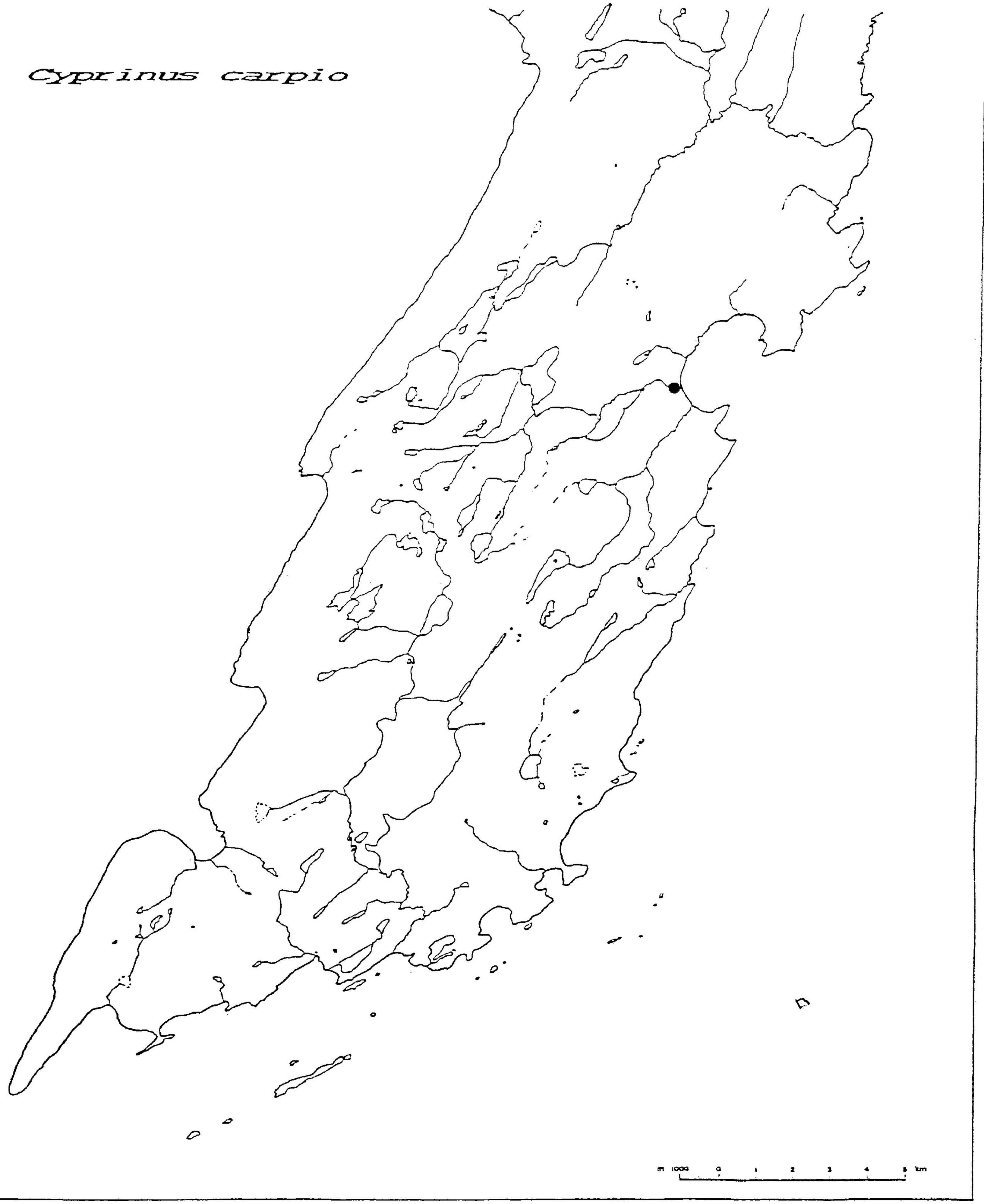
Esox lucius

Phoxinus eos



Phoxinus neogaeus


Couesius plumbeus



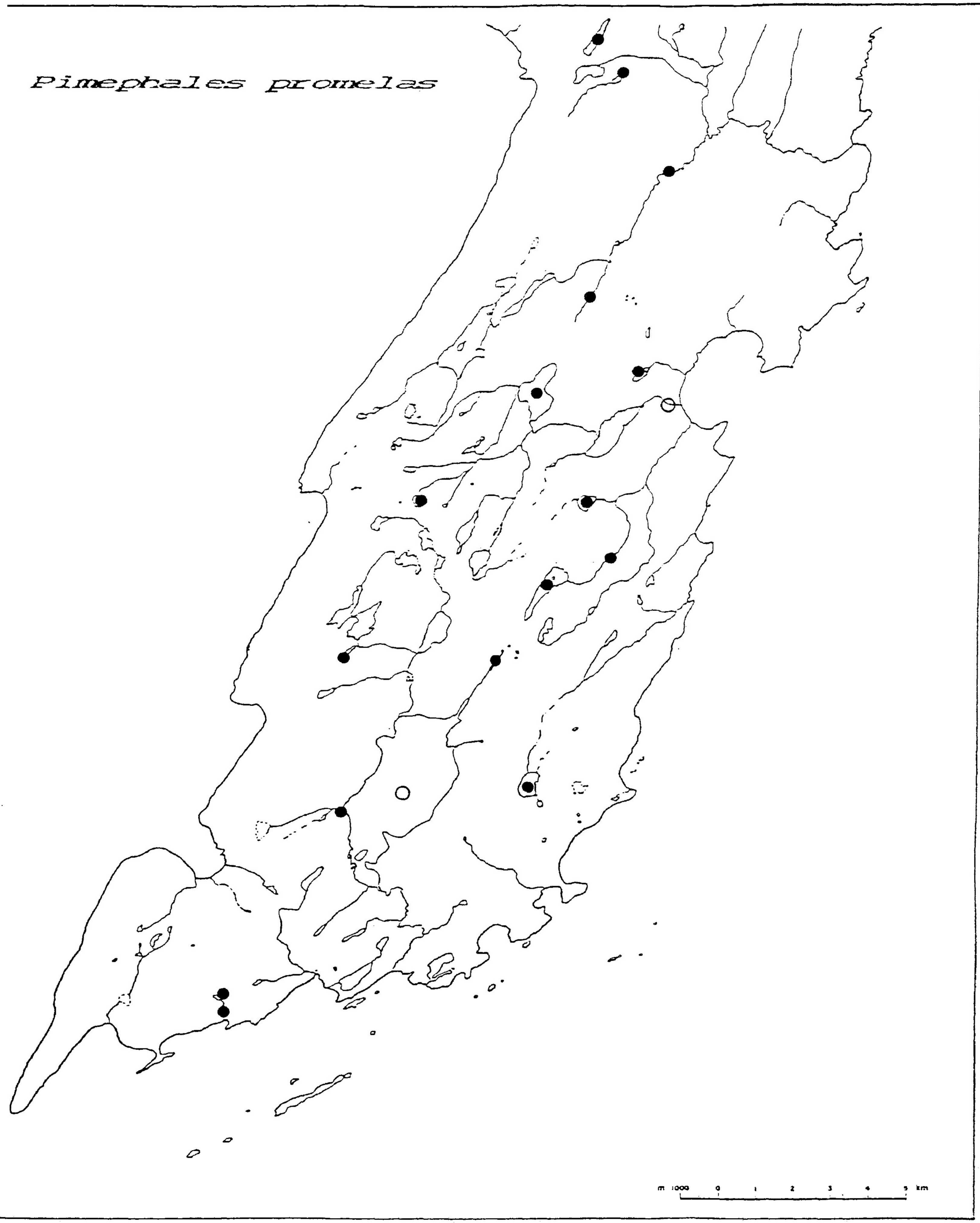
Cyprinus carpio

Notemigonus crysoleucas

Notropis atherinoides

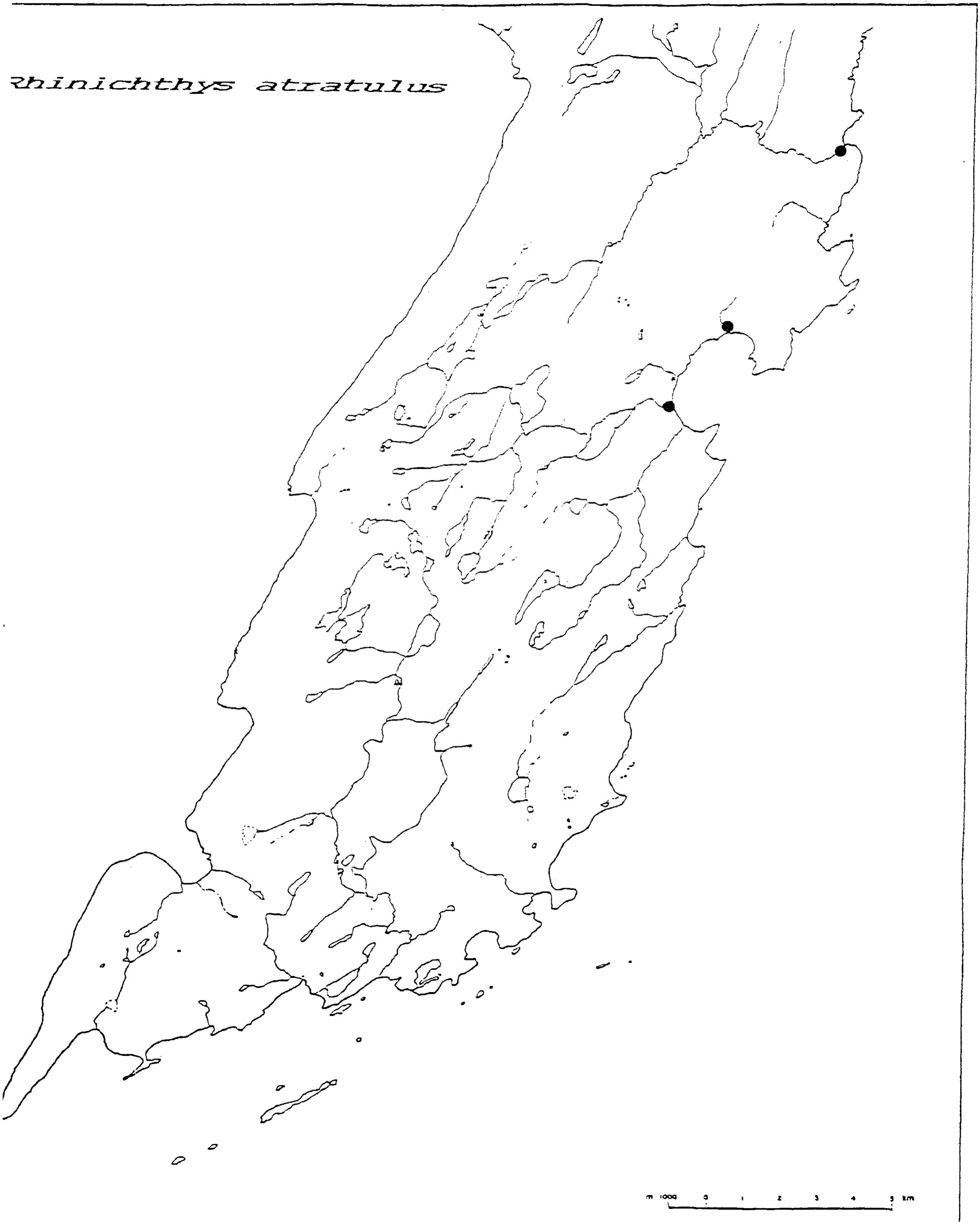
Notropis heterolepis

Notropis hudsonius



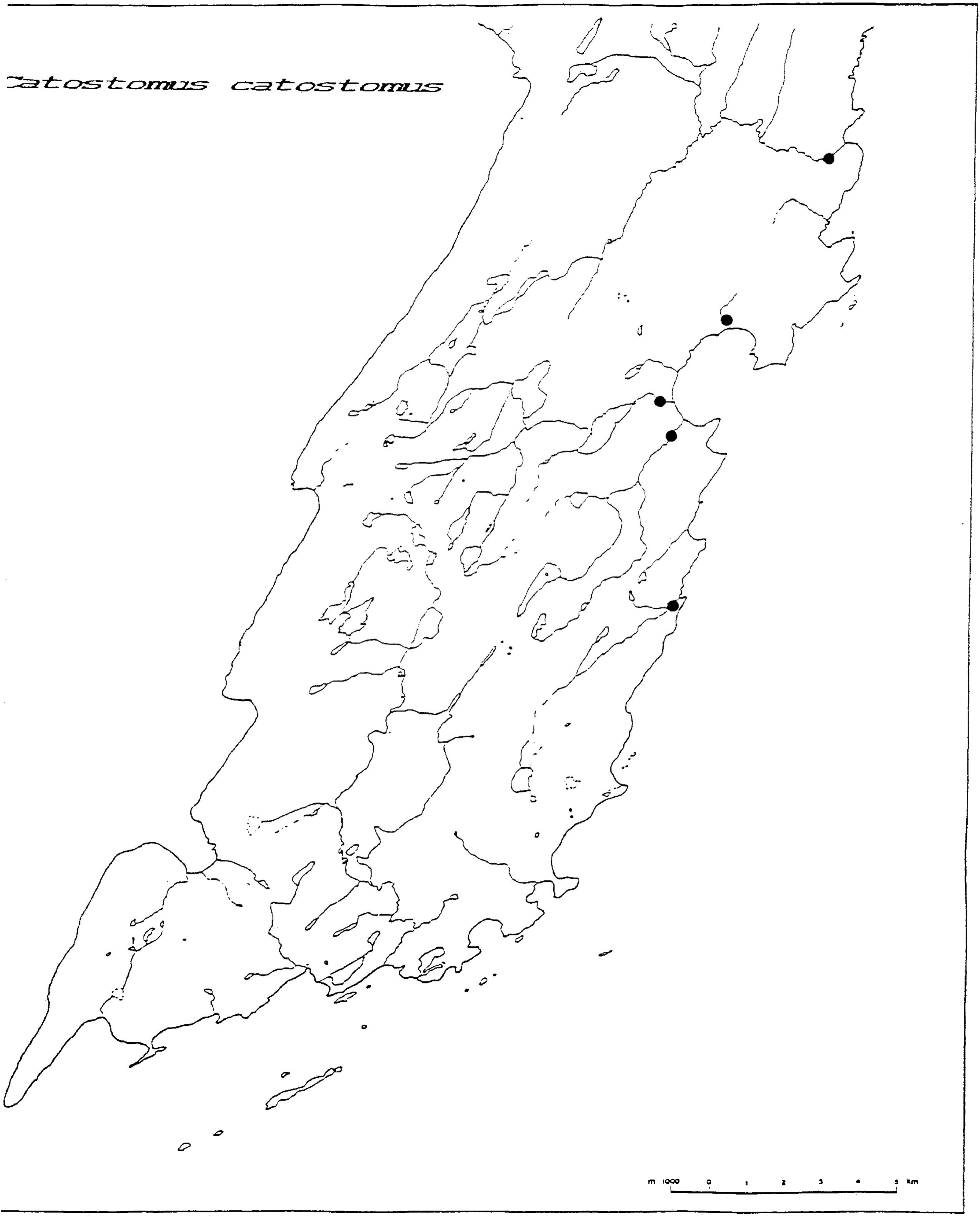
Pimephales promelas

Rhinichthys atratulus

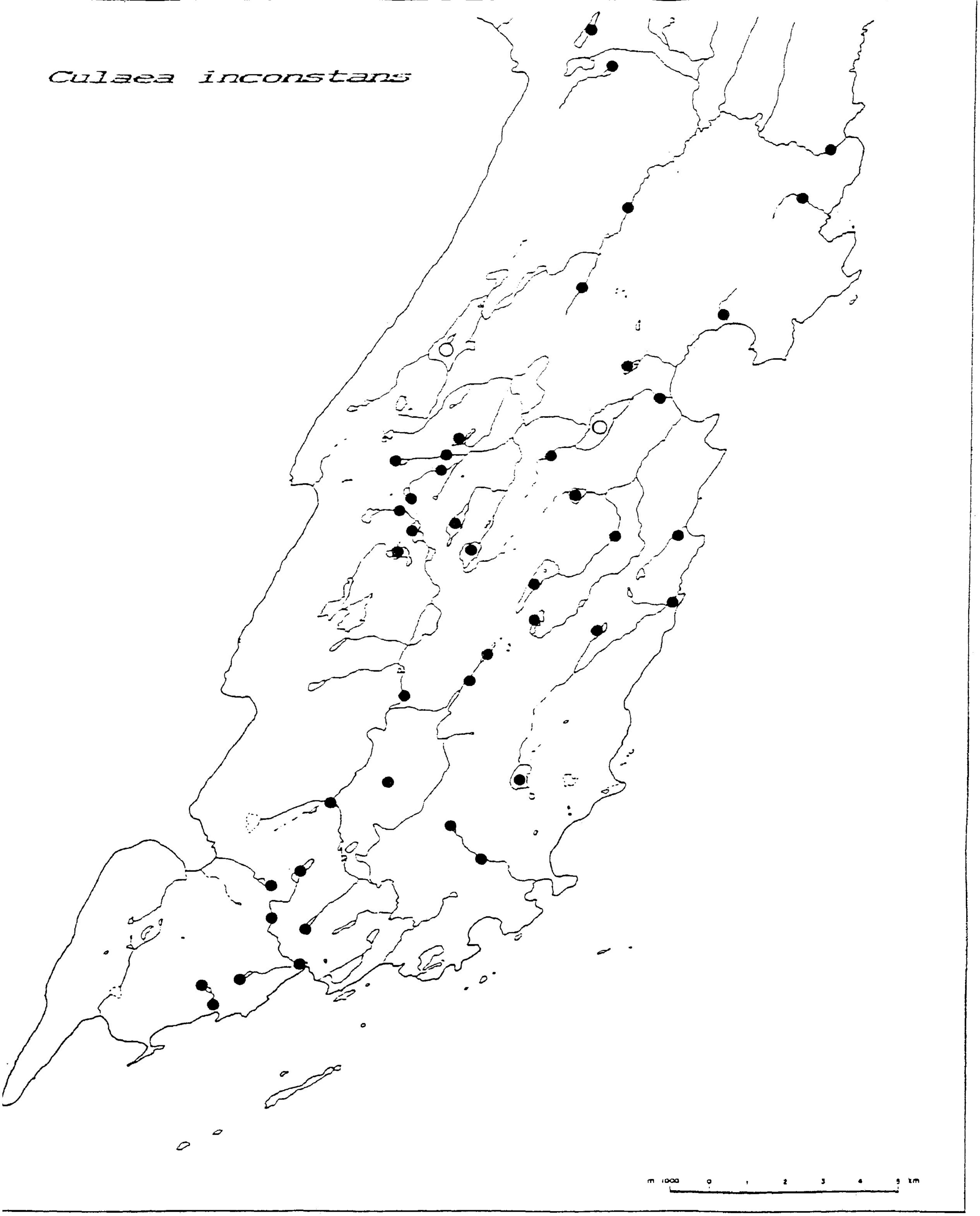


Rhinichthys cataractae

Semotilus margarita


Catostomus catostomus
m 1000 0 1 2 3 4 5 km


Catostomus commersoni
m 1000 0 1 2 3 4 5 km

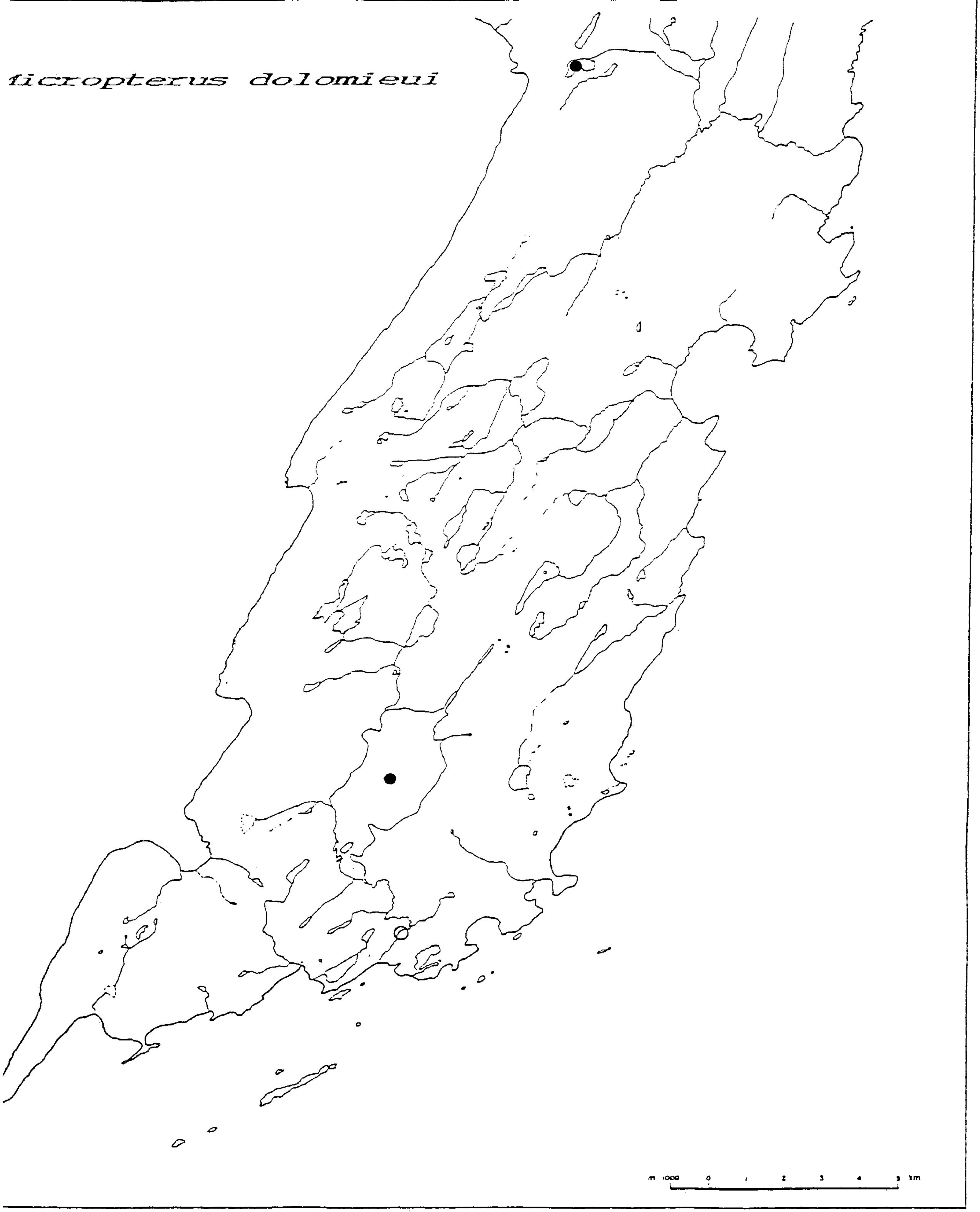


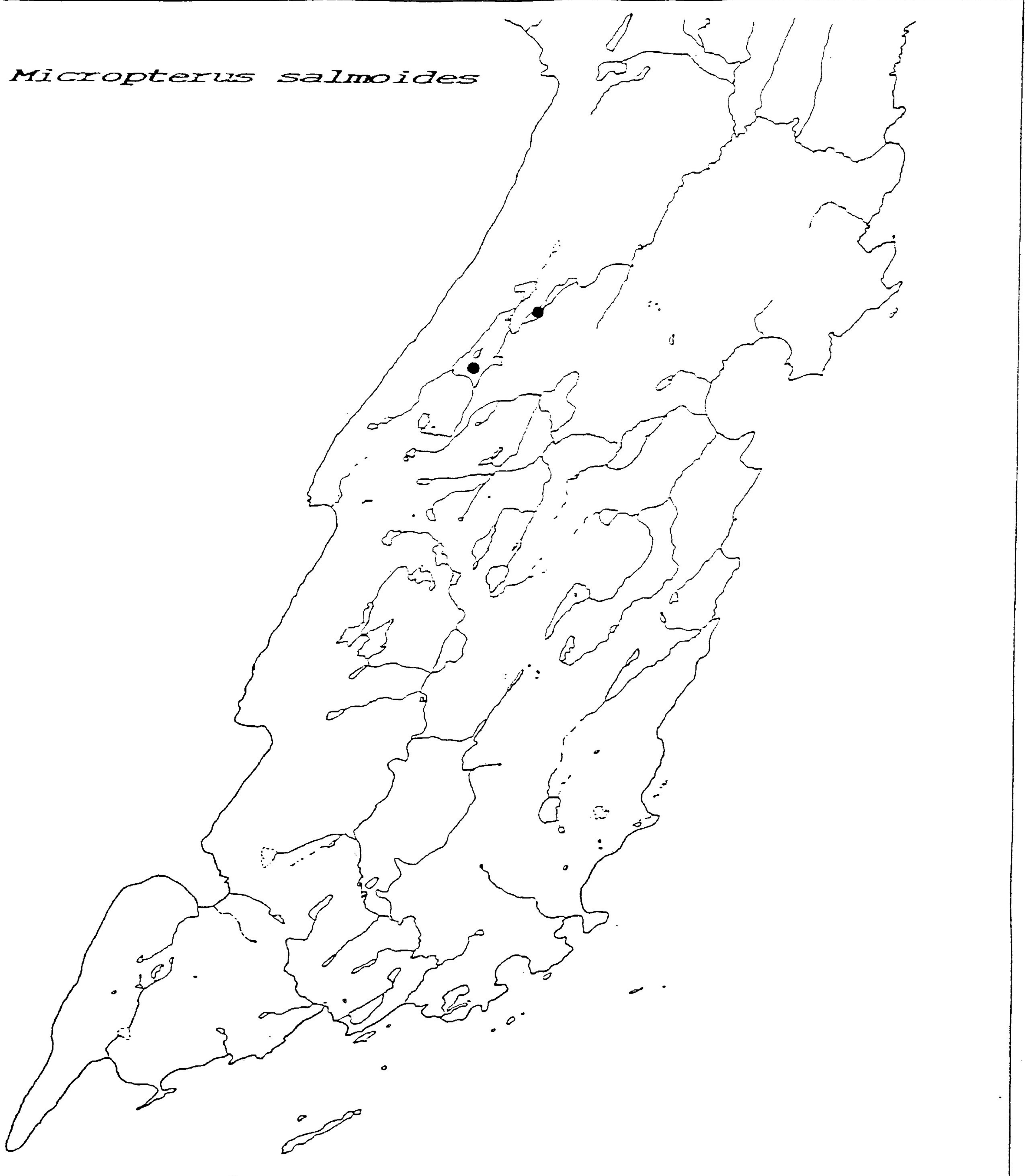
Culaea inconstans

Pungitius pungitius

Percopsis omiscomaycus

Pomoxis nigromaculatus


Micropterus dolomieui
m 1000 0 1 2 3 4 5 km



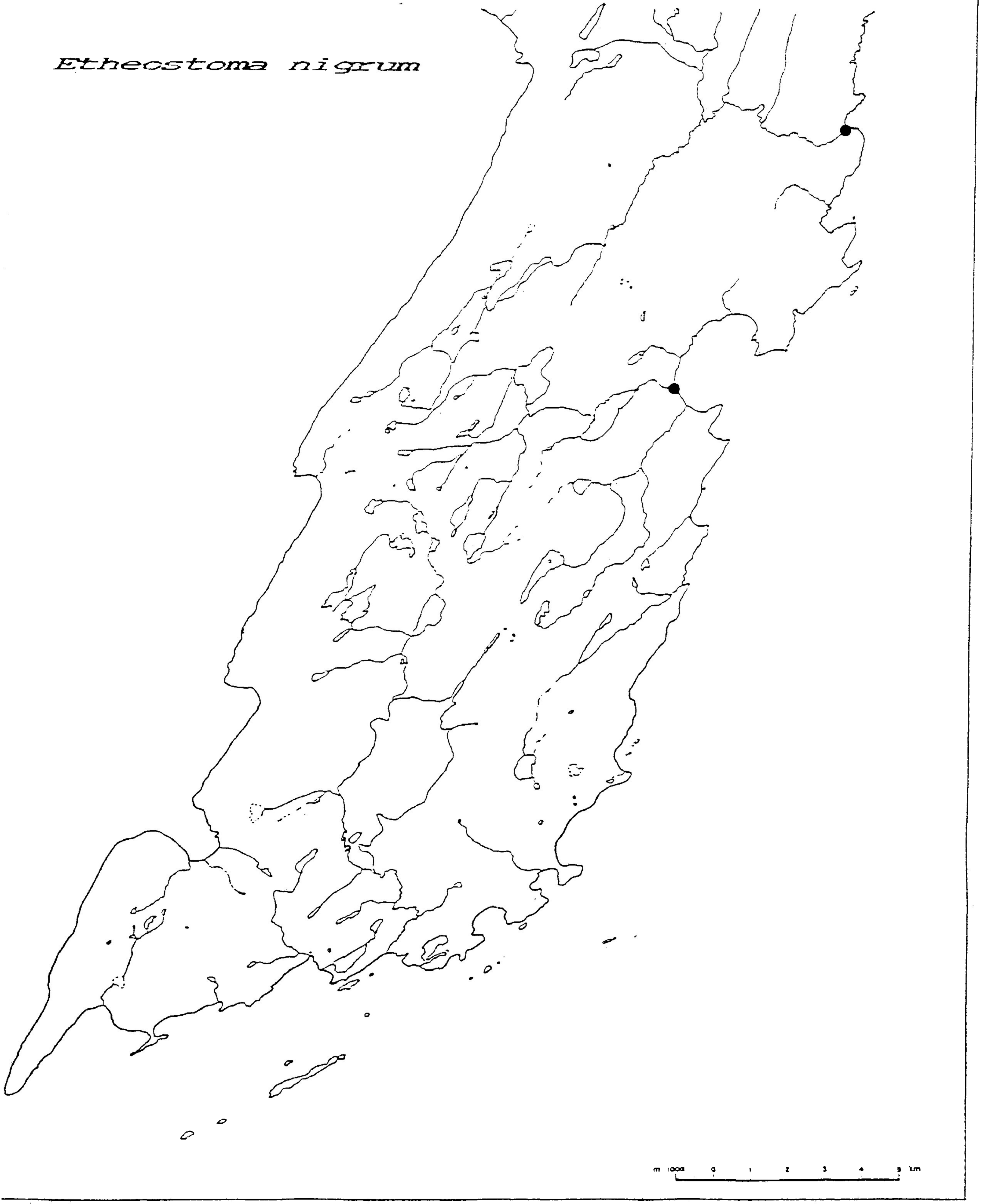
Micropterus salmoides

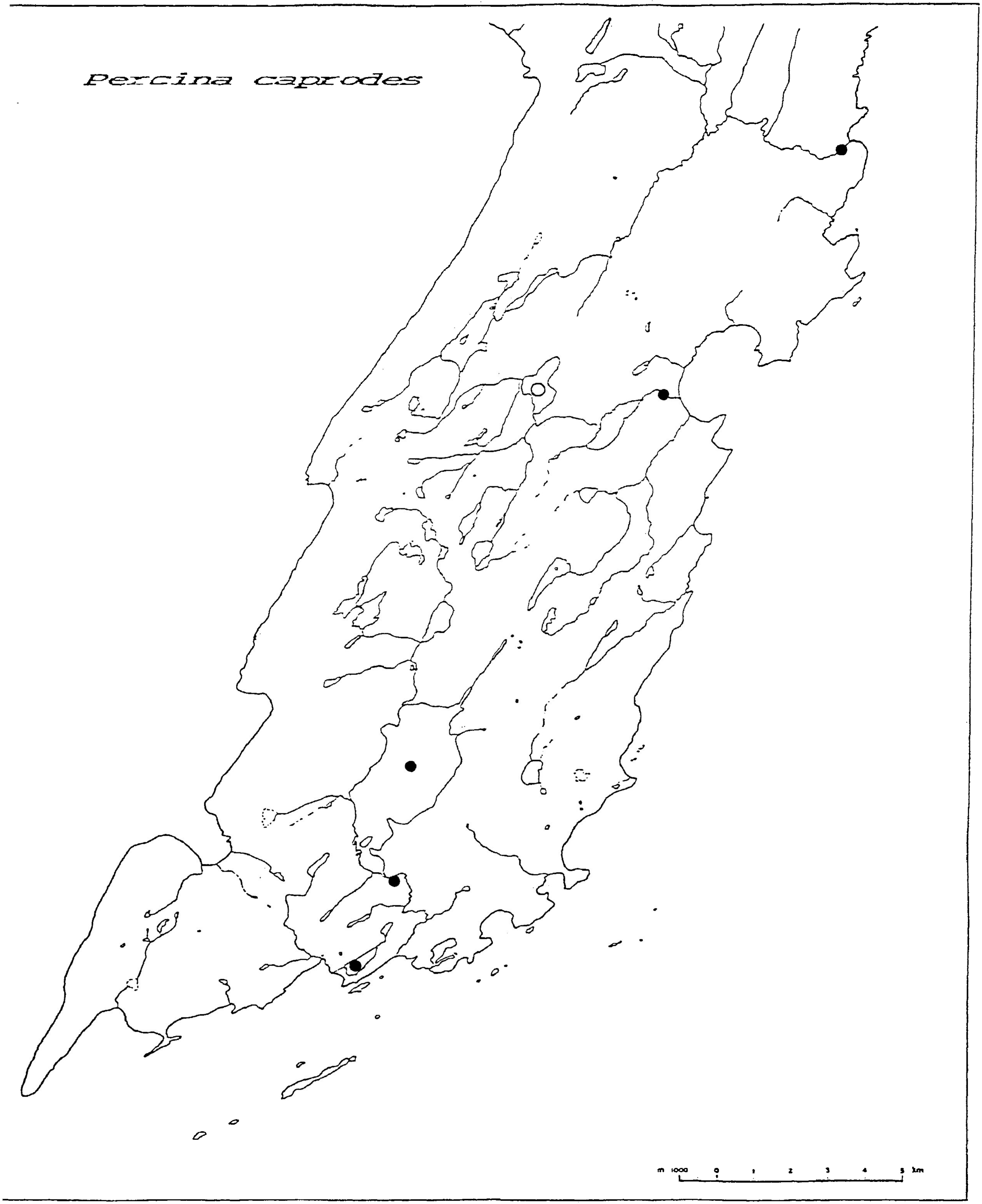

Perca flavescens
m 1000 0 1 2 3 4 5 km

Stizostedion vitreum

Etheostoma exile

Etheostoma nigrum





Percina caprodes

Cottus bairdi

Cottus cognatus

APPENDIX B

LAKE ELEVATION AND SPECIES LISTS
(metres ASL/ metres ALS)

S = Stephenson: 1989-90 collection
M or M/H = Momot or Momot and Hartviksen: Lakehead University collections
OMNR = Ontario Ministry of Natural Resources historic surveys
ROM = Royal Ontario Museum collections

Norwegian Lat 48^0 26'5" L 88^0 48'0" 292 / 108.7 m
Esox lucius OMNR
Phoxinus eos S
Semotilus margarita S
Catostomus commersoni S
Culaea inconstans S

*Upper Pass Lat 48^0 34'2" L 88^0 43'7" 281 / 97.7 m
Phoxinus eos S
Phoxinus neogaeus S
Pimephales promelas S
Semotilus margarita S
Catostomus commersoni S
Culaea inconstans S

Holt Lat 48^0 27'2" L 88^0 47'9" 278 / 94.7 m
Phoxinus eos S
Pimephales promelas S
Culaea inconstans S

Picnic Lat 48^0 28'0" L 88^0 46'6" 280 - 270 / 96.7 - 86.7 m
Culaea inconstans S

Twinpine Lat 48^0 25'3" L 88^0 49'0" 271 / 87.7 m
Esox lucius S
Notemigonus crysoleucas S
Notropis heterolepis S
Catostomus commersoni S
Perca flavescens S
Etheostoma exile S

Holt #1 Lat 48^0 27'8" L 88^0 48'0" 270 - 260 / 86.7 - 76.7 m
Phoxinus neogaeus S
Culaea inconstans S
Etheostoma exile S

Crest Lat 48^0 26'8" L 88^0 47'7" 264 / 80.7 m
Phoxinus eos S
Semotilus margarita S
Percopsis omiscomaycus S
Culaea inconstans S

Twinpine #1 Lat 48° 25'4" L 88° 48'8" 263 / 79.7 m
Esox lucius S
Notropis heterolepis S
Pimephales promelas S
Perca flavescens S
Etheostoma exile S

Milkshake Lat 48° 30'4" L 88° 46'9" 261 / 77.7 m
Esox lucius S
Perca flavescens S

Pounsford Lat 48° 29'5" L 88° 46'4" 256 / 72.7 m
Esox lucius M/H
Notropis hudsonius S
Notropis heterolepis S
Couesius plumbeus S
Catostomus commersoni S
Culaea inconstans ROM
Micropterus salmoides S (introduction)
Perca flavescens S
Stizostedion vitreum OMNR (introduction - likely extirpated)
Etheostoma exile S
Cottus cognatus M/H

*Sorenson's Lat 48° 33'0" L 88° 44'0" 256 / 72.7 m
Phoxinus eos S
Phoxinus neogaeus S
Pimephales promelas S
Culaea inconstans S

*Pass Lat 48° 33'0" L 88° 44'0" 254 / 70.7 m
Coregonus artedii OMNR
Osmerus mordax S
Esox lucius S
Catostomus commersoni OMNR
Notropis heterolepis S
Micropterus dolomieui S
Perca flavescens S

Wiswell Lat 48° 30'1" L 88° 45'7" 252 / 68.7 m
Catostomus commersoni S
Micropterus salmoides S
Perca flavescens S
Stizostedion vitreum S
Etheostoma exile S

East Pickerel Lat 48° 25'4" L 88° 45'0" 251 / 67.7 m
Culaea inconstans S

Lower Crest Lat 48° 26'4" L 88° 47'4" 248 / 64.7 m
Esox lucius S
Notropis heterolepis S
Notropis hudsonius S
Perca flavescens S

Red Sandstone Lat 48° 20'8" L 88° 49'7" 247 / 63.7 m
Culaea inconstans S

Addison Lat 48° 26'8" L 88° 46'5" 247 / 63.7 m
Esox lucius S
Notropis heterolepis S
Culaea inconstans S
Perca flavescens S
Etheostoma exile S

Sifting Lat 48° 26'2" L 88° 46'2" 239 / 55.7 m
Esox lucius S
Umbra limi S
Notemigonus crysoleucas S
Notropis hudsonius S
Notropis heterolepis S
Culaea inconstans S
Perca flavescens S

Otter Lat 48° 25'0" L 88° 46'0" 240 - 230 / 56.7 - 46.7 m
Esox lucius S
Phoxinus neogaeus S
Notemigonus crysoleucas S
Pimephales promelas S
Semotilus margarita S
Catostomus commersoni S
Culaea inconstans S
Perca flavescens S
Etheostoma exile S

Joe Boy #1 Lat 48° 27'8" L 88° 44'8" 240 - 230 / 56.7 - 46.7 m
Phoxinus eos S
Culaea inconstans S

Gardner Lat 48° 25'2" L 88° 47'7" 235 / 51.7 m
Esox lucius S
Notemigonus crysoleucas S
Notropis heterolepis S
Catostomus commersoni S
Perca flavescens S
Etheostoma exile S

Sawbill Lat 48° 21'6" L 88° 51'9" 234 / 50.7 m
Culaea inconstans S

Tarn Lat 48^{0} 21'4" L 88^{0} 50'8" 234 / 50.7 m
Phoxinus eos S
Culaea inconstans S

Pickerel Lat 48^{0} 25'7" L 88^{0} 45'2" 231 / 47.7 m
Phoxinus eos S
Phoxinus neogaeus S
Pimephales promelas S
Semotilus margarita S
Culaea inconstans S
Etheostoma exile S

Demers Lat 48^{0} 25'3" L 88^{0} 43'5" 231 / 47.7 m
Culaea inconstans S

Ferns Lat 48^{0} 23'0" L 88^{0} 45'4" 231 / 47.7 m
Umbra limi S
Phoxinus eos S
Pimephales promelas S
Culaea inconstans S

Wampum Lat 48^{0} 23'7" L 88^{0} 46'4" 229 / 45.7 m
Phoxinus neogaeus S
Culaea inconstans S

Marie Louise Lat 48^{0} 22'0" L 88^{0} 47'0" 228 / 44.7 m
Coregonus artedii S
Esox lucius S
Notemigonus crysoleucas S
Notropis heterolepis S
Notropis hudsonius S
Pimephales promelas S
Catostomus commersoni S
Culaea inconstans S
Percopsis omiscomaycus S
Micropterus dolomieui S
Perca flavescens S
Stizostedion vitreum OMNR (introduction - likely extirpated)
Etheostoma exile S
Percina caprodes S
Cottus cognatus S

Lizard Lat 48^{0} 28'9" L 88^{0} 45'5" 223 / 39.7 m
Esox lucius S
Umbra limi S
Notropis heterolepis S
Notropis hudsonius M/H
Pimephales promelas S
Catostomus commersoni M/H
Perca flavescens S
Etheostoma exile S
Percina caprodes M/H

Rita Lat 48° 27'2" L 88° 44'1" 221 / 37.7 m
Esox lucius OMNR (questionable record)
Umbra limi S
Phoxinus eos ROM
Phoxinus neogaeus S
Pimephales promelas S
Culaea inconstans S
Etheostoma exile S

Kay Lat 48° 29'2" L 88° 42'9" 219 / 35.7 m
Phoxinus eos S
Pimephales promelas S
Culaea inconstans S

Calcite Lat 48° 20'1" L 88° 51'0" 218 / 34.7 m
Phoxinus eos S
Culaea inconstans S

Shuniah Lat 48° 19'8" L 88° 51'9" 215 / 31.7 m
Phoxinus eos S
Phoxinus neogaeus S
Pimephales promelas S
Culaea inconstans S

Grassy Lat 48° 20'6" L 88° 48'7" 207 / 23.7 m
Phoxinus eos S

Joe Boy Lat 48° 28'2" L 88° 43'3" 206 / 22.7 m
Esox lucius S
Umbra limi S
Notropis heterolepis S
Culaea inconstans M
Perca flavescens S
Etheostoma exile M

Surprise Lat 48° 20'1" L 88° 49'1" 187 / 3.7 m
Coregonus artedii S
Oncorhynchus mykiss OMNR (introduction - likely extirpated)
Salvelinus fontinalis OMNR (introduction - likely extirpated)
Osmerus mordax S
Phoxinus eos S
Phoxinus neogaeus S
Notropis hudsonius S
Notropis heterolepis S
Catostomus commersoni S
Perca flavescens S
Etheostoma exile S
Percina caprodes S

Lake Superior 183.3 m

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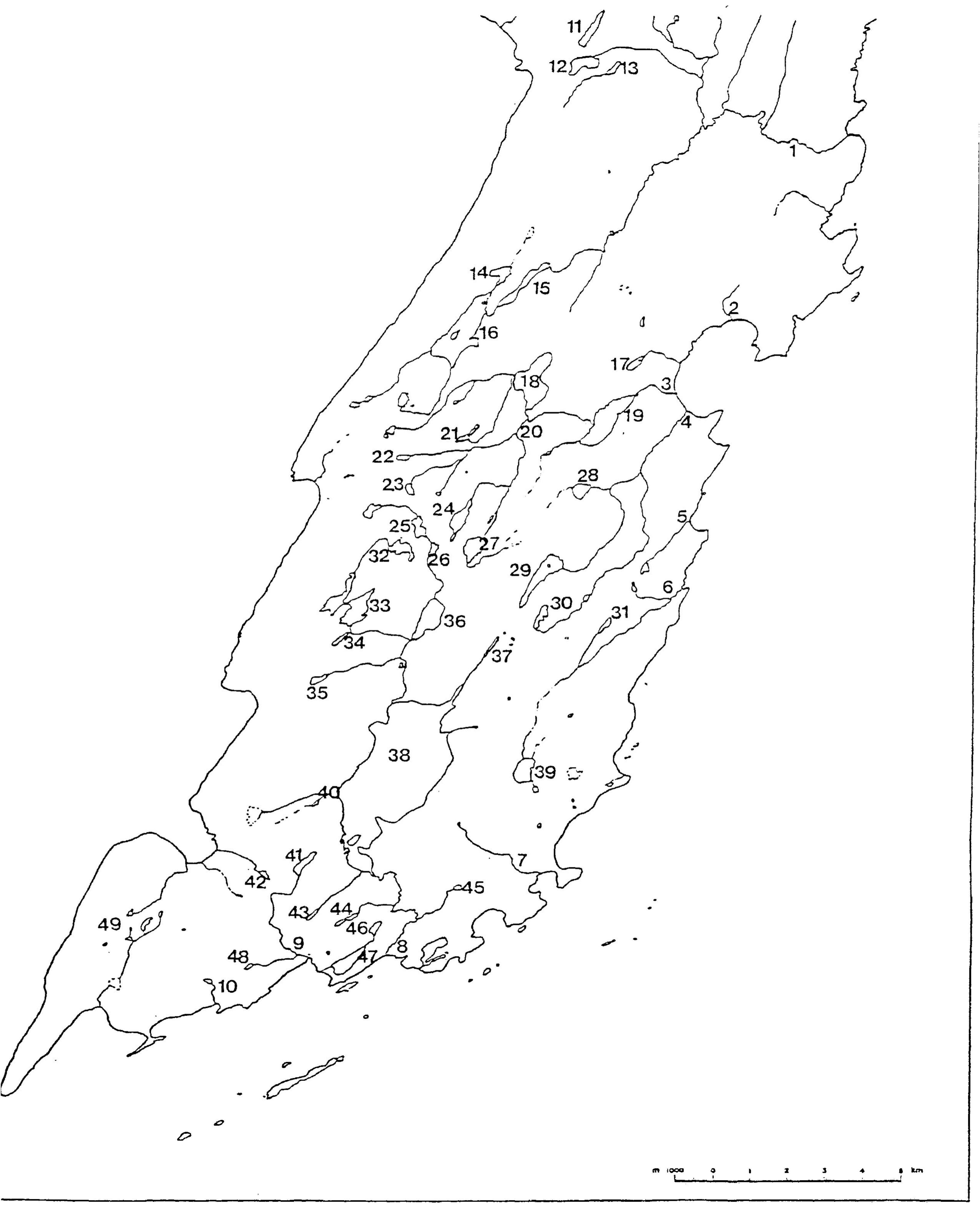
* Denotes those lakes not within Sleeping Giant Provincial Park boundaries.

APPENDIX C

Sibley Peninsula Lakes and Streams

1. Portage Creek
2. Squaw Bay Creek
3. Joe Boy Creek
4. Pickerel Creek
5. Demer's Point Creek
6. Demer's Creek
7. Wampum Lake Creek
8. Sibley Creek
9. Sawbill Creek
10. Shuniah Lake and Shuniah Creek
11. Upper Pass Lake
12. Pass Lake
13. Sorenson's Lake
14. Milkshake Lake
15. Wiswell Lake
16. Pounsford Lake
17. Kay Lake
18. Lizard Lake
19. Joe Boy Lake
20. Sand Creek
21. Picnic Lake
22. Holt Lake #1
23. Holt Lake
24. Addison Lake
25. Crest Lake
26. Lower Crest Lake
27. Sifting Lake
28. Rita Lake
29. Pickerel Lake
30. East Pickerel Lake
31. Demers Lake
32. Norwegian Lake
33. Twinpine Lake
34. Twinpine Lake #1
35. Verandah Lake
36. Gardner Lake
37. Otter Lake
38. Marie Louise Lake
39. Ferns Lake
40. Scum Creek and Scum Lake
41. Sawbill Lake
42. Tarn Lake
43. Red Sandstone Lake
44. Ravine Lake
45. Berry Blue Lake and Creek
46. Grassy Lake
47. Surprise Lake
48. Calcite Lake
49. "Sleeping Giant" lakes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