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FISHES OF ISLE ROYALE, LAKE SUPERIOR, MICHIGAN *

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Introduction

THIS paper on the fish fauna of Isle Royale (Fig. 1) is meant to serve several purposes. In the first place it is a contribution to the long-continued ichthyological survey of the State of Michigan. Toward this end the record stations for each species have been added currently to our distributional spot maps of the state. It is likewise a contribution to the analysis of the fish fauna of the Great Lakes. Some of the data have been utilized in our preliminary general treatises on that fauna (Hubbs and Lagler, 1939, 1941, 1947). This study also bears on problems of postglacial reinvasion, dispersal, faunal origin, isolation, and speciation, and in this way transcends the restricted limits of systematic ichthyology. Finally, this publication makes known a major segment in the fauna of one of our national parks. As such we hope it may con-

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tribute to the wise management, preservation, general appreciation, and further study of an important recreational and cultural resource.

Field Work, Collections, and Hydrographic Observations

Knowledge of the fish fauna of Isle Royale stems from several field studies. Some fish collections were made on the state geological and natural history survey expeditions of 1904 and 1905, which were reported upon by Ruthven (1906, 1909). The field work of these early parties was limited to some bays and coves and to a few inland lakes and streams. Several additional specimens were collected by Captain R. E. Ellsworth while on a fish patrol in 1920—in McCargoe Cove on August 12 and at the mouth of Washington River (at the Washington Club) on September 14.

An intensive study was made of the inland lakes and their fish faunas by Walter Koelz in 1929, as part of the scientific survey of Isle Royale that was conducted by the University of Michigan under a grant from the Fifty-fifth Legislature of the State of Michigan. Koelz's detailed report remains unpublished but has been extensively utilized in the preparation of this paper. A summary of the characteristics of each lake (Table I) and the list of the fishes present in each (Table IV) are drawn largely from Koelz's work. Hubbs collaborated with Koelz in the identification of the fishes that he collected, other than Coregonidae. An account of the coregonids, together with a brief description of the lakes that harbor them, was published by Koelz in 1931. In the field work he was assisted by George Stanley and John Brumm. In 1930 Stanley investigated the late geological history of the island, with particular reference to sequence of stages of the glacial Great Lakes. He collected a total of nine species at seven localities. Supplementary data were obtained from the commercial fishery reports to the Michigan Department of Conservation and, by verbal communication, from John Van Oosten, who in 1927 conducted a brief reconnaissance of the fisheries of the island and has kindly made his information available to us. H. F. Johnson furnished Van Oosten with a number of records and with data on the past abundance of commercial species. The commercial fishery reports of the U. S. Fish and Wildlife Service were also used, with the coöperation of Ralph Hile.

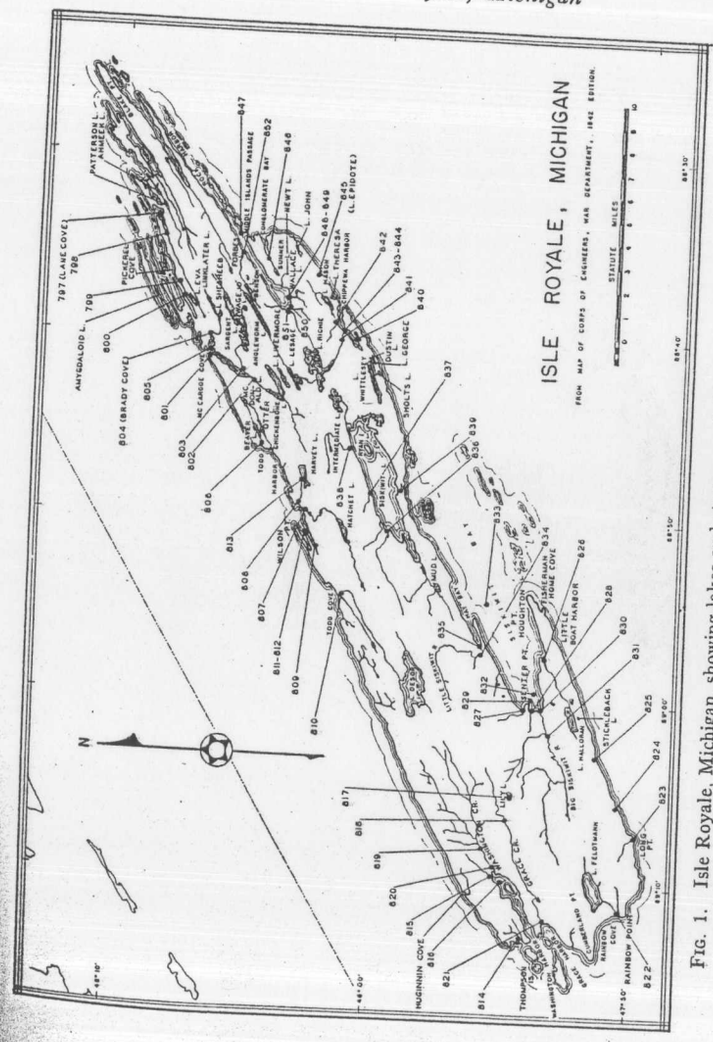
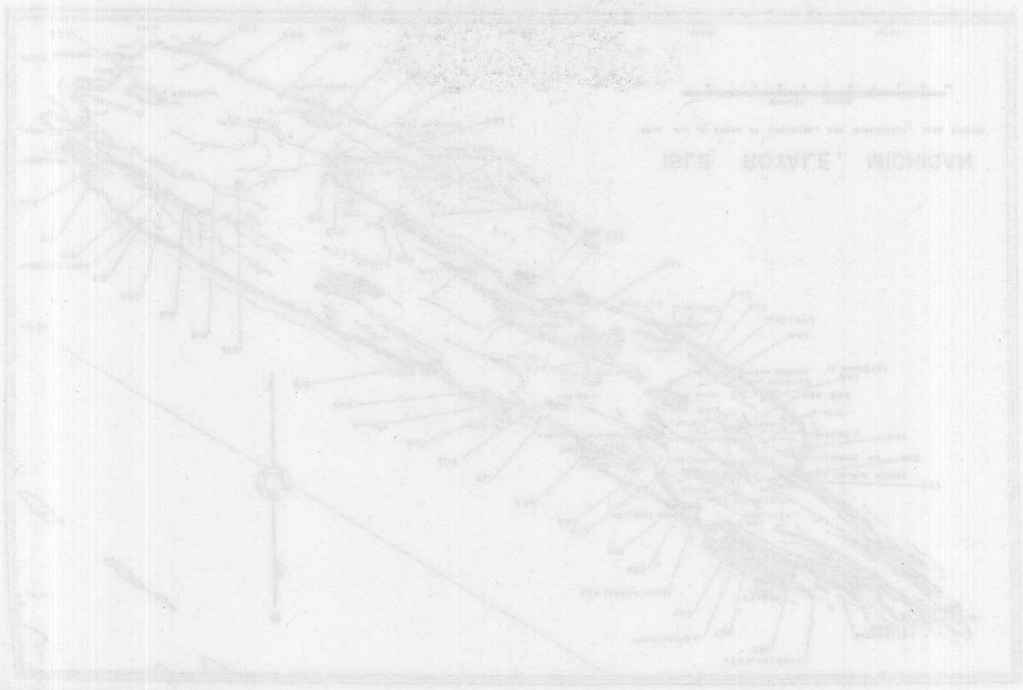


FIG. 1. Isle Royale, Michigan, showing lakes and streams and the stations (L 45:797 to L 45:851) where fishes were collected in 1945



Aided by a grant from the Horace H. Rackham School of Graduate Studies, University of Michigan, Lagler undertook during the summer of 1945 an expedition to supplement the previous fish collecting on Isle Royale. This field work was conducted as a part of the general fish survey of the state and as one element in Lagler's analysis of the fish fauna of the islands in the Great Lakes. M. E. (Fitzgibbon) Dimick and D. L. (Lundstrom) Puranen effectively assisted in the operations. The National Park Service extended collecting privileges, and the work on the island was expedited by Park Superintendent George Baggley and by Ranger Naturalist Karl Gilbert. The 1945 collections are listed below and are spotted on Figure 1. Supplementary records of larger species of fishes were provided by Karl Gilbert and by Fire Guard George Allen.

DATA ON COLLECTIONS MADE IN 1945 [1]

797. West arm of Lane Cove. Gill-net set at depth of 50 feet. July 15–16, overnight.

798. Stream entering west end of Lane Cove and Lane Cove at mouth of stream. Cedar swamp upstream with beaver dams. Seined to depth of 2 feet. July 17.

799. Small cove opening into Pickerel Cove, about 1,500 feet from mouth of Pickerel Cove. Bottom: silt, with aquatic plants. Seined to depth of 2 feet. July 17.

800. Outlet of Lake Eva into Pickerel Cove. Bottom: rock, silt, and detritus, with sparse aquatic plants. Seined to depth of 2.5 feet. July 17.

801. Mouths of McCargoe and Brady coves. Bottom: sand, rubble, and boulders, with algae on rocks. Gill-net set at depths from 6 to 30 feet. July 17–18, overnight.

802. Outlet of Chickenbone Lake, from mouth to one-half mile upstream, including small tributary entering from west in this section. Bottom: gravel, rubble, boulders, bedrock, silt, and peat, with some aquatic vegetation. Shore: marsh meadow near mouth; wooded upstream. Seined to depth of 3 feet. July 18.

803. Outlet of Sargent Lake into McCargoe Cove, from mouth to one-quarter mile upstream. Bottom: silt, detritus, and boulders. Shore: densely wooded. Seined to depth of 1.5 feet. July 18.

804. Stream entering east end of Brady Cove, vicinity of mouth. Bottom: pulpy peat, silt, and detritus, with some sedges. Seined. July 18.

805. Shore of Birch Island in McCargoe Cove. Bottom: sand, gravel, rubble, and boulders. Seined. Night of July 18.

[1] Place names, distances, and drainage pattern mostly follow the map by Corps of Engineers, War Department, Isle Royale, Michigan (published by U. S. Lake Survey Office, 1940; Cat. No. 981). For locations see Figure 1. Collections were made during daylight except as otherwise stated. The numbers are all preceded by the series symbol, L45.

806. Outlet of Beaver Lake into Todd Harbor, from mouth to one-quarter mile upstream. Stream falls about one foot through rubble at mouth. Bottom: sand, silt, and detritus, with some algae and moss. Seined to depth of 10 inches. July 19.

807. Outlet of Hatchet Lake into Todd Harbor, from mouth to three-eighths mile upstream. Bottom: bedrock, silt, and detritus, with some algae and moss. Stream falls rapidly over bedrock at mouth; about one-quarter mile upstream it is impounded and sluggish. Seined to depth of 3 feet. July 19.

808. Outlet of Harvey Lake into Todd Harbor, from mouth to one-quarter mile upstream. Bottom: sand, gravel, silt, and detritus, with no vegetation. The mouth is partly blocked by a beach bar of gravel and detritus. The lower one-eighth mile of the stream is at Lake Superior level. Upstream, the bottom changes to sand and gravel, and there are riffles and pools. Seined to depth of 3 feet. July 19.

809. Stream entering extreme western end of Pickett Bay of Todd Harbor. Bottom: sand, silt, fibrous peat, and detritus, with some water plants. Shore: cedar and alder thicket and swampy. Temperature, 68° F. Seined to 2.5 feet. July 19.

810. Outlet of Lake Desor into Todd Cove to five-eighths mile upstream and small tributary entering this outlet from west near its mouth. Bottom: silt and fibrous and pulpy peat in lower reaches, with some aquatic plants; sand, gravel, and detritus upstream. Seined to depth of 3 feet. July 20.

811. Shore of Taylor Island in Todd Harbor. Bottom: gravel, rubble, and few boulders, with some algae. Seined to depth of 4 feet. July 20, night.

812. Todd Harbor in channel between Florence Point and Taylor Island. Gill-net set at depths from 8 to 22 feet. July 20–21, overnight.

813. Harvey Lake in vicinity of outlet and in outlet near source (Pl. I, Fig. 3). Bottom: sand, gravel, few boulders, silt, and detritus. Shore: waist-high poplars and abundant burned downed timber. Temperatures: air, 70° F.; water, 77° F. Seined to depth of 3 feet. July 21.

814. Cove at western end of Isle Royale just opposite (northeast of) Thompson Island, and small stream entering cove. Bottom: in cove, sand, silt, and detritus; in stream, bedrock and rubble. Steam flow: 15 gallons per minute. Temperatures: stream, 63° F.; lake, 61.5° F. Seined to depth of 3 feet. July 22.

815. Stream entering Washington Harbor about 1,000 feet west of mouth of Washington Creek, in mouth and upstream one-eighth mile. Bottom: sand, silt, gravel, and detritus (including large quantity of wood chips). Seined to depth of 2.5 feet. July 22.

816. Washington Harbor along edge of shoal area at east end. Aquatic vegetation (*Potamogeton* and *Myriophyllum*) moderately dense. Gill-net set at depth of 6 feet. July 22–23, overnight.

817. Lily Lake, about 3 miles east of the easternmost extremity of Washington Harbor. Water: light brown, slightly turbid. Bottom: fibrous and pulpy peat with white water lilies. Shore: encroaching bog mat, backed with cedar swamp; then rising to wooded ground. Estimated area: 14 acres. Seined to depth of 4 feet. July 23. (See p. 90.)

818. Grace Creek, tributary of Grace Harbor, about 4.7 miles upstream from mouth. Bottom: sand, silt, detritus, little rubble, and few boulders, with no vegetation. Banks: densely wooded. Seined to depth of 10 inches. July 23.

819. Washington Creek about one mile upstream from mouth and also near old Windigo Mine. Bottom: clay, silt, sand, gravel, rubble, and detritus. Seined to depth of 2.5 feet. July 24.

820. Washington Creek, from mouth to one-quarter mile upstream. Stream broad and at base level; rising tide causing current to move upstream. Bottom: sand, silt, clay, and detritus. Seined to depth of 3 feet. July 24.

821. Grace Creek from mouth to first beaver dam upstream (about one-quarter mile). Seined to depth of 2.5 feet. July 25.

822. Outlet of Lake Feldtmann at mouth into Rainbow Cove and for one-quarter mile upstream. Bottom: sand, gravel, rubble, and some silt. Temperature of stream, 73° F.; of Lake Superior off mouth of stream, 51° F. Seined to depth of 2 feet. July 25.

823. Stream entering Lake Superior at Long Point. Bottom: silt and gravel. Temperature in stream where wooded, 65° F.; in beach pool, 80° F.; in Lake Superior off mouth of stream, 45.5° F. Seined to depth of 2.5 feet. July 25.

824. Bog pond 100 feet inshore from Lake Superior, about 1.25 miles east of Long Point. Bottom: pulpy and fibrous peat and detritus over gravel. Seined to depth of 2.5 feet. July 25.

825. McCormick Beach Creek, tributary to Lake Superior about 4 miles east of Long Point. Bottom: bedrock, sandstone, and silt. Seined to depth of 1.5 feet. July 25.

826. Outlet of Lake Halloran into Siskiwit Bay from mouth to one-quarter mile upstream. Within 100 feet of shore the stream is dammed by beaver; upstream it is swampy. Bottom: sand, boulders, silt, and detritus. Seined to depth of 2.5 feet. July 26.

827. Tributary of Siskiwit Bay about one-half mile north of Senter Point. Small stream with beach pool at mouth and beaver ponds upstream. Seined to depth of 2.5 feet. July 26.

828. Tributary of Siskiwit Bay at southwest base of Senter Point. Bottom: sand, silt, and detritus. Banks: alder and cedar thicket. Water: brown and stagnant, in disconnected pools. Seined to depth of one foot. July 26.

829. Siskiwit Bay just off Senter Point. Gill-net set to depth of 20 feet. July 26–27, overnight.

830. Big Siskiwit River in mouth and near by in Siskiwit Bay. Bottom: sand, gravel, and detritus. Seined to depth of 3 feet. July 26, night.

831. Big Siskiwit River about 2 miles upstream from mouth. Bottom: sand, silt, gravel, and detritus. Banks: alder thicket. Seined to depth of 1.5 feet. July 27.

832. Siskiwit Bay about 1,000 feet off mouth of Big Siskiwit River. Trolling with brass spoon. July 27.

833. Siskiwit Bay about one-quarter mile off Point Hay. Commercial gill-net set at depth of about 30 feet. July 28.

834. Little Siskiwit River to about one-half mile upstream from mouth into Hay Bay. Bottom: bedrock, gravel, sand, rubble, and boulders. No fish above barrier falls about one-quarter mile upstream from mouth. Seined to depth of 2.5 feet. July 28.

835. Hay Bay at mouth of Little Siskiwit River. Bottom: sand and gravel. Seined to depth of 3 feet. July 28.

836. Tributary entering Siskiwit Lake about 2 miles northeast of extreme western end of lake. Bottom: sand, gravel, and rubble. Temperature: 57° F. Seined to depth of 1.5 feet. July 29.

837. Siskiwit Lake and mouth of small stream entering from north, opposite lake outlet. Bottom: sand, gravel, and rubble. Seined to depth of 1.5 feet. July 29.

838. Stream entering Siskiwit Lake from north, opposite Ryan Island. Bottom: sand, gravel, boulders, bedrock, and detritus. Estimated flow, 75 gallons per minute. A series of small cascades lead to a few large pools at lake level. Seined to depth of 2.5 feet. July 29.

839. Outlet of Siskiwit Lake just downstream from falls at Siskiwit Lake. Bottom: bedrock and rubble. Width: to 50 feet. Current: rapid. Temperature, 72° F. Seined to depth of 1.5 feet. July 29.

840. Chippewa Harbor at its westernmost tributary and in lower reaches of tributary. Bottom: sand, silt, boulders, bedrock, and detritus. Vegetation moderately dense. Seined to depth of 2.5 feet. July 30.

841. Outlet of Lake Richie into Chippewa Harbor, at mouth and for one-half mile upstream. Bottom: in lower reaches, silt and detritus; upstream about one-half mile, sand, gravel, and rubble. Flow: 20 gallons per minute. Seined to depth of 4.5 feet, and fished with rod and line. July 30.

842. Outlet of Mason Lake from mouth into Chippewa Harbor to one-half mile upstream. Bottom: sand, silt, and detritus. Vegetation moderate in sluggish flow at base level. Flow (upstream about one-fifth mile) less than 15 gallons per minute. Seined to depth of 2 feet and fished with hook and line. July 30.

843. Chippewa Harbor about mouth of Lake Richie outlet. July 30, night.

844. Chippewa Harbor at narrows below Lake Richie outlet. Gill-net set at depth of about 30 feet. July 30–31, overnight.

845. Lake Epidote and its outlet about 1.25 miles east of Chippewa Harbor, near Lake Superior shore. Bottom: bedrock, slab rubble, boulders, silt, and detritus. Seined to depth of 2 feet. July 31.

846. Outlet of Sumner Lake into Conglomerate Bay; in bay about mouth and to about one-eighth mile upstream. Bottom: sand, silt, gravel, and detritus. Flow: about 50 gallons per minute. Seined to depth of 1.5 feet. July 31.

847. Middle Islands Passage from Rock Harbor to Lake Superior. Gill-net set at depth of 20–35 feet. July 31—August 1, overnight.

848. Rock Harbor, southwesternmost extremity. Bottom: sand, silt, and detritus. Seined to depth of 3 feet. August 1.

849. Outlet of Wallace Lake into Rock Harbor, from mouth to one-quarter mile

TABLE 1

SOME CHARACTERISTICS OF ISLE ROYALE LAKES*

The lakes are listed in the order of their maximum depths.

Lake	Approximate elevation above Lake Superior (feet)	Maximum depth (feet)	Length of longest axis	Bottom
Mud	<100	3	½ mi.	Mire
Stickleback	<100	3	600 ft.	Bog
Epidote	<10	5	350 ft.	Bedrock, boulders, sandy mud
Newt	100–200	4+	...	...
Sholts	<100	5	900 ft.	Mud, rock
Theresa	<100	8	¼ mi.	Mire
Ahmeek	<100	10	...	Mud
Feldtmann	<100	10	1½ mi.	Sand, mud
George	<100	10	...	Stony, mud
Halloran	<100	10	1 mi.	Mud, sand, peat, detritus
Wagejo	200–300	10	...	...
Wallace	<100	10	¼ mi.+	Mire
Sumner	<100	12	½ mi.—	Mire
Patterson	<100	13	½ mi.	Mire
Harvey†	168	13	...	Sand, peat, detritus
Benson†	About 190	14	1 mi.	Sand, mud
John	100–200	14	½ mi.	Soft
McDonald	<100	14	½ mi.	Sand, mud
Otter	<100	14	...	Mud, clay, sand
Beaver	<100	17	¾ mi.	...
Hatchet†	145	18	1¼ mi.	Sand, gravel, boulders, mud, snags
Livermore†	190	19	1 mi.—	Gravel, mud, snags, bedrock
Shesheeb	<100	20	½ mi.	Mud
Chickenbone	<100	21	1¾ mi.	Soft, muddy
Forbes†	About 190	21	¼ mi.	Mire, sand, gravel, stone, silt
Linklater	<100	21	1 mi.	Mud
Dustin	<100	22	...	Mud, stone
Eva	<100	24	⅝ mi.	Mud
Intermediate	<100	24	1⅛ mi.	Mud, sand, rocks
Mason	<100	26	1 mi.—	Mud, sand, gravel
Amygdaloid	<100	29	...	Mud, bedrock, rocky
Angleworm†	About 190	30	2¼ mi.	Mud, sand, boulders
Lesage†	About 190	30	⅞ mi.	Muddy
Whittlesey	<100	30	2 mi.—	Soft mud, sand
Richie	<100	39	2 mi.	Soft mud, sand, clay
Sargent	<100	45	2¾ mi.	Mud, silt, sand, bedrock
Desor†	235	55	3 mi.—	Sand, gravel, boulders, clay
Lily	<400	..	...	Fibrous and pulpy peat, detritus
Siskiwit†	57	142	7 mi.	Silt, rocks, clay, detritus

* Physical features (except elevations) mostly as determined by Walter Koelz in 1929.

† Elevation from levels run by George M. Stanley. Other elevations are approximated from 100-foot contours on the map referred to in footnote 1, p. 76.

upstream. Bottom: near mouth, sand, silt, clay, detritus, and a few boulders; upstream, bedrock and boulders. Seined to depth of 2.5 feet. August 1.

850. Stream entering southwesternmost extremity of Rock Harbor (first tributary west of Wallace Lake outlet). Bottom: sand, silt, and detritus. Several beaver dams in stream. Seined to depth of 2.5 feet. August 1.

851. Stream entering Rock Harbor near its southwestern end (the first tributary northwest of Park Camp Ground). Bottom: sand, silt, and detritus. Seined to depth of 3 feet. August 1.

SUPPLEMENTARY HYDROGRAPHIC OBSERVATIONS MADE IN 1945

Tributaries entering Stockly, Five Finger, and Duncan bays from west were extensively dammed by beaver. Small impoundments and beaver swamps have resulted. July 15–17.

Tributary entering western extremity of Todd Cove was a mere trickle with no fish. July 20.

Beaver Lake outlet was dry. July 19.

Tributary of Lake Superior at Thompsonite Beach dropped at its mouth about 20 feet in a falls impassable by fish. Only newt larvae (*Triturus viridescens*) were found above falls. July 20.

Stream channel entering Huginnin Cove was dry. July 22.

Small stream channel entering cove just south of station 814 (see Fig. 1) was dry. July 22.

Small stream channel entering Grace Harbor about one and five-eighths miles southwest of station 821 was dry. July 25.

Small stream channel tributary to Rainbow Cove about 400 feet south of mouth of Lake Feldtmann outlet was dry. July 25.

Small tributary channel entering Rock Harbor (Newt Lake outlet) just southwest of Sumner Lake was dry. August 1.

ZOOGEOGRAPHICAL ANALYSIS OF THE FISH FAUNA

As now known, the fauna of Isle Royale includes 49 kinds of fish, representing 41 species, 31 genera, and 14 families. With three exceptions all the species are regarded as native to the waters on and about the island, and even these three have reached the island by natural dispersal from other parts of the Great Lakes. *Petromyzon marinus* has expanded its range through the Great Lakes after it reached these waters by passing through canals. *Osmerus mordax* has spread from relatively recent local stockings. *Salmo gairdnerii irideus* has long been established through the Great Lakes as the result of early stocking by man. Another exotic species, *Salmo trutta fario*, was once introduced, but, fortunately, it failed to become established. Koelz (1929 manuscript) ob-

TABLE II

NUMERICAL AND PROPORTIONAL REPRESENTATION OF THE GREAT LAKES FISH FAUNA IN THE WATERS OF ISLE ROYALE

Family	Numbers of genera, species, and forms						Percentage occurring on Isle Royale		
	Entire Great Lakes*			Isle Royale					
	Genera	Species	Forms	Genera	Species	Forms	Genera	Species	Forms
Petromyzonidae	3	5	5	1†	1†	1†	33†	20†	20†
Polyodontidae	1	1	1	0	0	0	0	0	0
Acipenseridae	1	1	1	1	1	1	100	100	100
Lepisosteidae	1	2	2	0	0	0	0	0	0
Amiidae	1	1	1	0	0	0	0	0	0
Hiodontidae	1	1	1	0	0	0	0	0	0
Clupeidae	1	1	1	0	0	0	0	0	0
Salmonidae	3	3	3	0	0	0	0	0	0
Coregonidae	4	7	11	3	3	4	75	43	36
Thymallidae	3	13	44	3	5‡	9‡	100	38‡	20‡
Osmeridae	1	1	1	0	0	0	0	0	0
Catostomidae	1	1	1	1	1	1	100	100	100
Cyprinidae	11	19	23	1§	2§	2§	9§	11§	9§
Ameiuridae	25	49	65	9	13	16	36	27	25
Umbridae	5	12	12	0	0	0	0	0	0
Esocidae	1	1	1	0	0	0	0	0	0
Anguillidae	1	4	4	1	2	2	100	50	50
Cyprinodontidae	1	1	1	0	0	0	0	0	0
Poeciliidae	1	3	4	0	0	0	0	0	0
Gadidae	1	1	2	0	0	0	0	0	0
Percopsidae	1	1	1	1	1	1	100	100	100
Aphredoderidae	1	1	1	1	1	1	100	100	100
Serranidae	1	1	1	0	0	0	0	0	0
Percidae	1	1	1	0	0	0	0	0	0
Centrarchidae	2	2	2	0	0	0	0	0	0
Atherinidae	11	21	26	4	4	4	36	19	15
Sciaenidae	5	12	12	1	1	1	20	8	8
Cottidae	1	1	1	0	0	0	0	0	0
Gasterosteidae	1	1	1	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0
	2	4	5	2	4	4	100	100	80
	3	3	3	2	2	2	67	67	67
Total	94	173	236	31	41	49	33	24	21

* As listed by Hubbs and Lagler (1947), with the addition of the three new subspecies described in this report.

† More than the one introduced species of lamprey will perhaps be found about Isle Royale on further exploration.

‡ Other species of Coregonidae will no doubt be added to the Isle Royale fauna when the deeper surrounding waters are fished.

§ Another catostomid may be indicated by the reports of "mullet" and "carp" in the commercial fishery.

tained evidence that *Stizostedion v. vitreum* had been stocked as fry, but it was no doubt a native species, since Isle Royale is well within its natural range.

The fish fauna of Isle Royale is rather depauperate (Table II), but not surprisingly so, in view of the northern latitude and the isolated position of the island in a large cold lake. No representatives are known of thirteen families that penetrate the Great Lakes basin from the south,

namely, Polyodontidae, Lepisosteidae, Amiidae, Hiodontidae, Clupeidae, Ameiuridae, Anguillidae, Cyprinodontidae, Poeciliidae, Aphredoderidae, Serranidae, Atherinidae, and Sciaenidae. A few species of Polyodontidae, Hiodontidae, Ameiuridae, and Sciaenidae are known from Canada north of the Great Lakes (Dymond, 1947), but appear not to have become established about Isle Royale. The Isle Royale fauna has a poor representation of several other families that are essentially southern as related to the Great Lakes, namely, the Petromyzonidae (the one representative is a recent invader; other species may be discovered), Catostomidae, and Centrarchidae. Of the Cyprinidae that reached the Great Lakes more than one third of the genera and more than one fourth of the species have populated Isle Royale—a tribute to the ability of this group to predominate. A good showing is made by the Percidae. There is a large representation of the Salmonidae, Coregonidae, and Esocidae—essentially northern groups. The coregonids would be better accounted for had the deep waters about Isle Royale been explored. The Isle Royale fauna includes all the Great Lakes representatives of Acipenseridae, Osmeridae (introduced), Gadidae, Percopsidae, and Cottidae (except for one mainland subspecies), and two of the three species of Gasterosteidae; these six families are all of northern distribution. The lack of Umbridae on Isle Royale is attributable to the failure of *Umbra limi* to range so far north in the Great Lakes. The absence of Thymallidae is related to the highly localized distribution of grayling in the southern part of its range. In approximate figures the Isle Royale fish fauna comprises one half of the Great Lakes fauna in terms of families; one third in terms of genera; one fourth in terms of species; one fifth in terms of total kinds.

The occurrence of each species in the Isle Royale fish fauna is primarily attributable to incursion; secondarily, to survival or differentiation. Like other parts of the Great Lakes region, Isle Royale was populated during and after the melting of the last continental ice sheet (Greene, 1935; Radforth, 1944; Hubbs and Lagler, 1947). Recession of the Wisconsin glacier opened channels for the reinvasion of the waters of Lake Superior by the fishes that had survived in nonglaciated areas in Alaska and in the upper Mississippi Valley and probably also in meltwater around the margins of the glacial lobes. From the northwest or from the meltwater, perhaps from both sources, probably came such northern types as: the Salmonidae, other than the introduced rainbow trout; the Coregonidae; possibly the Esocidae (*Esox lucius* and *Esox m.*

masquinongy); the Gadidae (*Lota lota maculosa*); the Cottidae; and one of the Gasterosteidae, namely, *Pungitius pungitius*.

Some of these species may also have reinvaded the Great Lakes from the upper Mississippi Pleistocene refuge (the Driftless Area). All species other than those listed above, except, of course, the three that have spread to Isle Royale in modern times, presumably reached the Great Lakes and ultimately the island from the Mississippi basin, through one of the several glacial outlets and thence through the glacial Great Lakes. They are among the species which are supposed to have reinvaded the Great Lakes through most or all of the main outlets, after which they dispersed widely through the Great Lakes basin.

As Ruthven (1909:329) remarked, it is difficult to understand how some of the species that now occur in the lakes and streams of Isle Royale reached such habitats from any other favorable waters; how certain of the weaker fishes and certain of the pond types could ever have swum across the wide, deep channel of almost icy water that separates Isle Royale from the adjacent mainland shore, which in itself is not particularly favorable to such fishes. As Koelz put it, in his manuscript report: "A journey of twenty-five miles across a depth largely over 600 feet, in water that for most of the year is near freezing, is hardly to be expected from fish that do not regularly grow larger than three inches and prefer to live on warm shoals." The Isle Royale species that we have in mind in this connection are those that were seldom or never collected around the Lake Superior shore and those that are not represented in Lake Superior by closely related types. These are: *Semotilus a. atromaculatus, Margariscus margarita* (two subspecies), *Pfrille neogaea, Chrosomus eos, Notemigonus crysoleucas auratus, Notropis heterodon, Notropis v. volucellus, Notropis heterolepis* (two subspecies), *Pimephales promelas* (two subspecies), *Percina caprodes semifasciata, Poecilichthys exilis, Lepomis gibbosus,* and *Eucalia inconstans* (which occurred in one shore collection, obviously as a straggler).

Several theories might be advanced to explain how such fishes reached Isle Royale:

(1) They may have been brought to the island by some such fortuitous means as the transport of eggs or of some other stage by birds or by high winds, with or without the aid of rafts. Such an idea seems inherently improbable, though it is strengthened by the circumstances that *Semotilus a. atromaculatus* and *Notropis heterodon* were each taken at

only one place and that several other species seem to be restricted to a small part of the island. Thus *Poecilichthys exilis* has been taken only in Chickenbone and Sargent lakes, both tributary to McCargoe Cove, and *Percina caprodes semifasciata* is known only from Lake Siskiwit and its outlet and from Lake Whittesey and Dustin Lake not far distant.

(2) They may have followed smaller watercourses on a land bridge or on the Lake Superior bottom when and if it was exposed during the evolution of the present Great Lakes. Such a route of incursion was favored by Koelz, but the survey of the Pleistocene geology of the island by George Stanley in 1930 leaves no reason to believe that any fish could have reached the island by any means other than swimming from the mainland across the intervening channel, no matter how wide, deep, and cold it may have been. There is no evidence of any postglacial land connection between Isle Royale and the mainland. Had such a connection existed it would probably have made possible the invasion of the island by *Cottus b. bairdii* and perhaps by other creek fishes.

(3) They may have, or have had, greater powers of dispersal across cold deep waters than is generally recognized. There is some evidence that waters ecologically unsuited to a species may serve as a channel of dispersal rather than as a barrier. For example, the open waters of Lake Michigan were found by Hubbs (unpublished notes, 1917–20) to be the probable route by which small-stream fishes reached creeks north of Chicago that flow in V-shaped valleys and that obviously were never connected with any body of water other than Lake Michigan. Such fishes would not be expected to inhabit the waters of Lake Michigan, and none were disclosed there by seining or by observation until huge fish populations, killed by bad water conditions, were washed ashore in windrows. Then a few examples of each of the creek species were found to have been living in the lake. Such ecological misfits would undoubtedly have entered any small creek that they encountered. Similarly, any pond or creek fish that became lost in the unfavorable waters of Lake Superior might have wandered widely, and a few might have reached Isle Royale. Perhaps some that were washed into the lake during floods accompanied brush that floated to the island. Since any fish in the latitude of Isle Royale are forced to live in icy water for several months each winter, their ability to survive for a considerable time in Lake Superior is to be expected. Crossings from the mainland may have been very rare events—as is typical in the populating of an island by any kind of animal—but thousands of years have elapsed since the Lake

Superior basin became filled with water in place of ice. The occurrence in Lake Superior and in immediately adjacent lowland waters of thirty-eight kinds of fish (more than 70 per cent of the island fauna) argues for the ability of fishes to live in the big lake.

(4) During a warm postglacial period, such as has been postulated on the basis of pollen studies, Lake Superior may have interposed a less formidable barrier against the invasion of fishes from the mainland. The occurrence of warm-water relicts in the north, as in Wisconsin (Greene, 1935) and in the northern parts of the mainland of Michigan, strongly suggests that southern types temporarily became much more widely dispersed to the north than they are at present. To us it seems highly plausible that some of the fishes listed on page 84 may be warm-water postglacial relicts in the interior waters of Isle Royale. Perhaps some of the fishes that occur also around the marginal shores reached the island at a time when Lake Superior became much warmer for a longer part of the year.

Although Lake Superior has served as a passageway from the mainland to Isle Royale even for creek and pond fishes, it apparently has been a barrier to a few others—or, these species, having once crossed, did not find in Isle Royale conditions favorable enough to effect their perpetuation. Of the thirty-six kinds of fish reported by Smith and Moyle (1944 : 115–124) from the Lake Superior tributaries along the Minnesota north shore, the only ones that have not become established on Isle Royale are: *Salmo trutta fario* (introduced); *Rhinichthys atratulus meleagris* (creek fish, locally abundant here, at northern end of range); *Notropis cornutus frontalis* (common stream fish, but near northern end of range); *Hybognathus hankinsoni* (uncommon; a bog-water species at northern end of range); *Bolesoma n. nigrum* (a small fish of sand bottoms, not likely to wander far in open water); *Micropterus d. dolomieu* (probably introduced); *Lepomis m. macrochirus* (possibly introduced); and *Cottus b. bairdii* (the stream form, less likely than *C. b. kumlieni* to negotiate the barrier).

Fishes which occur along the Canadian north shore of Lake Superior or on both sides of that region, but which apparently have not attained Isle Royale waters, are indicated, from the distributional data given by Radforth (1944) and by Dymond (1947), to be: *Salmo trutta fario*, *Moxostoma aureolum* and *M. anisurum* (these may be the fishes that

[2] For comments see list in preceding paragraph. In these lists we disregard the deep-water coregonids that have not been sampled on Isle Royale.

were commercially listed as "mullet" and "carp" from Isle Royale); *Notropis cornutus frontalis;*[2] *Hyborhynchus notatus* (a small, rather inactive bottom dweller); *Stizostedion c. canadense* (of spotted distribution in the north); *Bolesoma n. nigrum;*[2] *Micropterus d. dolomieu* (of restricted occurrence as a native fish in the northern end of its range); possibly also the largemouth bass, *Micropterus salmoides; Ambloplites r. rupestris; Cottus b. bairdii.*[2]

Considering the data for Lake Nipigon (Dymond, 1926) and Nipigon River we add to this list only one coregonid, *Leucichthys nipigon,* which is restricted to Canadian lakes.

It is obvious that the sparsity of kinds of fish on Isle Royale is attributable much more to the very limited fauna of the adjacent shores of Lake Superior than to the barrier of cold deep water. Most of the species that have come within reasonable reach of Isle Royale have somehow been able to cross this barrier and have survived on the island, at least locally. The species that appear not to have traversed the channel are of either rare or local occurrence so far north or appear to have been relatively recent arrivals from the south. They may not have had time to disperse to the island or may have arrived subsequent to the warm postglacial period, when the barrier was less effective.

It is improbable that all fish immigrants to Isle Royale have survived. It may be assumed that there has been at least local extirpation, particularly of the cold-water, clear-water pioneers. Thus most of the inland lakes were no doubt at first occupied by coregonids, which have vanished in all but the four largest and deepest lakes (p. 95). Two species, *Cristivomer namaycush* and *Catostomus c. catostomus,* though now absent, were in all probability originally present in the higher lakes of Isle Royale, for they occur, as relatively very ancient relicts, above falls in the higher lakes of the Huron Mountains on the south shore of Lake Superior (Hubbs, 1929). The occurrence of *C. c. commersonnii* in the higher lakes of Isle Royale but of *C. c. catostomus* in those of the Huron Mountains may reflect a strong competition between these species of suckers where living in restricted waters. Two other species that occur in the Huron Mountain lakes, namely, *Salvelinus fontinalis* and *Couesius p. plumbeus,* have each survived in only one of the higher lakes on Isle Royale.

At comparably high levels above Lake Superior, however, the fish fauna of the Isle Royale lakes is richer and more varied than is that of the Huron Mountain lakes (Table III) and comprises a number of spe-

TABLE III

DISTRIBUTION OF FISHES IN HIGH LAKES OF ISLE ROYALE AND ON THE SOUTH SHORE OF LAKE SUPERIOR

Region	Isle Royale			Huron Mts.			Porcupine Mts.	
Lake	Others	Desor	Lily	Ives	Others	Cliff	Carp†	Little Carp‡
Present elevation of lakes above Lake Superior	100′–200′	235′	400′	153′	233′–243′	315′	500′	950′
Estimated elevation of lakes above Minong Beach*	−40′–+60′	120′	300′	173′	253′–263′	335′	580′	1030′
Leucichthys artedi, subspecies	..	+	..	..	..	..	..	+
Leucichthys artedi annensis	..	..	..	..	+	..	..	..
Leucichthys artedi clemensi	..	..	..	+	+	..	..	..
Leucichthys hubbsi	..	..	..	+	..	..	..	..
Coregonus clupeaformis dustini	..	+	..	..	..	..	..	..
Salvelinus f. fontinalis	+	+	..	..	+	..	..	..
Salvelinus fontinalis, subspecies	..	..	..	..	..	..	..	+
Cristivomer n. namaycush	..	..	..	+	+	..	..	..
Catostomus c. commersonnii	+	+	..	..	..	..	+	+
Catostomus c. catostomus	..	..	..	+	+	..	..	..
Semotilus a. atromaculatus	+	..	..	..	..	..	+	+
Margariscus margarita nachtriebi	+	+	..	..	..	..	+	?
Margariscus margarita koelzi	+	..	..	..	..	..	..	..
Couesius plumbeus plumbeus	..	+	..	+	+	..	..	?
Rhinichthys atratulus meleagris	..	..	..	..	..	..	+	+
Pfrille neogaea	+	..	+	..	..	..	..	..
Chrosomus eos	..	..	..	..	..	..	+	+
Notropis cornutus frontalis	..	..	..	..	..	..	..	?
Notropis h. hudsonius	..	..	..	..	..	..	+	..
Notropis h. heterolepis	+	..	..	..	..	..	+	..
Notropis h. regalis	+	..	..	..	..	..	..	..
Pimephales p. promelas	+	..	+	..	..	..	+	+
Pimephales p. harveyensis	+	..	..	..	..	..	..	..
Hyborhynchus notatus	..	..	..	..	+	..	..	..
Esox lucius	+	..	..	..	..	..	..	..
Percopsis omiscomaycus	+	+	..	..	..	..	+	..
Perca flavescens	+	..	..	+	+	..	+	..
Cottus ricei	..	+	..	..	..	..	..	..
Cottus cognatus gracilis	..	+	..	..	..	..	..	..
Eucalia inconstans	+	+	+	..	+	..	..	+
Pungitius pungitius	+	+	..	..	..	..	..	+
Total no. of species	15	11	3	6	9	0	10	8, 9 or 10

* From George Stanley's estimates; the Minong water plane, extrapolated from positions known on Isle Royale and on the Keweenaw Peninsula, lies from 10 to 80 feet below Lake Superior near the Porcupine Mountains, and from 20 feet above to 20 below the lake near the Huron Mountains.

† Data from Ruthven (1906: 107–108) and from the Michigan Institute for Fisheries Research (1938, 1945). *Micropterus d. dolomieu* and *Lepomis m. macrochirus* have been stocked in the lake (1935, 1936). Carp Lake is now called Lake of the Clouds.

‡ Data from Ruthven (1906: 107–108) and from surveys by the Institute for Fisheries Research, August 29–30, 1941, and summer and fall of 1947. Included are a few species reported by Ruthven from Little Carp River just above the lake. Little Carp Lake is now often called Mirror Lake. Ruthven's record of *Couesius plumbeus* from Little Carp River is questioned because it is thought very possible that it was based on *Margariscus margarita nachtriebi*, with which *Couesius p. plumbeus* was confused (Hankinson, 1917). The pertinent specimens appear to be no longer extant. Nor could the specimens identified as *Nototropis cornutus* be found, nor is there any record of them in the catalog of the University of Michigan Museum.

cies that are presumed to have reëntered the Lake Superior basin later in the sequence of postglacial reinvasion. This difference may be attributed to two causes.

In the first place, after the Isle Royale lakes had been formed by the receding levels of the glacial Great Lakes, fishes were less abruptly and less completely isolated. The outlets of the higher lakes on the island are not blocked by such impassable barriers as exist in the outlets of all higher Huron Mountain lakes other than Trout (Hubbs, 1929). At present most of the outlets on Isle Royale are too small to serve effectively as channels by which fishes can ascend to the lakes, but during some moister postglacial period there was presumably a more ample discharge.

In the second place, the Isle Royale lakes were cut off from the antecedent of Lake Superior at a later time than were the Huron Mountain lakes. They are now, it is true, about as high above Lake Superior, but this elevation is due in large part to tilting of the land surface during the postglacial isostatic readjustment. The relative age of the lakes is indicated much better by their height above the Minong water plane than by their present elevation above Lake Superior (Table III). The Minong beach represents a lake stage intermediate between Lake Algonquin and Lake Nipissing. On Isle Royale, according to George Stanley's personal communication, it grades from about 165 feet above Lake Superior in the northeastern part of the island to only 80 feet near the southwestern end. By extrapolation of Stanley's estimates the Minong level near the Huron Mountains lies from 20 feet below to 20 above present Lake Superior. Except for Lake Desor and Lily Lake the higher Isle Royale lakes lie from about 40 feet below to about 60 feet above the Minong plane, whereas the fish-containing Huron Mountain lakes are situated about 170 to 260 feet above the same plane, according to Stanley's estimates. Though Lake Desor is 235 feet above Lake Superior, it is only about 120 feet above the Minong plane and, therefore, is less ancient than the Huron Mountain lakes that are at almost exactly the same elevation above Superior. Lily Lake lies nearly 400 feet above Superior and about 300 feet above the Minong water plane.

The higher Isle Royale lakes harbor several kinds of fish that do not occur in the older, originally higher, Huron Mountain lakes, or are represented there only in Trout Lake. These forms fall into several categories:

(1) Glacial Great Lakes relicts, in Lake Desor, that are represented by cognates in the higher Huron Mountain lakes: *Leucichthys artedi*, subspecies, and *Coregonus clupeaformis*, subspecies.

(2) Species that occur in none of the higher Huron Mountain lakes and are not represented there by cognates. Included are northern types that are probably glacial Great Lakes relicts, which have become extirpated in the Huron Mountain lakes, just as other relicts have become extinct in the Isle Royale lakes (p. 87). Included also are more southern types that are presumed to have arrived in the Superior basin after the Huron Mountain lakes were cut off by barriers in the outlets. Not all the species are readily assignable to either category, but, tentatively, they may be listed in the following sequence of decreasing age as inhabitants of the Superior basin: 1, *Pungitius pungitius;* 2, *Cottus cognatus gracilis;* 3, *Cottus ricei;* 4, *Esox lucius;* 5, *Percopsis omiscomaycus;* 6, *Margariscus margarita* (two subspecies); 7, *Pfrille neogaea;* 8, *Catostomus c. commersonnii;* 9, *Notropis heterolepis* (two subspecies); 10, *Pimephales promelas* (two subspecies); 11, *Semotilus a. atromaculatus.* Toward the middle of this list the assigned sequence is particularly arbitrary.

(3) Kinds not represented in higher Huron Mountain lakes, except in Trout Lake, which has no impassable barrier in its outlet: *Salvelinus f. fontinalis* and *Eucalia inconstans.*

Lake Desor, the highest of the Isle Royale lakes, with the exception of the pond named Lily Lake, has eleven fish species, nearly twice as many as are native in any of the upper Huron Mountain lakes. Its large size and its varied habitats are the apparent reasons for the retention of early postglacial arrivals, and the gradient of its outlet seems to have permitted the entry of *Catostomus c. commersonnii, Semotilus a. atromaculatus, Margariscus margarita nachtriebi,* and *Eucalia inconstans,* if any or all of these arrived in the region after Lake Desor was formed.

The Lily Lake fauna comprises three northern bog-water fishes, *Pfrille, Pimephales,* and *Eucalia.* These may have entered by an outlet, or they may be relicts dating from the ancient origin of the lake. If they are relicts here, they probably occurred originally in the higher Huron Mountain lakes but failed to survive because of rather unfavorable conditions. At present Lily Lake lies in a shallow trough, but at an earlier, moister, period it may have risen high enough to discharge over the lowest point in the surrounding rim, either to the north or to the south. The pertinent physiographic evidence should be checked.

	Patterson	Richie	Sargent	Sheheeb	Sholts	Siskiwit	Stickleback	Sumner	Superior*	Theresa	Wagejo	Wallace	Whittlesey	No. of lakes per species
Petromyzon	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Acipenser f	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Salmo gaird	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Salvelinus f	..	..	..	..	..	R	..	..	+	..	..	..	..	4
Cristivomer	..	..	..	..	..	+	..	..	+	..	..	..	..	2
Cristivomer	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Leucichthy	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Leucichthy	..	+	..	..	..	..	..	..	..	..	..	..	..	1
Leucichthy	..	..	+	..	..	..	..	..	..	..	..	..	..	1
Leucichthy	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Leucichthy	..	..	..	..	..	+	..	..	..	..	..	..	..	1
Leucichthy	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Coregonus	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Coregonus	..	..	..	..	..	+	..	..	..	..	..	..	..	1
Coregonus	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Prosopium	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Osmerus m	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Catostomus	..	+	+	..	+	+	..	..	+	..	..	+	+	16
Catostomus	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Semotilus a	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Margariscu	..	..	..	..	..	..	..	..	..	..	..	..	..	3
Margariscu	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Couesius p	..	..	..	..	..	..	..	..	+	..	..	..	..	2
Rhinichthy	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Pfrille neog	..	..	..	..	..	..	..	+	+	..	..	+	..	5
Chrosomus	..	..	..	..	..	..	..	..	+	..	..	+	..	2
Notemigon	..	+	+	+	..	..	..	..	+	..	..	..	..	11
Notropis at	..	..	..	..	..	+	..	..	+	..	..	..	..	2
Notropis h	..	+	+	..	..	+	..	..	+	..	..	..	+	11
Notropis h	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Notropis v	..	+	..	..	..	..	..	..	+	..	..	..	..	2
Notropis h	..	+	+	+	+	+	..	+	+	+	..	+	..	22
Notropis h	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Pimephales	..	..	..	..	..	..	..	+	+	..	..	+	..	5
Pimephales	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Esox lucius	+	+	+	+	+	+	..	..	+	..	+	..	+	30
Esox m. m	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Lota lota n	..	..	..	..	..	+	..	..	+	..	..	..	..	2
Percopsis o	..	+	..	..	..	+	..	..	+	..	..	..	+	7
Perca flave	+	+	+	+	+	+	..	..	+	..	..	..	+	29
Stizostedio	..	..	..	..	..	..	..	..	+	..	..	..	+	4
Percina ca	..	..	..	..	..	+	..	..	+	..	..	..	+	4
Poecilichth	..	..	+	..	..	..	..	..	..	..	..	..	..	2
Lepomis gi	..	+	..	..	..	..	..	..	+	..	..	..	..	3
Triglopsis	..	..	..	..	..	..	..	..	+	..	..	..	..	1
Cottus rice	..	..	..	..	..	+	..	..	+	..	..	..	+	4
Cottus bai	..	..	..	..	..	..	..	..	+	..	..	..	..	2
Cottus cog	..	+	+	..	..	+	..	..	+	..	..	..	..	7
Eucalia ine	..	..	..	..	..	+	+	+	+	+	..	+	..	10
Pungitius	..	..	..	..	..	+	..	..	+	..	..	..	..	4
Number	2	11	9	4	4	17	1	4	38	2	1	6	8	

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F. Lagler

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lakes: *Leucichthys artedi,*
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TABLE IV

DISTRIBUTIONAL SYNOPSIS OF FISHES IN ISLE ROYALE LAKES

Based mostly on data obtained by Walter Koelz in 1929. +, records based on specimens. R, presumably reliable reports

Species	Ahmeek	Amygdaloid	Angleworm	Beaver	Benson	Chickenbone	Desor	Dustin	Epidote	Eva	Feldtmann	Forbes	George	Halloran	Harvey	Hatchet	Intermediate	John	Lesage	Lily	Linklater	Livermore	Mason	McDonald	Mud	Newt	Otter	Pettegrew	Pickle	Sargent	Shoalcoob	Sholtz	Siskiwit	Stockbeck	Sumner	Superior*	Theresa	Wagejo	Wallace	Whittlesey	No. of lakes per species
Petromyzon marinus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Acipenser fulvescens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Salmo gairdnerii irideus	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													1
Salvelinus f. fontinalis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+									..	..	..													4
Cristivomer n. namaycush	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..						+							2
Cristivomer namaycush siscowet	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..						+							1
Leucichthys artedi, subspecies	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													1
Leucichthys artedi, subspecies	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Leucichthys artedi sargenti	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Leucichthys artedi arcturus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Leucichthys bartletti	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Leucichthys nigripinnis cyanopterus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Coregonus c. clupeaformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Coregonus clupeaformis, subspecies	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Coregonus clupeaformis dustini	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													1
Prosopium cylindraceum quadrilaterale	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Osmerus mordax	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Catostomus c. commersonnii	..	..	..	..	..	+	+	+	..	..	+	..	..	..	+	+	+	+							+	..	..						+					+	+	16
Catostomus c. catostomus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	++									..	..	..													1
Semotilus a. atromaculatus	..	..	..	..	..	..	+	..	..	..	..	+	..	..	..										..	..	..													1
Margariscus margarita nachtriebi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+										..	..	..													3
Margariscus margarita koelzi	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													1
Couesius p. plumbeus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													2
Rhinichthys c. cataractae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Pfrille neogaea	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..										..	..	..													5
Chrosomus eos	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													2
Notemigonus crysoleucas auratus	..	..	..	+	..	..	..	..	..	+	..	..	..	+	..		+						+		..	..	+													11
Notropis atherinoides: acutus × atherinoides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		+								..	..	+													2
Notropis h. hudsonius	..	+	..	+	..	+	..	..	..	+	..	..	..	..	..		+								..	..	+													11
Notropis heterodon	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Notropis v. volucellus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													2
Notropis h. heterolepis	..	..	..	+	..	..	..	+	..	+	..	+	..	+	..		+	+				+	+		+	..	+													22
Notropis heterolepis regalis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+					+					..	..	..													1
Pimephales p. promelas	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+									..	..	..													5
Pimephales promelas harveyensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+										..	..	+													1
Esox lucius	+	+	+	+	R	+	..	+	+	+	+	..	+	+	+		+	+	+	+	+	+	+	+	+	..	+						+							30
Esox m. masquinongy	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Lota lota maculosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													2
Percopsis omiscomaycus	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	+	+								..	..	..													7
Perca flavescens	+	+	+	+	+	+	..	+	+	..	+	+	+	+	+		+	+	+	+	+	+	+	+	..	..	+						+							29
Stizostedion v. vitreum	..	..	..	..	..	+	..	+	..	..	..	..	..	..	..										..	..	..													4
Percina caprodes semifasciata	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..										..	..	..													4
Poecilichthys exilis	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..										..	..	..													2
Lepomis gibbosus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													3
Triglopsis thompsonii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..										..	..	..													1
Cottus ricei	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													4
Cottus bairdii kumlieni	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..										..	..	..													2
Cottus cognatus gracilis	..	..	..	..	..	+	+	..	..	..	..	..	..	..	..										..	..	..													7
Eucalia inconstans	..	..	..	..	..	..	+	..	..	..	..	..	..	..	+										..	..	..													10
Pungitius pungitius	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..										..	..	..													4
Number of kinds per lake†	2	3	2	5	4	8	11	6	2	4	3	3	2	4	6	8	4	4	4	3	4	3	6	2	3	0	5	7	11	6	4	4	17	1	4	38	2	1	6	8	

* Including adjacent stream mouths, marshes, and ponds not more than twenty-five feet higher than the Lake Superior

† The percentages of the fauna occurring in each lake are approximately twice the number of kinds.

In several fish-faunal respects the higher Isle Royale lakes agree with Carp Lake (Lake of the Clouds) and Little Carp Lake (Mirror Lake), which lie high in the Porcupine Mountains (Ruthven, 1906). These high lakes on Isle Royale and in the Porcupine Mountains are inhabited by several species that do not occur in the higher waters of the Huron Mountains (Table III and Hubbs, 1929). Some may have existed there at an early date, but if so, they appear not to have survived. Others probably arrived in the Lake Superior basin after the Huron Mountain lakes were cut off. The time when the species that occur in the Porcupine Mountain lakes arrived may eventually be measured by a dating, in glacial lake terms, of the falls in the lower and mid sections of the outlet streams (Carp River and Little Carp River). This sort of study is much needed in the analysis of the past and present distribution of fishes in the Great Lakes region.

The richness of the Isle Royale fish fauna decreases with elevation (Fig. 2). The number of species in the five main elevation categories decreases as follows: 40, 20, 15, 11, 3 (the percentage composition is approximately twice the number of species). Part of this decrease is due to the fewer waters and less varied habitats at the higher reaches. Historical factors, however, are probably also prominently involved. Many of the species that are confined to the lower waters probably arrived late in the sequence of postglacial redispersal and have not been able to ascend the generally small and intermittent streams of Isle Royale to the higher lakes.

In the waters of Isle Royale the fishes are scatteringly distributed, as though chance may have played an important rôle in dispersal and survival (Table IV). Twenty-four kinds, comprising nearly half of the Isle Royale fish fauna, are not known to occur in more than one lake. Eight kinds are known to inhabit only two lakes. Combinations of four lakes make up the habitat of five forms. Further considering the number of lakes per species, we find that three lakes, five lakes, seven lakes, and eleven lakes comprise the entire known habitat of two species. Of five ubiquitous kinds, one occurs in ten lakes, one in sixteen lakes, another in twenty-two lakes, another in twenty-nine lakes, and yet another in thirty lakes. The limited habitat of many of the forms is in part accounted for by the local differentiation of several of the species.

In general, the larger as well as the lower lakes have the higher number of species. In the order of known number of kinds of fish the lakes rank as follows:

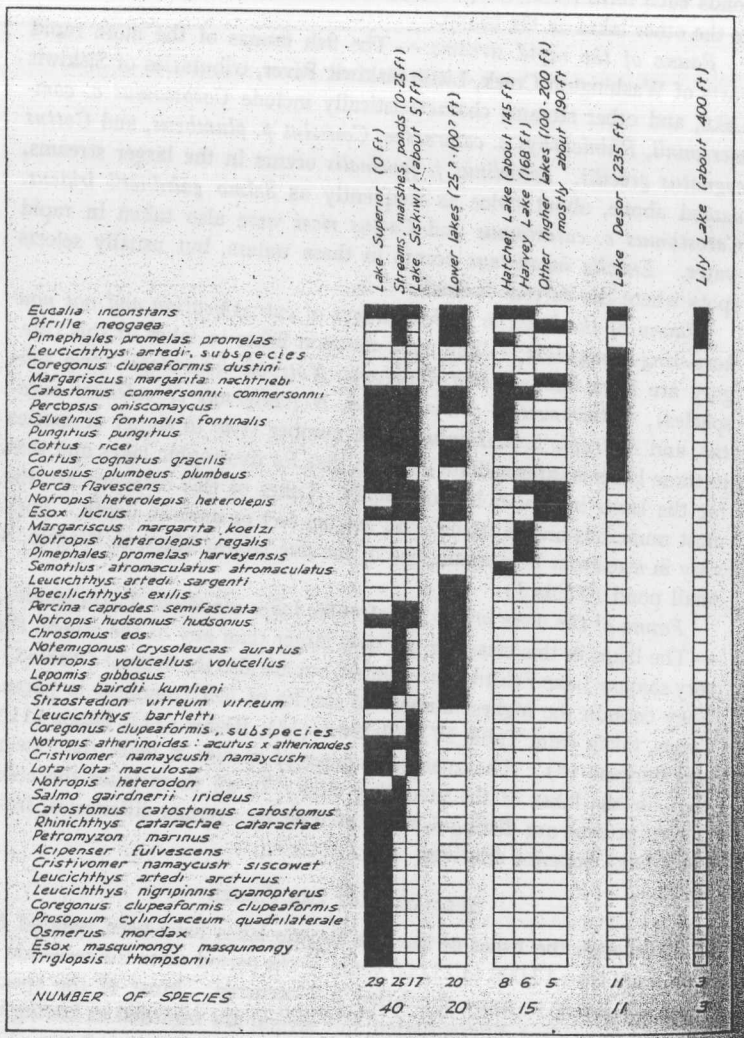


FIG. 2. Analysis of the Isle Royale fish fauna, mostly by lakes and by groups of lakes having similar elevation

Thirty-eight kinds: Lake Superior and adjacent stream mouths, ponds, and marshes less than 25 feet higher than the main lake.

Seventeen kinds: Siskiwit Lake, by far the largest of the inland lakes and one of the lower in elevation (57 feet).

Eleven kinds: Lakes Richie and Desor, next in order of size, except perhaps for Lake Feldtmann (a low-elevation but very shallow lake, in which only three species were caught). Lake Richie is one of the lower lakes (less than 100 feet elevation), but Lake Desor is the highest (235 feet) of the main lakes.

Nine kinds: Sargent Lake, next in order of size, and one of the lower lakes.

Zero to eight kinds: other inland lakes in which there seems to be very little correlation between number of species and either the size of the lake or its elevation.

Ecological Analysis of the Fauna

On and about Isle Royale we recognize seven major habitat types that appear to harbor distinctive fish associations: (1) Lake Superior, from a depth of eight fathoms to the shore zone; (2) the exposed shore; (3) the stream mouths, base-level portions of streams, and sheltered, sometimes vegetated, coves; (4) the boggy streams, beaver ponds, and dystrophic lakes; (5) the rapid streams; (6) the lakes in various stages of eutrophication but not harboring coregonids; (7) the more or less oligotrophic lakes inhabited by coregonids.

Fauna of Lake Superior from a depth of eight fathoms to the shore zone. — The fishes that characteristically dwell in less than fifty feet of water during summer months, twenty kinds, are known from our experimental gill-net collections, from the commercial fish take, and from anglers' reports. They are: *Petromyzon marinus, Acipenser fulvescens, Salmo gairdnerii irideus, Salvelinus f. fontinalis, Cristivomer n. namaycush, C. n. siscowet* (perhaps chiefly in still deeper water), *Leucichthys artedi arcturus, L. nigripinnis cyanopterus* (generally in deeper water), *Coregonus c. clupeaformis, Prosopium cylindraceum quadrilaterale, Osmerus mordax* (probably), *Catostomus c. commersonnii, C. c. catostomus, Couesius p. plumbeus, Esox lucius, E. m. masquinongy* (if Ruthven's 1906 record is correct), *Lota lota maculosa, Perca flavescens, Stizostedion v. vitreum, Triglopsis thompsonii* (probably). Obviously these kinds differ in abundance and vary in numbers with the seasons. In

addition to the forms cited, others, such as deep-water coregonids, may enter the habitat for spawning purposes. Some of the species listed are more characteristic of these and deeper waters than are others. For example, *Catostomus catostomus* is more typical of this portion of Lake Superior than is *C. commersonnii*.

Fauna of the exposed shore. — Another assemblage of species inhabits the rocky, often precipitous parts of the Isle Royale shore that are exposed to wave action. This habitat is not continuous around the island, but is interrupted by sheltered coves or by stretches of sharp drop-off. In practice it has been treated as the exposed hard-bottomed section of the shore zone that is seinable by wading. The most common associates are *Couesius p. plumbeus*, *Rhinichthys c. cataractae*, the young of the two species of *Catostomus*, *Percopsis omiscomaycus*, *Cottus bairdii kumlieni*, *C. cognatus gracilis*, and *Pungitius pungitius*. Other kinds occur less frequently, or are thought to occur, to bring the probable total to twenty.

Fauna of the stream mouths, base-level parts of streams, and sheltered, sometimes vegetated, coves. — Most common here are *Catostomus c. commersonnii*, *Couesius p. plumbeus*, *Rhinichthys c. cataractae*, *Percopsis omiscomaycus*, *Cottus cognatus gracilis*, *Eucalia inconstans*, and *Pungitius pungitius*. Other fishes inhabiting sheltered waters of this sort are strays from zones where they are more abundant. The species listed are the typical elements, but a total of about thirty-one kinds may be represented.

Fauna of the boggy streams, beaver ponds, and dystrophic lakes. — Although they range in elevation from some of the lowest bodies of water (almost base-level beaver ponds) to the highest water studied (Lily Lake), such senescent waters have fish-faunal elements in common. *Eucalia inconstans* occurs in nearly all of them. *Pfrille neogaea*, *Chrosomus eos*, and *Pimephales p. promelas* are, however, most characteristic elements, since on the island they are common in and are largely confined to such boggy situations. Such habitats are characteristic of these species through Michigan. The nine kinds that are represented include, in addition to the species named above, *Catostomus c. commersonnii*, *Notemigonus crysoleucas auratus*, *Notropis h. heterolepis*, *Esox lucius*, and *Perca flavescens*. The waters involved are all shallow, soft-bottomed, and brownish. The lakes included are those that have predominantly bog borders and are mostly not over ten feet deep, namely, Ahmeek, Wallace, Sumner, Theresa, Mud, Sholts, Stickleback, and Lily (see Table I). These lakes as well as several unnamed ponds each have six or fewer fish species — on the average fewer than do the other lakes on the island.

Fauna of the rapid streams. — The fish faunas of the more rapid parts of Washington Creek, Little Siskiwit River, tributaries of Siskiwit Lake, and other streams characteristically include *Catostomus c. commersonnii*, *Rhinichthys c. cataractae*, *Couesius p. plumbeus*, and *Cottus cognatus gracilis*. *Salvelinus f. fontinalis* occurs in the larger streams, named above, about twice as frequently as *Salmo gairdnerii irideus*. *Catostomus c. catostomus* and *Cottus ricei* were also taken in rapid water. *Eucalia inconstans* occurs in these waters, but usually selects spots where the current is slack.

Fauna of the lakes in various stages of eutrophication and not now harboring coregonids. — The most common fishes in lakes of this category are *Esox lucius*, *Perca flavescens*, *Notropis heterolepis* (two subspecies), *Catostomus c. commersonnii*, *Notemigonus crysoleucas auratus*, and *Notropis h. hudsonius*. The number (two to eight) of species in these lakes is intermediate between that for dystrophic lakes and that for the lakes inhabited by coregonids. Lakes of this category are the most numerous on the island. All are ten feet or more in depth. They vary in size from Feldtmann, one of the five largest lakes, to Wagejo, a small pond (Table I).

Fauna of the more or less oligotrophic lakes inhabited by coregonids. — The lakes in this class are not only larger than any of the others, the very shallow Lake Feldtmann excepted, but are also the deepest (Table I). They contain the highest number of species of fish (numbers in parentheses, taken from Table IV): Siskiwit (17), Richie (11), Desor (11), and Sargent (9). The average number of species is more than twice that for the lakes of the preceding class. In all these lakes the coregonids present are distinguishable, at least by average differences, from their Lake Superior relatives.

Speciation of the Fishes

Although the fishes of the Isle Royale lakes have been isolated for not more than 12,000 to 25,000 years — the period since the recession of the last icecap — some speciation has occurred. Most of the species exhibit no evident differentiation, but several are regarded as having become subspecifically modified in certain of the lakes, and one, *Leucichthys bartletti* of Siskiwit Lake, is interpreted as specifically distinct.

The most notable differentiation is, perhaps, that of three minnows (Cyprinidae) in Harvey Lake (Pl. I). In seeking to explain why *Margariscus margarita, Notropis heterolepis,* and *Pimephales promelas* have become so changed in this one lake as to warrant subspecific separation, whereas they have remained scarcely or much less modified in other lakes on the island, our thoughts center on isolation rather than on any peculiar ecological conditions. Harvey Lake lies 168 feet above Lake Superior near the middle of the north shore (Fig. 1), therefore well above the Minong water plane (according to the findings of George Stanley). Hence its fishes may have been isolated for about 15,000 years, for Lake Nipissing is dated back about 4,000 years and the Minong stage as 6,000 to 12,000 years still farther back (estimates by Stanley). The outlet is so small and in part so steep that it has probably been a barrier to the further invasion of the lake by minnows since the lake was formed by the lowering of the Great Lakes. The outlet (into Todd Harbor) is scarcely more than one mile long — shorter than that of other Isle Royale lakes of similar elevation (Fig. 1). So far as we know, the stream has not been completely traversed to determine whether any barriers exist that may have been totally impassable to fish. In the other lakes inhabited by the same species in unmodified form the period of isolation has been shorter; or probably less complete, on account of repeated incursions. Or in other lakes the species may have been isolated equally long, or longer, but may not have speciated. It is well recognized that time is not a precise correlate of speciation.

The physical characteristics of Harvey Lake, as observed by Koelz (1929 manuscript) and by Lagler (Pl. I), offer no explanation for the differentiation of the three minnows. It is of moderate size, being little more than one mile long and one-fourth mile wide. Like many of the other lakes it is shallow; 190 soundings by Koelz indicate that there are extensive shoal areas less than six feet deep and a maximum depth, over a broad area, of thirteen feet. As in many lakes occupied by the species in unmodified form, the bottom is mostly mud, with some sand and peat in two coves and with many snags along the shore. There are no extensive lateral marshes, and the low shoreline, with areas of broken rock and vegetation, is moderately varied by coves and by three islands. When Koelz visited the lake in 1929 the surrounding area was well timbered with birch, cedar, Norway pine, white pine, and other trees characteristic of the region (in 1936 fire destroyed these woods, and recovery was slight by 1945). Pondweeds (*Potamogeton*) grow on the bottom in some abundance to depths of about ten feet. Before the water plants became heavily browsed by moose, the vegetation was probably more abundant, as it often is in lakes that are inhabited by the minnows in question. The temperature, as expected in such a lake, is rather warm (about midday on September 1, 1929, Koelz reported a range from 25.8° C. at the surface to 20.0° C. at the thirteen-foot bottom). The water is turbid, again as expected (the thermometer disappeared from sight at three feet). The chemistry of the water has not been studied, but there is no reason to suspect any outstandingly distinctive chemical features.

More extreme yet briefer differentiation seems to be exhibited by *Leucichthys bartletti,* the specifically endemic coregonid described by Koelz (1931:368–370, pl. 39) from Siskiwit Lake. Its ancestor has not been definitely determined. Its variability is perhaps due to hybridization in the past (p. 106). Its period of isolation probably approaches 5,000 years, for Siskiwit Lake lies, as determined by Stanley (personal communication), fifty-seven feet above Lake Superior, slightly higher than the Nipissing beach. Since it inhabits deep water, the species probably has remained completely isolated. It is unlikely that either it or its ancestor penetrated into the lake through the outlet, which, moreover, has a low cascade near its source. Specific differentiation is also claimed for another inland-lake form of the genus, namely, *Leucichthys hubbsi* Koelz (1929b) of Ives Lake in the Huron Mountains, but that cisco has been isolated much longer, for Ives Lake has an impassable chutelike outlet (Hubbs, 1929) and lies far above the Minong water plane.

All other coregonids of the lakes on Isle Royale are measurably different from, though conspecific, with those of Lake Superior, from the ancestors of which they were probably derived.

The *Coregonus* of Lake Desor was distinguished by Koelz (1931: 379) on the basis of a higher average number of scales, a longer head, a larger mouth, longer pectoral fins, and a slenderer body. These differences probably arose during the time since this fish became isolated, before the Minong stage (p. 89). Koelz referred to this subspecies the race in Trout Lake, Wisconsin, but we think that the two forms are distinct enough to be treated as subspecifically different, that their resemblance is due to convergence, and that *C. c. dustini* is endemic in Lake Desor.

The *Coregonus* of Siskiwit Lake, although isolated only since Lake Nipissing time, also appears to have become subspecifically differenti-

ated from the Lake Superior whitefish, although at present it seems impracticable to name the subspecies (pp. 106–109).

The ciscoes (*Leucichthys artedi*) of the Isle Royale lakes appear to be differentiated from one another and from those of inland lakes elsewhere, as well as from the Lake Superior form, *L. a. arcturus*, though their separation is attended with some doubt (see pp. 102–104). The only distinctively named race is *L. a. sargenti* of Sargent Lake. The Lake Richie form has been identified with it, but the condition of the specimens renders impossible its definite identification. The Siskiwit Lake "herring" has also been referred to *L. a. sargenti*, but we regard it as the young of *L. bartletti*. The cisco of Lake Desor as well as that of Chautauqua Lake, New York, was illogically identified by Koelz with *L. a. huronicus*, a local form of Rush Lake, at the base of the Huron Mountains, on the south side of Lake Superior. Like the *Coregonus clupeaformis* of Siskiwit Lake, the *Leucichthys artedi* of Lake Desor appears to represent a distinct subspecific endemic, though the granting now of a name seems unwise. In Lake Desor, though the isolation has been equally long, the *Leucichthys* seems to have changed less than the *Coregonus* has. But the differentiation of both appears to have been local. Resemblances between the end products of speciation in distant, unconnected lakes is attributable to convergence, or merely to coincidence.

Other species may have become more or less differentiated on Isle Royale. As is noted on page 127, the three inland-lake populations of *Stizostedion v. vitreum* are very peculiar in appearance and may represent local differentiates.

There are some indications that ecotypic subspecies or races of *Leucichthys artedi* and of *Cristivomer namaycush* occur along the Lake Superior shores of Isle Royale.

Conservation and Preservation of the Fish Fauna

As one of us pointed out (Hubbs, 1940), aquatic life had long been neglected in the nature-preservation policies of the national parks. A definite policy, more acceptable to preservationists, is now in force, but the pressure to build up and maintain angling in the parks is so great as to demand constant vigilance on the part of all who are concerned with the implementation of the enlightened policy. We urge that a permanent ban be placed on the introduction into Isle Royale of any exotic fishes, including exotic stocks of native game species. Trout are

particularly subject to raciation. Every effort should be made to maintain the indigenous races. The depletion of the native species and races should be prevented by fishing regulations and by the maintenance of productive natural conditions in the lakes and streams. Commercial fishing also should be regulated so as to prevent depletion of native stocks.

Annotated Species List

Under each species heading that follows there is given a synopsis of the known distribution on Isle Royale, along with some notes on habitat and habits, remarks on the characters and taxonomy of certain species, and diagnoses of the three new subspecies of Cyprinidae.

The fishes collected on the island have been identified by means of the criteria that have been developed in the University of Michigan Museum of Zoology since 1920. These characters are briefly and incompletely summarized in our keys to the Great Lakes fishes (Hubbs and Lagler, 1939, 1941, 1947). The last of these treatises is followed in matters of nomenclature and sequence of species. In the Coregonidae our work is based largely on the monographs by Koelz (1929a, 1931), though we take issue with a number of his conclusions regarding the systematics of the races in the inland lakes. The taxonomy of Great Lakes fishes has been treated in the publications just cited, as well as in the annotated check-list by Hubbs (1926), with supplements by Hubbs and Greene (1928) and by Hubbs (1930).

All collections on which this report is based are deposited in the University of Michigan Museum of Zoology. The directors and fish curators of that museum have granted full use of all available material and reports.

Petromyzonidae — Lamprey Family

Petromyzon marinus Linnaeus

Sea lamprey

A recent capture indicates that the sea lamprey has finally reached Isle Royale, in the course of its rapid spread through the Great Lakes, after its entry into Lake Erie through Welland Canal (Hubbs and Pope, 1937). A 9.5-inch specimen was taken from a ten-pound lake trout off Rock Harbor on August 15, 1946, by commercial fishermen, who reported their catch and sent the lamprey to Dr. John Van Oosten. The record has been published by Creaser (1947).

ACIPENSERIDAE — STURGEON FAMILY

Acipenser fulvescens Rafinesque

Rock sturgeon

No specimens of sturgeon have been collected about Isle Royale, but Karl Gilbert reports that the species is occasionally encountered by commercial fishermen in Washington Harbor. Isle Royale is well within the natural range of the species, and it is known from other localities in Lake Superior.

SALMONIDAE — SALMON FAMILY

Salmo gairdnerii irideus Gibbons

Common rainbow trout

As a result of stocking in past years, the rainbow trout (or "steelhead," as larger lake-run individuals are often called in this region) is well established in the streams and about the shore of Isle Royale. It is particularly common in Washington (Windigo) Creek and in Washington Harbor. At the east end of this harbor it was repeatedly seen with the common brook trout (*Salvelinus f. fontinalis*) in schools of ten- to twelve-inch individuals moving along the shore in about fifteen feet of water. Commercial fishermen reported to Dr. John Van Oosten in 1927 that they occasionally caught this trout about this embayment. It provides good sport fishing in Washington Creek. The first Isle Royale specimen was collected from this stream by Captain R. E. Ellsworth on September 14, 1920. The 1945 collections are L45 : 808, 810, 816, and 819 (pp. 77–78).

The brown trout, *Salmo trutta fario* Linnaeus, is reported to have been stocked inadvertently during recent years in a few localities on Isle Royale. None have been reported as having been seen or caught since the planting, and none were secured in 1945 during the seining of the streams in which the species is presumed to have been planted. It is probable that this trout failed to become established. From the standpoint of sound national park policy it is very fortunate that this exotic species did not persist, for it might have become a serious competitor with and predator upon the indigenous fishes.

Salvelinus fontinalis fontinalis (Mitchill)

Common brook trout

The brook trout is native to Isle Royale, as it is to other Lake Superior waters. It has also been stocked, which is unfortunate, since it

cannot now be assured that the local populations are strictly indigenous. It now occurs in at least two lakes, in several streams and their mouths, and in Lake Superior about the island. Particular centers of abundance were found to be the Little Siskiwit River below the falls, the shoal waters at the east end of Washington Harbor, and Washington Creek. Ruthven (1906 : 109; 1909 : 330) recorded it from this stream and harbor and, as *Cristivomer namaycush,* from Benson Brook (see below). Koelz's records are from Hatchet Lake and Lake Desor. He also indicated it as probably occurring in Siskiwit Lake, from which anglers also report it. In 1930 Stanley took specimens in Desor Creek (Lake Desor outlet), just above Todd Cove, and it occurred again in this stream in our 1945 collections. "Coasters" (lake-run brook trout) are reported from Rock Harbor in the vicinity of Mott Island. The 1945 collecting stations are L45 : 802, 810, 818, 819, 825, 834, and 852 (pp. 76–81).

Cristivomer namaycush namaycush (Walbaum)

Common lake trout

As would be expected from its northern range, the lake trout (also called "Mackinaw trout") occurs on the shoals as well as in deeper waters all around the island. Koelz obtained it also in Siskiwit Lake. Smaller individuals, about twelve to eighteen inches long, were taken in our experimental gill-nets in depths of thirty-five feet and less. The 1945 collecting stations are L45 : 801, 812, 832, 844, and 847 (pp. 76–79). Commercial fish returns, conferences with fishermen, and catch inspections indicate captures in all the principal bays and coves and about most of the named islands. Specific localities mentioned in the commercial fishermen's returns include Amygdaloid Channel, Belle Harbor, Belle Isle, Chippewa Harbor, Fisherman Home Cove, Hay Bay, Johnson Island, Little Boat Harbor, Malone Island, Rock Harbor, Siskiwit Bay, Tobin Harbor, Todd Harbor, Washington Harbor, Washington Island, and Wright Island. According to Fire Guard George Allen, lake trout were taken regularly off Blake Point, on Three Foot Shoal, and in Rock Harbor during the summer of 1945. Ruthven (1906: 109; 1909 : 330) reported the species from Washington Harbor, the north shore of the island, Rock Harbor, and off the "east" coast of the island. The fingerling (41 mm. long) from Benson Brook, identified by Ruthven as *Cristivomer namaycush,* proves on reëxamination, with the better material now available, to be a brook trout (*Salvelinus f. fontinalis*).

"Deep-sea" trolling for lake trout provides great sport for visitors to the Isle Royale National Park. This species and the whitefish comprise the bulk of the commercial fish catch of the island.

Commercial fishermen about Isle Royale, as elsewhere in the Great Lakes, make the plausible claim that in addition to the siscowet there are two kinds of lake trout in the shoal waters. An investigation of the trout races is urgently needed.

Cristivomer namaycush siscowet (Agassiz)

Siscowet lake trout

The robust and fat deep-water form of lake trout known as "siscowet" is recognized readily by commercial fishermen about the island. It is probably uncommon, however. In 1927 Dr. Van Oosten saw some trout from off Good Little Boat Harbor that he supposed to be siscowets. H. F. Johnson reported to him that catches were made about Chippewa Harbor. Scotland and Anderson accurately described the fish to Lagler and told of occasionally taking it in Amygdaloid Channel and elsewhere along the north shore.

The genetic validity of the subspecies *C. n. siscowet* has yet to be established. One argument in favor of its validity is the occurrence in Rush Lake, Huron Mountains, Michigan, of typical lake trout as well as of a dwarfed type that resembles *C. n. siscowet* in several respects but differs in not being fat (Hubbs, 1929 : 155). No such type has been found in the lakes of Isle Royale.

Coregonidae — Whitefish Family

Leucichthys artedi, subspecies

Lake Desor cisco

The cisco of Lake Desor was referred by Ruthven (1909 : 330) to *Argyrosomus artedi* and by Koelz (1931 : 318) to *Leucichthys artedi huronicus*. We regard as illogical and unjustified the identification of the race of Lake Desor, as well as that of Lake Chautauqua, New York, with a subspecies (*huronicus*), the type locality of which is Rush Lake, at the base of the Huron Mountains on the south side of Lake Superior. Examination of Koelz's own data (1931 : 311, 318, 396–400) shows that the reference of the Chautauqua population to *huronicus* was without sound foundation, and an examination of the specimens he used confirms this view. The three usable specimens from Lake Desor also look

unlike the types of *huronicus* in some respects. The head is flatter on the sides and in dorsal contour, which, instead of being markedly convex and down-curved in the mouth region, is nearly straight to the more horizontal and sharper premaxillaries. The mandible is more oblique, projects more strongly, and has a more definite symphyseal knob. The head is deeper, particularly in the midsection; the depth at the vertical through the posterior border of the orbit is as long as or longer (instead of shorter) than the distance from the tip of the snout to the posterior border of the orbit. On the average the paired fins are larger, as Koelz (1931 : 399) showed for the pectoral. In view of these differences we regard the two races as distinct and do not consider the long-isolated form of Lake Desor properly referable to *L. a. huronicus*. We believe that the peculiarities of the Desor stock are an expression of isolation and endemism. It may eventually be given a separate subspecies name, but for the present we do not regard it as wise to do so. Some authors, Dymond (1943 : 213; 1947 : 8–9), for example, have gone so far as to propose that no subspecies be recognized in the *Leucichthys artedi* complex. So extreme a stand we do not care to take, although we do recognize it as possible that many of the characters used by Koelz to separate the subspecies are environmentally induced. That some of the distinctions are subject to great nonracial modification has been proved by Hile (1937). The problem calls urgently for more study and for more critical analysis.

Leucichthys artedi sargenti Koelz

Sargent Lake cisco

The local race of cisco in Sargent Lake was described by Koelz (1931 : 320), whose data indicate that on the average it has fewer scales, a deeper body, and decidedly longer paired fins than the Lake Desor race. The differences are probably due to raciation during isolation. The earlier origin of the Lake Desor stock is involved.

With more or less doubt Koelz referred to *L. a. sargenti* the inadequate samples from Siskiwit Lake and from Lake Richie. The "herring" from Siskiwit we identify (p. 105) as the young of the endemic chub *L. bartletti*. On the basis of the counts and measurements taken by Koelz, the Lake Richie cisco appears to agree fairly well with *L. a. sargenti*, but the few specimens are so small and so badly injured (all or most were from stomachs of other fishes) that the identification cannot be accepted.

Leucichthys artedi arcturus Jordan and Evermann
Lake Superior cisco

The Lake Superior cisco, locally called "herring," is caught by commercial fishermen around the entire shore of Isle Royale. It was recorded from Washington and Rock harbors by Ruthven in 1906 and 1909, respectively, as *Argyrosomus artedi.*

Hankinson (unpublished notes) identified nine young specimens about an inch and a half long from the head of Tobin Harbor, July 20, 1905, as *Leucichthys*. They probably represent *L. artedi arcturus,* as do shore-seined young in our collection (L45 : 814) from the western end of Isle Royale, in the cove opposite Thompson Island.

Experimental gill-nets set in less than fifty feet of water in July–August, 1945, took specimens in Lane Cove, McCargoe Cove, Todd Harbor, Washington Harbor, Siskiwit Bay, Chippewa Harbor, and Middle Islands Passage (Stations L45 : 797, 801, 829, 833, and 847). Some of these individuals might pass as subspecies *artedi,* but they are mostly more terete and shorter-headed.

Commercial fishing returns indicate the catching of "herring," presumably of this subspecies, about the following localities: Belle Isle, Chippewa Harbor, Fisherman Home Cove, Hay Bay, Johnson Island, Malone Island, Rock Harbor, Siskiwit Bay, and Tobin Harbor.

H. F. Johnson, fishing in Chippewa Harbor in 1927, told Dr. John Van Oosten that he believed there were two kinds of shallow-water "herring" in that vicinity, one spawning near the surface over deep water and the other, looking like a tullibee (*L. a. tullibee*), spawning on sand in shallow water. It is quite possible that there are two subspecies of *L. artedi* in Lake Superior about Isle Royale. Koelz (1929 : 500; 1931 : 352) indicated the presence, in the north-shore bays of Lake Superior, of a deep-bodied race that is different from the more terete form of the open waters. The problem posed by these suspected ecotypes of *Leucichthys artedi,* as well as by those of *Cristivomer namaycush,* demands detailed and critical study.

Leucichthys bartletti Koelz
Siskiwit Lake cisco

This cisco is known only from Siskiwit Lake, from which Koelz (1931 : 368) described it as a distinct species. From the same lake

Koelz (1931 : 321) reported a number of young ciscoes, referring them to *L. a. sargenti* with the reservation that, "On account of their being so very small, it is impossible to determine the identity of these specimens." He (p. 369) contrasted *sargenti* ("herring") and *bartletti* ("chubs") as follows: "A form of *Leucichthys artedi,* probably *sargenti,* is also found in the lake. *L. bartletti* is distinguishable from this by having a reduced number of gillrakers, a much longer snout and much less body depth. It also undoubtedly lives in much deeper water and probably grows larger."

The specimens identified as *"artedi"* were found dead on the beach or floating. Those named *bartletti* were taken in gill-nets and in fish stomachs.

A close study of this material leads to the conclusion that the specimens called *"artedi"* are merely the young of *bartletti.* Some specimens, it is true, have more gill-rakers, 40 to 42, than any of the *bartletti* counted, but several others have only 25 to 37 gill-rakers, as in that species. Although we cannot explain readily why variation is greater than would be expected on the basis of counts by Koelz (1929a : 560–561; 1931 : 387, 397, 401, 405, 412–413, 421), we do not believe that the data warrant the assumption that there are two forms of *Leucichthys* in Siskiwit Lake. The difference in the length of the snout is an average one only; as measured from the anterior rim of the orbit to the tip of the premaxillaries, the snout length enters the head length 2.7 to 3.2 times in the young (*"artedi"*) and 2.5 to 2.8 times in the adult. Some of the larger of the young have the snout quite as long and the head quite as slender and rakish as in types of *bartletti.* In the young of true *L. a. sargenti* the snout is only one fifth as long as the head. In the length and form of the mandible also these young ciscoes from Siskiwit Lake agree with *bartletti* rather than with *sargenti;* the mandible is slightly more instead of decidedly less than half as long as the head, and it is slenderer, distinctly projecting, and somewhat hooked upward at its tip. Many of the young are quite as slender as the adults. The differences noted in size and habitat are, of course, merely an index of age. The scale rows, as counted in about a dozen of the young specimens, range from 62 to 76. This is not an unusual amount of variation for a cisco (see counts by Koelz, 1929a : 562–563; 1931 : 388, 398, 402, 411, 414–416).

It is therefore concluded that there is only one form of *Leucichthys*

in Siskiwit Lake. With what Great Lakes species this form is allied can hardly be guessed at now. It is not at all impossible that it, like most of the inland forms, is a representative of *L. artedi* that through convergence has come to resemble the deep-water species of the Great Lakes. Whatever its origin may have been, its specific differentiation since about the time of Lake Nipissing, thus in a period of about 5,000 years, is remarkable.

Another strong possibility is that the characteristics of the Siskiwit Lake cisco are in part due to the introgression of one character, high gill-raker number, through the past hybridization of *L. artedi* with a deep-water form, followed by inbreeding. Such a speciational situation, involving a markedly skew distribution of gill-raker counts, is evident in the cyprinid genus *Siphateles* in Nevada (Hubbs and Miller, MS). A parallel case, involving scute numbers, has been demonstrated by Heuts (1947: 43–48) for *Gasterosteus*. That hybridization does occur in nature between genera of Coregonidae is demonstrated by data given by Koelz (1929a: 539–541). Furthermore, on strong circumstantial evidence, certain specimens from Lake Superior have been interpreted (Hubbs, unpublished notes) as hybrids between *Leucichthys artedi arcturus* and *L. kiyi kiyi*. A thoroughgoing analysis of the Siskiwit Lake cisco is called for.

Leucichthys nigripinnis cyanopterus Jordan and Evermann
Bluefin

This usually deep-water form, the Lake Superior representative of the "blackfin," was reported for Rock Harbor by Ruthven (1909 : 330) under the name then current, *Argyrosomus nigripinnis*.

H. F. Johnson, who has fished commercially about Chippewa Harbor since 1904, told Dr. John Van Oosten in 1927 that "blackfins" were taken in abundance in 1904, almost disappeared in 1905, and were caught in small numbers from then until 1927.

Occasional returns or reports given in the commercial fish statistics for "chubs" or "longjaws" from Chippewa Harbor and Washington Harbor may apply to this species. Such returns, however, do not distinguish between the deep-water species of coregonids, and there is little reason to doubt that some or all of the four other deep-water ciscoes of Lake Superior (see Koelz, 1929a) occur about Isle Royale. These species are shortjaw chub, *L. zenithicus*, Superior shortnose chub, *L. reighardi dymondi*, Michigan kiyi, *L. k. kiyi*, and Great Lakes bloater, *L. hoyi*. The last-named species was probably the "bloater" that Mr.

Johnson reported to Dr. Van Oosten as occasionally being caught in herring nets at Chippewa Harbor.

Coregonus clupeaformis clupeaformis Mitchill
Great Lakes whitefish

The Great Lakes whitefish is common all around the island. Young were seined on the shore, and half-grown individuals were taken in experimental gill-nets set at depths less than fifty feet. The 1945 collecting stations are L45 : 797, 801, 805, 812, 814, 816, 821, 830, 835, 844, and 847 (pp. 76–79). Commercial nets take larger specimens. Fishermen reported catches at Belle Isle, Chippewa Harbor, Rock Harbor, Siskiwit Bay, Tobin Harbor, Washington Harbor, Washington Island, and Wright Island.

Hankinson (unpublished notes) identified as of this species a young individual 1.75 inches long taken on July 20, 1905, at the head of Tobin Harbor.

The whitefish shares with the lake trout the position of greatest importance in the local commercial fishery. Some "jumbos," large individuals weighing more than four pounds, are still taken, but, according to the comments of fishermen, not so commonly as formerly.

Coregonus clupeaformis, subspecies
Siskiwit Lake whitefish

Koelz (1931 : 377) found a whitefish to be common in Lake Siskiwit. It is a rather slender form, especially in the head, and superficially somewhat resembles the Menominee whitefish, *Prosopium*. This resemblance we presume to be the basis of Ruthven's record (1909 : 330) of *"Coregonus quadrilateralis"* from Siskiwit Lake, for neither Koelz nor we took the Menominee in this body of water.

Whether the Lake Siskiwit whitefish is genetically distinct and if so, whether it warrants subspecific separation, are questions that call for consideration, although in the present state of coregonid systematics we can hardly expect to arrive at a final decision. It was identified by Koelz (1931 : 377) as *C. c. neo-hantoniensis*, with the reservation that it seems to have a slightly longer maxillary. But this identification is to be questioned, for the subspecies has been attributed to inland lakes in general, between the populations of which no genetic connection can be assumed. Furthermore, there is serious doubt regarding the validity of

the chief diagnostic feature attributed by Koelz to *neo-hantoniensis*, namely, the greater length of the paired fins. On the basis of the long pectorals Koelz (1931 : 375, 428) identified as *C. c. neo-hantoniensis* the whitefish of St. Mary's Lake, Glacier National Park, in which the Great Lakes whitefish (*C. c. clupeaformis* or *C. c. latus*) had been stocked (Schultz, 1941 : 40). The population sampled may or may not have been the result of the stocking. Furthermore, runt brook trout (*Salvelinus f. fontinalis*) in cold creeks have very large paired fins. So do poeciliid fishes when stunted in aquaria. The character certainly is subject to environmental influence, and as expressed in *Coregonus clupeaformis* may have no genetic basis.

In one character, presumably of genetic significance, the Siskiwit Lake whitefish does seem to have differentiated racially from the Lake Superior form. The average number of gill-rakers is markedly reduced (Table V).

TABLE V

NUMBER OF GILL-RAKERS IN WHITEFISH (COREGONUS CLUPEAFORMIS) FROM LAKE SUPERIOR AND FROM SISKIWIT LAKE

The data for Lake Superior are from Koelz (1929a : 560), and those for Siskiwit Lake are from Koelz (1931 : 425).

	Number of gill-rakers (total on first arch)						N	M	SE	$\frac{M_1 - M_2}{\sqrt{SE_1^2 + SE_2^2}}$
	25	26	27	28	29	30				
Superior	2	24	34	32	15	2	109	27.37	±.14	9
Siskiwit	13	8	4	..	..	..	25	25.64	±.14	
Superior	26 (24%)		83 (76 %)				..	..	..	..
Siskiwit	21 (84%)		4 (16 %)				..	..	..	..

The difference between the counts is reliable statistically. On the basis of the "percentage identifiable" it would seemingly be possible to separate the Superior and Siskiwit races subspecifically if only these were known, for more than three fourths of the specimens of each form are separable on gill-raker counts alone, when we place the dividing line so as to maximize the difference (see lower part of Table V). But the data published by Koelz (1929a, 1931) indicate such a maze of local forms that subspecific separation at present appears impracticable. The differentiation of the Siskiwit Lake whitefish from that of Lake Superior can, nevertheless, be regarded as having reached the subspecies level.

Coregonus clupeaformis dustini Koelz
Lake Desor whitefish

Koelz (1931 : 379) described this very peculiar type of whitefish from Lake Desor, where he found it to abound. He also referred to this subspecies the whitefish of Trout Lake, northern Wisconsin, but noted some difference between the specimens from the two lakes. It is presumed that the resemblances are due to convergence and that the form in Lake Desor is endemic, the product of local speciation. According to Koelz's own figures (his Table XXXIX, p. 427), the Trout Lake *Coregonus* does not have the increased scale number, a prime distinguishing feature of *dustini*. The difference in scale count is probably of the subspecies level. If we assume that the count for Trout Lake is 86 or fewer and that for Lake Desor 87 or more, we find the percentage typical (i.e. the percentage identifiable) to be 79 per cent for Trout Lake and 87 per cent for Lake Desor. On the identical basis we can separate 87 per cent of the Desor fish from 86 per cent of the Lake Superior population, as indicated by the counts of Koelz (1929a : 562–563).

The large mouth and slender form of this endemic whitefish may well be adaptations to its fish-eating habits, enforced by the paucity of normal whitefish food in Lake Desor.

Prosopium cylindraceum quadrilaterale (Richardson)
Round whitefish

The round whitefish, locally known also as the "pilot" or "Menominee," occurs all around the island. As explained above (p. 107), however, it seems probable that the one previously published record of this species from Isle Royale (for Siskiwit Lake) was based on *Coregonus clupeaformis*, subspecies. We have taken young in shore seining and half-grown and adults in experimental gill-nets set in water less than fifty feet deep at stations L45 : 797, 801, 812, 814, 816, 829, 830, 844 (report), and 847 (pp. 76–79). It is reported from Good Small Boat Harbor (Van Oosten), vicinity of Gull Rocks (Scotland and Anderson),

and Rock Harbor (Baggley and Allen). The commercial fish records show catches about Rock Harbor, Siskiwit Bay, and Wright Island.

Osmeridae — Smelt Family

Osmerus mordax (Mitchill)

American smelt

Young smelt were abundant in the shallows of the west end of Siskiwit Bay about the mouth of the Big Siskiwit River on July 26, 1945, when they were seined in darkness from 10:15 to 11:15 P.M. (L45 : 830). It seems probable that spawning runs have become established in this river. The occurrence of this cold-water fish on Isle Royale is evidence of its ability to traverse considerable stretches of open water. Not indigenous to the Great Lakes, the species was introduced at various times from 1912 through 1921 into Michigan waters. In 1932 the westernmost record in Lake Superior was for Keweenaw Bay (Van Oosten, 1937). Raymond E. Johnson, of the Minnesota Department of Conservation, tells us that the smelt was reported from Minnesota's north shore of Lake Superior by commercial fishermen in 1945 and was taken in the spring of 1946 at the mouth of the French River and from the St. Louis River. The species has thus about completed its spread through the Great Lakes.

Catostomidae — Sucker Family

Catostomus commersonnii commersonnii (Lacépède)

Common white sucker

In contrast to *Catostomus c. catostomus,* which is most abundant in the waters margining the island and which lives inland in only a few streams, *C. c. commersonnii* occurs extensively in streams and their mouths and in many inland lakes, as well as about the shore and in the shallower waters of Lake Superior. It was taken by Koelz in fifteen inland lakes (Table IV) and by Lagler during the 1945 survey at stations L45 : 798, 800, 801, 803, 808, 809, 811 to 814, 816, 819 to 822, 826, 829, 830, 837, 838, 840, 841, 843, 846, 850, and 851 (pp. 76–81). This sucker was reported by Ruthven (1906 : 109; 1909 : 330) from Washington and Rock harbors. Captain Ellsworth collected specimens in the mouth of Washington River and in McCargoe Cove. Stanley took it in Pickerel Cove, a feeder to Lake Desor, Siskiwit Lake, mouth of

Little Siskiwit River, and outlet of Lake Shesheeb. Commercial fish returns list "white suckers" from Washington Harbor and Washington Island. Single entries in these records and verbal reports of fishermen in 1945 for an occasional "mullet" or "carp" may refer either to the common white sucker or to some species of redhorse (*Moxostoma*).

Catostomus catostomus catostomus (Forster)

Eastern sturgeon sucker

This sucker occurs principally in waters margining the island. The young are most common about the shore, and the subadults and adults frequent the shallower offshore zones. Collections were obtained in 1945 at stations L45 : 797, 798, 800, 801, 805, 809, 811, 812, 814, 816, 819 to 821, 829, 830, 841, 844, and 847 (pp. 76–79). Previously Captain Ellsworth had taken one in McCargoe Cove, and commercial fish returns indicated its presence at Washington Harbor. The species occurs only sparingly in the streams of the island and, so far as known, not at all in the inland lakes — a remarkable circumstance, considering the distribution of the species in other waters about Lake Superior (Hubbs, 1929). It was presumably originally present in the higher inland lakes but has not survived in them (p. 87). Its local distribution is largely complementary to that of the common white sucker (*Catostomus c. commersonnii*). Both kinds, however, spawn in the streams. One male collected on July 21 (at station L45 : 812) had milt running.

Cyprinidae — Minnow Family

Semotilus atromaculatus atromaculatus (Mitchill)

Northern creek chub

The only locality where this species is known on Isle Royale is Hatchet Lake, where Koelz took very large specimens. This isolated record is surprising. Were it not for the remoteness of Isle Royale one might attribute the occurrence to the escape of bait minnows. That the species was a rather early postglacial migrant and could be native in Hatchet Lake is attested by its abundance in the high lakes of the Porcupine Mountains on the south side of Lake Michigan, above falls in the lower courses of the outlet streams (Ruthven, 1906 : 107), and by its widespread occurrence in the north-shore tributaries of Lake Superior in Minnesota (Smith and Moyle, 1944 : 120).

Margariscus margarita nachtriebi (Cox)
Northern pearl dace
(Pl. II, Fig. 2)

This dace was taken by Koelz in Hatchet, Desor, and Forbes lakes. On the island it is apparently restricted to these bodies of water, for it has not been found elsewhere during the extensive collecting. The specimens from these three well-separated lakes appear to be typical of this widely spread northern subspecies. Only those from Forbes Lake approach the endemic subspecies of Harvey Lake. *Margariscus m. nachtriebi* ranges northward through most of Canada south of the tundra (Dymond, 1926:46; 1947:19).

Margariscus margarita ***koelzi,*** new subspecies
Harvey Lake pearl dace
(Pl. II, Fig. 1)

In Harvey Lake *Margariscus margarita,* like *Pimephales promelas* and *Notropis heterolepis,* is represented by an endemic subspecies.

Type specimens.—The holotype, an adult specimen 84 mm. in standard length, was collected by Walter Koelz on the shoals of Harvey Lake, Isle Royale, on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (Cat. No. 100010). The paratypes comprise thirty-five specimens, 43 to 82 mm. long (U.M.M.Z., No. 100011), collected with the holotype, and twelve examples, 22 to 101 mm. long (U.M.M.Z., 144473), collected by Karl F. Lagler and his party at station L45:813, in the same lake about the source of the outlet, July 21, 1945 (Pl. I, Fig. 3).

Diagnosis.—Like *M. m. nachtriebi,* but head slenderer and more conic, lips thinner, and gape less curved.

The slenderer and more conic head of *M. m. koelzi* is illustrated on Plate II, which compares the holotype of this species with a specimen of *M. m. nachtriebi* of like size from Lake Desor. The slenderness of the head is a rather consistent character (Table VI). The specimens from Hatchet Lake and Lake Desor are typical of *M. m. nachtriebi,* but those from Forbes Lake are intermediate, though probably closer to *nachtriebi* than to *koelzi.* Samples from various places in the wide range of the northern subspecies (*nachtriebi*) in general contrast sharply with *koelzi* in this character. The outstanding exception is furnished by a series of specimens collected by Walter Koelz on August 2, 1922, in a small lake

TABLE VI

RELATIVE HEAD DEPTH IN NORTHERN SUBSPECIES OF MARGARISCUS MARGARITA

As here used, the relative head depth is the distance from the occiput to the isthmus, expressed as hundredths of the head length to the margin of the opercular membrane. The measurements were made with precision calipers. The averages were computed from the uncombined data expressed in thousandths of the head length.

Subspecies and locality	Relative head depth																			
	57–58	59–60	61–62	63–64	65–66	67–68	69–70	71–73	N	M	57–62		63–73	
M. m. koelzi														
Harvey Lake, Isle Royale	7	19	19	3	..	..	..	..	48	60.2	45	(94%)	3	(6%)
M. m. nachtriebi														
Forbes Lake, Isle Royale	1	2	1	5	1	..	..	..	10	62.5	4	(40%)	6	(60%)
Hatchet Lake, Isle Royale	..	..	..	1	3	..	..	..	4	65.1	..		4	(100%)
Lake Desor, Isle Royale	..	..	1	1	2	1	..	..	5	64.6	1	(20%)	4	(80%)
Porcupine Mts., Michigan	..	..	2	4	..	1	..	..	7	63.5	2	(29%)	5	(71%)
Upper Peninsula, Michigan	..	..	1	1	1	..	3	..	6	66.6	1	(17%)	5	(83%)
Lower Peninsula, Michigan	..	..	1	4	6	4	1	1	17	66.1	1	(6%)	16	(94%)
Glacier National Park, Montana	..	..	2	7	1	..	..	..	10	63.2	2	(20%)	8	(80%)
Sand Hills region, Nebraska	..	..	4	3	2	1	..	..	10	63.3	4	(40%)	6	(60%)
Missouri R. basin, North Dakota	..	..	2	3	2	1	..	..	8	63.9	2	(25%)	6	(75%)
Souris R., North Dakota	..	..	..	..	..	1	..	..	1	68.4	..		1	(100%)
Mississippi R. basin, Minnesota	..	..	1	2	..	..	..	..	3	63.3	1	(33%)	2	(67%)
Near Lake Nipigon, Ontario	..	2	6	3	..	..	..	..	11	61.2	8	(73%)	3	(27%)
Hudson Bay drainage, Ontario	..	..	2	7	11	11	3	2	36	66.2	2	(6%)	34	(94%)
Grand Lake, Quebec	..	..	..	..	1	..	1	1	3	68.7	..		3	(100%)
Miramichi, New Brunswick	..	..	..	..	1	1	..	..	2	66.1	..		2	(100%)
Penobscot R. basin, Maine	..	..	..	2	1	..	..	..	3	64.0	..		3	(100%)
Summary														
M. m. koelzi	7	19	19	3	..	..	..	..	48	60.2	45	(94%)	3	(6%)
M. m. nachtriebi	1	4	23	43	32	21	8	4	136	64.7	28	(21%)	108	(79%)

tributary to Lake Nipigon, between Orient Bay and Macdiarmid, Ontario. But these minnows are abnormally dwarfed and have a very long head with massive muzzle. Their relatively slenderer heads are attributable to an unfavorable environment. The next closest approach to *koelzi* is exhibited by specimens from Sand Hills, Nebraska, and these, too, are considerably dwarfed and, as a result, long-headed. The Sand Hills specimens approach *koelzi* also in the thinness of the lips, but in this respect the series from near Lake Nipigon is typical of *nachtriebi* (Table VII).

We name this subspecies for Dr. Walter Koelz, as a partial recognition of his contribution to the ichthyology of Isle Royale.

Couesius plumbeus plumbeus (Agassiz)

Lake northern chub

This minnow was reported by Ruthven (1906 : 109) for Washington Harbor, where Stanley also found it. Koelz took it only in Lake Desor. Ellsworth collected it in McCargoe Cove. In our 1945 collecting it proved to be one of the commonest fishes in the lower reaches of streams and about the entire shore of the island. Specimens were seined at stations L45 : 798, 800, 802, 803, 805, 806, 808 to 811, 814, 820, 821, 826, 830, 840, 845, 847, 849, and 851 (pp. 76–81). Seven-inch adults were taken in our experimental gill-nets, set in twenty to thirty-five feet of water in Middle Islands Passage (L45 : 847). That this chub has presumably inhabited Isle Royale for a long time is indicated by its isolated occurrence in Lake Desor, at an elevation of 235 feet above Lake Superior. That it was an early postglacial reinvader is suggested not only by its wide distribution in Canada (Dymond, 1947 : 19), but also by its place in the fauna of completely isolated lakes in the Huron Mountains on the south side of Lake Superior (Hubbs, 1929).

One hybrid between this species and the longnose dace, *Couesius p. plumbeus* × *Rhinichthys c. cataractae*, was identified in a series of lake northern chubs from the sluggish brown stream entering the extreme western end of Pickett Bay of Todd Harbor (L45 : 809).

Rhinichthys cataractae cataractae (Valenciennes)

Great Lakes longnose dace

In harmony with its far-northern limits (Dymond, 1947 : 20), this dace occurs commonly all around the island in effluent streams and stream mouths, and in Siskiwit Lake about the shore and in one tribu-

TABLE VII

Width of Lips in Northern Subspecies of Margariscus margarita

The over-all width across the lips near the middle is expressed as thousandths of the head length.

Subspecies and locality	N	R	M	42–57	58–87
M. m. koelzi					
Harvey Lake, Isle Royale	47	42–75	57.5	31 (66%)	16 (34%)
M. m. nachtriebi					
Forbes Lake, Isle Royale	10	56–71	64.9	3 (30%)	7 (70%)
Hatchet Lake, Isle Royale	4	66–73	70.0	..	4 (100%)
Lake Desor, Isle Royale	5	67–83	75.8	..	5 (100%)
Porcupine Mts., Michigan	7	43–77	64.1	2 (29%)	5 (71%)
Upper Peninsula, Michigan	6	63–83	71.3	..	6 (100%)
Lower Peninsula, Michigan	17	56–81	67.6	1 (6%)	16 (94%)
Glacier National Park, Montana	10	57–71	62.7	1 (10%)	9 (90%)
Sand Hills region, Nebraska	10	54–66	60.2	4 (40%)	6 (60%)
Missouri R. basin, North Dakota	8	56–70	62.9	1 (13%)	7 (87%)
Souris R., North Dakota	1	62	61.7	..	1 (100%)
Mississippi R. basin, Minnesota	3	60–67	64.3	..	3 (100%)
Near Lake Nipigon, Ontario	11	46–76	64.1	2 (18%)	9 (82%)
Hudson Bay drainage, Ontario	36	54–87	71.7	1 (3%)	35 (97%)
Grand Lake, Quebec	3	73–82	77.3	..	3 (100%)
Miramichi, New Brunswick	2	65–78	71.5	..	2 (100%)
Penobscot R. basin, Maine	3	56–61	59.7	1 (33%)	2 (67%)
Summary					
M. m. koelzi	47	42–75	57.5	31 (66%)	16 (34%)
M. m. nachtriebi	136	43–87	67.4	16 (12%)	120 (88%)

tary. Stanley seined some young specimens at the mouth of the Little Siskiwit River, but in 1945 we failed to get it either there or upstream to one-half mile above the mouth. The 1945 collecting stations were L45 : 800, 802, 803, 806, 808, 810, 811, 819 to 821, 826, 830, 838, 839, 841, 848, and 849 (pp. 76–81). An adult male specimen taken on July 19 (L45: 806) was still in breeding color.

Pfrille neogaea (Cope)

Finescale dace

This northern species is quite rare on Isle Royale. It was recorded from Sumner Lake by Ruthven (1909 : 300) and was obtained in the same lake and in an adjacent marsh pool by Koelz, who also collected it in Benson and Wallace lakes. In 1945 we took it in sluggish water in the outlet of Hatchet Lake (L45 : 807); in the small bog pond about 100 feet inshore, approximately 1.25 miles east of Long Point (L45 : 824); in the lower, slow-moving part of the outlet of Lake Halloran (L45 : 826); and abundantly in high-lying Lily Lake (L45 : 817). Its occurrence at this high elevation (about 400 feet above Lake Superior) suggests that it first arrived long ago on Isle Royale. This suggestion is in harmony with the fact that the species is very widely spread in Canada (Dymond, 1947 : 20).

Chrosomus eos Cope

Northern redbelly dace

The northern redbelly dace is also rare on Isle Royale. Koelz took it only in Wallace Lake. In our collections it was found in the boggy stream entering the west end of Pickett Bay of Todd Cove (L45 : 809); near the Lake Superior shore in the small bog pond about 1.25 miles east of Long Point (L45 : 824); and in the lower reaches of the outlet of Wallace Lake (L45 : 849). On the island, as elsewhere, its distribution is obviously related to that of the finescale dace (*Pfrille*). They occurred together in two of our 1945 collections (L45 : 809 and 824). At station L45 : 824 a hybrid, *Chrosomus eos* × *Pfrille neogaea*, was taken (these species often hybridize). *Chrosomus eos* ranges throughout Ontario to 52° N. Lat. (Dymond, 1947 : 20).

Notemigonus crysoleucas auratus (Rafinesque)

Western golden shiner

This sluggish-water fish was taken by Koelz in ten of the inland lakes (Table IV). It occurred in six of our 1945 collections: L45 : 798, 802, 803, 814, 840, and 843 (pp. 76–79). Four of these stations were in lake outlets (including those of three lakes in which Koelz found the fish), and two were in and about the mouths of streams entering sheltered coves of Lake Superior. On Isle Royale *Notemigonus* occurs only in the lower waters and finds there its approximate northern limit, east of the plains. It is known in Ontario north to Lake Abitibi, but has not been reported from Lake Nipigon (Dymond, 1947 : 20). For these reasons it is regarded as one of the latest reinvaders of northern glaciated areas.

Notropis atherinoides : *acutus* Lapham × *atherinoides* Rafinesque

Emerald shiner intergrades

Isle Royale specimens of this shiner are interpreted as intergrades between the lake emerald shiner and the river emerald shiner. The intergrades are intermediate in the diagnostic characters (Table VIII). In three of the six characters they incline toward *atherinoides;* in two they are almost exactly intermediate; and in one they approach *acutus*.

TABLE VIII

COMPARISON OF ISLE ROYALE INTERGRADES WITH NOTROPIS ATHERINOIDES ACUTUS (FROM LAKE MICHIGAN) AND N. A. ATHERINOIDES (FROM LAKE ERIE)

The comparisons are based on well-preserved adults. The measurements were made according to the methods proposed by Hubbs and Lagler (1941, 1947). The data for the two subspecies are taken from Hubbs, 1945 : 15. The nine Isle Royale specimens measured were 56 to 58 mm. in standard length. Eight were from collection L45 : 800 and one was from L45 : 820.

Character	*N. a. acutus*	Isle Royale intergrades Average (range)	*N. a. atherinoides*
Body depth / Body width	< 2.0	1.98 (1.9–2.1)	> 2.0
Head length / Body width	< 2.0	2.17 (2.0–2.5)	> 2.0
Length of depressed dorsal fin / Body width	Typically 1.4–1.5 Range 1.2–1.7	1.71 (1.6–2.0)	Typically 1.6–1.8 Range 1.4–2.0
Standard length / Head length	> 4.0	4.09 (3.9–4.3)	< 4.0
Distance from dorsal fin to occiput / Length of depressed dorsal fin	> 2.0	1.89 (1.7–2.1)	< 2.0
Head length / Upper jawlength	3.3–3.5	3.48 (3.3–3.6)	3.6–3.8

On Isle Royale proper this fish is known only from Siskiwit Lake, where it was collected by Koelz. In the marginal waters it proved much less common than was expected, since the species is abundant in some places around the mainland shores of Lake Superior. In our 1945 collecting it was found only in stream mouths (L45 : 800, 802, and 820).

Notropis hudsonius hudsonius (Clinton)
Northern spottail shiner

Koelz took the spottail shiner in ten inland lakes, including Siskiwit Lake (Table IV). In 1945 it was collected in the same lake and at five stations scattered around the island in the lower parts of streams and on the shore. The station numbers were L45 : 802, 803, 805, 838, 840, and 843 (pp. 76–79).

The spot at the base of the tail fin is extreme in this material, as it also is in specimens from Carp Lake in the Porcupine Mountains, on the south side of Lake Superior. It is about one third as wide as the caudal peduncle is at the same vertical, and it is intensely black and round. A single young specimen was found in sorting Koelz's collection from Harvey Lake, one of the higher bodies of water and the scene of subspeciation of the three other cyprinids present. It is thought almost certain that this fish was inadvertently mixed with this collection, but the circumstance is mentioned to induce future collectors to search for this minnow in Harvey Lake. Ruthven (1906 : 108) reported the species from Carp Lake. It ranges far northward in Canada (Dymond, 1947 : 21).

Notropis heterodon (Cope)
Blackchin shiner

The blackchin shiner is known on Isle Royale only from the outlet of Sargent Lake, near its mouth in McCargoe Cove (L45 : 803). The three specimens that were collected probably were strays from the lake, from which, however, the species has not been taken. They appear to be typical. Each has eight anal rays.

This species is a usual inhabitant of clear weedy lakes through the southern part of the glacial district and occurs elsewhere in the Lake Superior basin. Dymond (1947 : 21) recorded it as ranging northward in Ontario only to Sault Sainte Marie, but Smith and Moyle (1944 : 121) collected it in a Minnesota stream on the north shore of Lake Superior. It was probably one of the last postglacial immigrants.

Notropis volucellus volucellus (Cope)
Northern mimic shiner

Another fish of restricted occurrence on Isle Royale is the northern mimic shiner. Koelz took it only in Lake Richie, where he found it common. In 1945 we took it in the lower reaches of the westernmost tributary of Chippewa Harbor (L45 : 840), in the outlet of Lake Richie near its mouth (L45 : 841), and, downstream, in the Mason Lake outlet (L45 : 843). All these localities are in the drainage of Chippewa Harbor.

In Canada this minnow ranges at least to 52° N. Lat. (Dymond, 1947 : 21). It is the species that Dymond had listed earlier (1926 : 50) from Lake Nipigon as *Notropis deliciosus stramineus*.

Notropis heterolepis heterolepis Eigenmann and Eigenmann
Northern blacknose shiner

This shiner, which has a far northern range (Dymond, 1947 : 22), is the commonest cyprinid on the island. In 1929 Koelz took it in twenty-one inland lakes (Table IV); in 1930 Stanley collected a series in the mouth of Big Siskiwit River; and in 1945 Lagler secured it in one stream collection (L45 : 802 in part) and in five stream-mouth stations: L45 : 800, 802 in part, 803, 841, and 846 (pp. 76–79). The characters of the blacknose shiner from most of these localities are in general similar to those shown by the subspecies throughout its range. It is noteworthy, therefore, that Harvey Lake is inhabited by an apparently distinct subspecies. As is indicated below, however, the specimens from certain other lakes are intermediate in some respects.

Notropis heterolepis ***regalis,*** new subspecies
Harvey Lake blacknose shiner
(Pl. II, Fig. 3)

In its typical form this race of *Notropis heterolepis* appears to be confined to Harvey Lake, Isle Royale, which it occupies in company with two other endemic subspecies (*Margariscus margarita koelzi* and *Pimephales promelas harveyensis*).

Type specimens.—The holotype, 81 mm. in standard length, was collected by Walter Koelz on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (No. 100027), along with 108 paratypes 22 to 74 mm. long (U.M.M.Z., No. 100028). These

specimens were seined on the shoals (Pl. I, Fig. 2) of Harvey Lake. The 23 additional paratypes, 32 to 48.5 mm. long (U.M.M.Z., No. 144474), were collected by Lagler at station L45 : 813, under somewhat different conditions, at the source of the outlet (Pl. I, Fig. 3).

Diagnosis.—Like *N. h. heterolepis*, but reaching a relatively huge size (81 mm. in standard length), and with the head small, usually entering the standard length more than 4.0 times, the eye also small, and the lateral band rather solidly black. The differences in head and eye proportions are apparent not only between specimens of maximum size, but also between those of the same size.

The large size attained in Harvey Lake probably has some genetic basis, for it is the maximum known for the species, and the lake has no apparent peculiar richness; the other species in the lake are not particularly large or robust. Among 697 series of *N. h. heterolepis* catalogued in the University of Michigan Museum of Zoology, ranging from North Dakota to Maine and Nova Scotia and comprising 27,874 specimens, the maximum size very seldom reaches 60 mm., exceeds 62 mm. in only five lots, and exceeds 70 mm., reaching 71 mm., in only one series (U.M.M.Z., No. 108077), that from Muskellunge Lake, Vilas County, Wisconsin.

In the small size of the head and the eye (Tables IX–X) the Harvey Lake blacknose shiner contrasts sharply with typical *N. h. heterolepis* throughout its wide east–west expanse of range. After handling nearly all the material mentioned above, we recognized the difference. When the proportions at the different size groupings for Harvey Lake are compared with those for a series from Lake Odessa, Frontenac County, Ontario (selected because of the many well-preserved specimens of typical appearance), there is seen to be very little overlap. We believe that similar results would be obtained if the Harvey Lake fish were compared with those from most other localities. Several lots from Isle Royale have the head and eye as long as is usual in *N. h. heterolepis*, but those from some other lakes are intermediate for one or both characters in one or more size groups. In no other lot, however, is the average as low for either head or eye proportion as it is in the Harvey Lake fish. Furthermore, the approach toward *regalis* is almost confined to the smallest size group. The specimens from Muskellunge Lake, Wisconsin, where the species reaches the largest size known except in Harvey Lake, have the

TABLE IX

COMPARISON BY LAKES OF HEAD LENGTHS OF NOTROPIS HETEROLEPIS

In the body of the table the figures in the first line for each rubric are the observed range and, in parentheses, the mean; those in the second line are the number of specimens and, in parentheses, the percentage separable above (+) or below (—) the arbitrary line of separation indicated in column heading. The head length, including opercular membrane, is expressed in thousandths of the standard length.

Size group, mm. Line of separation	27–40 271–272	40–50 263–264	50–60 256–257	60–81 256–257
N. h. regalis				
Harvey L., Isle Royale	244–273 (259)	246–261 (251)	238–257 (246)	239–260 (246)
	49 (98 —)	7 (100 —)	15 (93 —)	32 (94 —)
N. h. heterolepis				
L. Odessa, Ontario	270–287 (280)	265–289 (278)	256–283 (273)	...
	26 (92 +)	14 (100 +)	46 (98 +)	...
Muskellunge L., Wisconsin	267–277 (271)	272–273 (273)	252	256–281 (267)
	9 (56 —)	2 (100 +)	1 (100 —)	14 (93 +)
N. h. heterolepis and intermediates				
Isle Royale lakes				
Beaver L.	269–283 (277)	266–301 (277)	...	...
	22 (95 +)	26 (100 +)	...	...
L. Benson	256–274 (264)	...	...	...
	10 (90 —)	...	...	...
Chickenbone L. outlet	269–285 (275)	272–288 (277)	...	...
	10 (70 +)	10 (100 +)	...	...
L. Eva	272	260	...	...
	1 (100 +)	1 (100 —)	...	...
Forbes L.	269–278 (272)	271	...	...
	5 (60 —)	1 (100 +)	...	...
Intermediate L.	264–279 (271)	265–282 (272)	...	...
	10 (50 ±)	10 (100 +)	...	...
L. John	266–283 (274)	...	...	...
	10 (60 +)	...	...	...
Linklater L.	262–268 (266)	...	...	...
	2 (100 —)	...	...	...
L. Livermore	263–272 (267)	263–272 (268)	...	...
	5 (80 —)	5 (80 +)	...	...
L. Mason	296–296 (296)	283	...	...
	2 (100 +)	1 (100 +)	...	...
Mud L.	262–270 (267)	...	...	...
	5 (100 —)	...	...	...
Otter L.	264–277 (270)	257–281 (271)	...	...
	5 (60 —)	5 (80 +)	...	...
L. Richie	276–290 (281)	268–293 (277)	...	...
	11 (100 +)	12 (100 +)	...	...
Sargent L. and outlet	268–285 (276)	270–277 (274)	...	...
	7 (57 +)	5 (100 +)	...	...
Sholts L.	267–280 (274)	...	...	...
	6 (50 ±)	...	...	...
Siskiwit L.	270–289 (278)	273–281 (277)	...	...
	17 (88 +)	5 (100 +)	...	...
Sumner L.	267–268 (267)	262–274 (267)	272–281 (277)	...
	2 (100 —)	5 (60 +)	2 (100 +)	...
L. Thérésa	268–287 (278)	267–288 (277)	...	...
	6 (60 +)	6 (100 +)	...	...
Wallace L.	268–280 (274)	...	...	...
	2 (50 ±)	...	...	...

head on the average almost as large as those in Lake Odessa, though the eye measurements are atypically low—owing to the unusual width of the soft margin of the orbit anteriorly.

TABLE X

COMPARISONS BY LAKES OF ORBIT LENGTHS OF NOTROPIS HETEROLEPIS

The format is explained in the subheading of Table IX. The orbit was measured between free rims, from just behind nostril to lower edge of dark lateral stripe.

Size group, mm. Line of separation	27–40 77–78	40–50 72–73	50–60 68–69	60–81 66–67
N. h. regalis				
Harvey L., Isle Royale	67–81 (74) 49 (80 —)	67–70 (68) 7 (100 —)	60–69 (65) 15 (87 —)	57–68 (63) 32 (94 —)
N. h. heterolepis				
L. Odessa, Ontario	73–91 (81) 26 (81 +)	74–83 (77) 14 (100 +)	68–79 (73) 46 (98 +)	... ...
Muskellunge L., Wisconsin	72–78 (75) 9 (78 —)	68–72 (70) 2 (100 —)	68 1 (100 —)	62–74 (68) 14 (57 +)
N. h. heterolepis and intermediates				
Isle Royale lakes				
Beaver L.	76–89 (83) 22 (95 +)	74–87 (80) 26 (100 +)	... ...	... ...
L. Benson	72–80 (76) 10 (80 —)	... ...	... ...	... ...
Chickenbone L. outlet	76–88 (82) 10 (90 +)	76–87 (81) 10 (100 +)	... ...	... ...
L. Eva	85 1 (100 +)	76 1 (100 +)	... ...	... ...
Forbes L.	76–83 (79) 5 (60 +)	76 1 (100 +)	... ...	... ...
Intermediate L.	72–87 (79) 10 (60 +)	74–82 (78) 10 (100 +)	... ...	... ...
L. John	72–78 (75) 10 (70 —)	... ...	... ...	... ...
Linklater L.	89–89 (89) 2 (100 +)	... ...	... ...	... ...
L. Livermore	74–82 (79) 5 (80 +)	74–78 (76) 5 (100 +)	... ...	... ...
L. Mason	77–79 (78) 2 (50 ±)	75 1 (100 +)	... ...	... ...
Mud L.	74–82 (80) 5 (80 +)	... ...	... ...	... ...
Otter L.	74–82 (79) 5 (60 +)	76–82 (79) 5 (100 +)	... ...	... ...
L. Richie	79–88 (83) 11 (100 +)	79–88 (83) 12 (100 +)	... ...	... ...
Sargent L. and outlet	78–90 (84) 7 (100 +)	77–84 (80) 5 (100 +)	... ...	... ...
Sholts L.	75–81 (79) 6 (83 +)	... ...	... ...	... ...
Siskiwit L.	79–90 (83) 17 (100 +)	79–85 (82) 5 (100 +)	... ...	... ...
Sumner L.	77–78 (77) 2 (50 ±)	70–82 (77) 5 (80 +)	73–74 (73) 2 (100 +)	... ...
L. Theresa	79–85 (82) 6 (100 +)	71–79 (75) 6 (83 +)	... ...	... ...
Wallace L.	85–88 (87) 2 (100 +)	... ...	... ...	... ...

We conclude that *N. h. regalis*, though rather sharply distinct from *N. h. heterolepis*, is approached by the races inhabiting certain other inland lakes, particularly those on Isle Royale. Were it not for such partial transition, full specific status might have been considered.

We apply the name *regalis* to this species in reference both to its large size and to its occurrence on Isle Royale.

Pimephales promelas promelas Rafinesque

Northern fathead minnow

In view of its northern range (Dymond, 1947 : 22), it is not surprising that this minnow has been taken on Isle Royale. The first island record, by Ruthven (1909 : 330), was for Sumner Lake. Koelz found it extremely abundant in this lake in 1929 and took it also in Hatchet and Wallace lakes. In 1945 it was obtained near Lake Superior in the outlet of Sumner Lake (L45 : 846). Large numbers were found in Lily Lake (L45 : 817), the highest body of water on the island. This isolated lake, which was not worked by Koelz, lies above the 1,000-foot contour in the western part of the island. At the suggestion of Karl Gilbert, it is designated "Lily Lake." Six northern fathead minnows from this small body of water have 46–50 scale rows, which is the normal number for the typical subspecies in this latitude. In all the island waters except Harvey Lake the characters of the fathead minnows agree well with those of *P. p. promelas* elsewhere in the far north. The Harvey Lake population is taken to represent an endemic subspecies.

Pimephales promelas harveyensis, new subspecies

Harvey Lake fathead minnow

(Pl. II, Fig. 4)

As Koelz pointed out to Hubbs, the fathead minnows of Harvey Lake are quite unlike those from other waters throughout the wide range of the species. They seem worthy of subspecific separation, as do the representatives in the same lake of *Margariscus margarita* and *Notropis heterolepis*.

Type specimens.—The holotype, 51 mm. in standard length, was collected by Walter Koelz in Harvey Lake on Isle Royale on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (No. 99989). Seventy-nine paratypes (U.M.M.Z., No. 99990), 22 to 48 mm. long, were collected at the same time and place. About the head of the outlet, on July 11, 1945, Lagler collected 24 additional

paratypes (U.M.M.Z., No. 144475): 15 young, 14 to 17 mm. long, and 9 half-grown to adult specimens, 36.5 to 47 mm. long.

Diagnosis.—Like *P. p. promelas*, but with finer scales (in 50–60 rows); dorsal fin inserted farther forward; caudal peduncle longer and slenderer; head short, slender, and subconic; eye small; mandible not very strongly oblique. The lateral line is short, as in *P. p. promelas* as contrasted with *P. p. confertus*.

On the basis of the scale count 90 per cent of the specimens of *P. p. harveyensis* from Harvey Lake can be separated from 94 to 100 per cent of the specimens of *P. p. promelas* from the other localities inhabited by the species on Isle Royale (Table XI).

TABLE XI

SCALE COUNTS ALONG SIDE OF BODY OF PIMEPHALES PROMELAS FROM ISLE ROYALE

Subspecies and locality	N	R	M	45–51	52–60
P. p. harveyensis					
Harvey Lake	78	50–60	54.0	8 (10%)	70 (90%)
P. p. promelas					
Hatchet Lake	10	45–50	47.6	10 (100%)	..
Sumner Lake	10	46–51	48.3	10 (100%)	..
Wallace Lake	17	45–53	48.8	16 (94%)	1 (6%)
Lily Lake	6	46–50	..	6 (100%)	..

The origin of the dorsal fin is unusually far forward. Its distance from the caudal base reaches, when measured forward, to any point from the anteriormost part of the eye to a location nearer to the tip of the snout than to the nostril. In Sumner Lake and Lily Lake specimens this measurement reaches to any point from well behind the eye to the anterior part of the eye. In this respect, as well as in other proportions, the Hatchet Lake specimens are somewhat intermediate.

The difference in proportions are already evident in the very young (14 to 17 mm. long) — a strong indication of genetic fixation. Furthermore, the melanophores of the back are fewer and larger than those in comparable young of *P. p. promelas* from Isle Royale, and the dark back is more restricted and is more sharply set off by a light streak from the dark lateral band.

Except for the darker color, the specimens collected by Lagler about the source of the outlet (Pl. I, Fig. 3) are essentially like those taken along the main lake shore (Pl. I, Fig. 2).

Although detailed comparison is not made with collections of *P. p. promelas* from various parts of the range of the typical subspecies, our experience with the group indicates that the characters of the Harvey Lake specimens are extreme and warrant the erection of this subspecies. The contrast is particularly sharp with the coarse-scaled, heavy-set race that occupies the southern part of the Great Lakes basin. As indicated by Hubbs and Black (1947:8), *P. p. promelas* will probably be broken up after detailed analysis, into two or more subspecies.

ESOCIDAE — PIKE FAMILY

Esox lucius Linnaeus

Northern pike

Pike are widely distributed in the inland lakes and around the shores of Isle Royale. Ruthven (1909:330) indicated Sargent Lake as the only Isle Royale record then known for this fish, but in 1929 Koelz found it not only there but also in twenty-seven other inland lakes (Table IV). On the authority of Karl Gilbert, Lake Benson may now be added to the list. In 1945 pike were collected in the lower parts of the outlets of Sargent Lake (L45:803) and in Lakes Richie (L45:841) and Mason (L45:842). According to reports of anglers and others, it occurs in most of the coves around the island, one of which is named Pickerel Cove. The 1945 shore records include: Todd Harbor (L45:812); Washington Harbor (report, Gilbert); and Duncan Bay (report, Allen). Catches of "grass pike," occasionally entered on the commercial fish tallies for Lake Superior around the island, are referable to this species.

Esox masquinongy masquinongy Mitchill

Great Lakes muskellunge

The muskellunge is included in the list of Isle Royale fishes solely on the basis of Ruthven's record (1906:109) of one caught in Washington Harbor. The specimen was probably not preserved, for it is not recorded in the University of Michigan Museum of Zoology. A confirmation of the report would therefore be welcome.

GADIDAE — COD FAMILY

Lota lota maculosa (LeSueur)

American burbot

Ruthven (1909:331) reported the burbot, locally called "lawyer," from Tobin and Rock harbors, and Dr. Van Oosten saw some that had

been caught in Chippewa Harbor. Lagler took specimens in experimental gill-nets at a depth of fifty feet in Lane Cove (L45 : 797) and at 20–35 feet in Middle Islands Passage (L45 : 847). Gilbert reported specimens taken by commercial fishermen in Washington Harbor. From these records and reports it is concluded that the fresh-water representative of the cod family is distributed all around the island. In the inland waters it must be of very restricted occurrence, since in his extensive gill-net collecting Koelz took it in Siskiwit Lake only.

The American representative of the Holarctic species *Lota lota* has a far northern range (Hubbs and Schultz, 1941:17–27).

Percopsidae — Troutperch Family

Percopsis omiscomaycus (Walbaum)

Troutperch

At Isle Royale the troutperch occurs in all marginal waters as well as in the interior. The first report, by Ruthven (1909 : 331), under the name *P. guttatus,* was for Tobin Harbor. Koelz collected it in six inland lakes (Table IV), and Stanley seined one young specimen at the mouth of the Little Siskiwit River. In 1945 the species was commonly encountered in the lower reaches of streams tributary to Lake Superior as well as along the shore. It was taken at stations L45 : 798, 802, 803, 805, 811, 820, 830, 839, 843, 849, and 850 (pp. 76–81). In line with experience elsewhere around the Great Lakes, in shore collections it was seined most commonly after dark. A ripe female obtained on July 18 at station L45 : 805 gave evidence of delayed spawning, attributable to the persistently low temperatures of Lake Superior waters. The species is one of far northern limits (Dymond, 1947 : 25).

Percidae — Perch Family

Perca flavescens (Mitchill)

Yellow perch

On Isle Royale the perch is principally a fish of the inland lakes, in most of which it occurs (in twenty-eight out of thirty-nine). It also lives, scatteringly, about the lake shore and in stream mouths. It was reported from Washington Harbor by Ruthven (1906 : 109), by commercial fishermen, and by Gilbert in 1945; from Forbes Lake by Ruthven (1909 : 331) and by Koelz; and from Harvey Lake by Koelz and by Lagler (L45 : 813). The other 1945 collections were L45 : 802, 803, 811, 840, 841, 843, and 845 (pp. 76–79). See also Table IV.

The perch ranges far to the north in Canada, as does the following species (Dymond, 1947 : 27).

Stizostedion vitreum vitreum (Mitchill)

Yellow pikeperch

This fish, sometimes locally called "walleye" or "yellow pickerel," was taken by Koelz from three lakes only (Chickenbone, Whittlesey, and Dustin). Examples from these inland lakes are very peculiar in appearance. When studied more closely they may prove to represent distinct local forms. The only commercial listing seen is of a catch made in Chippewa Harbor. Karl Gilbert reports that it is occasionally taken in Washington Harbor. The species no doubt occurs in other places about the shore of Isle Royale, since it is found elsewhere in Lake Superior and tributary waters.

Percina caprodes semifasciata (De Kay)

Northern logperch

Although it also has far northern limits (Dymond, 1947 : 27), the logperch is restricted in its known distribution to the central part of the island near the southern shore. It was collected by Koelz only in Siskiwit, Whittlesey, and Dustin lakes, all of which lie between the Nipissing and the Minong water planes. Lagler also found this darter in Siskiwit Lake (L45 : 836 and 838), as well as in the lake outlet below the falls (L45 : 839). The circumstance that *Percina* retains an air bladder during its juvenile midwater stage helps to explain how it may have crossed the deep channel that separates Isle Royale from the mainland. Though it ranges far north in Canada, its absence from the higher waters of Isle Royale, the Huron Mountains, and the Porcupine Mountains suggests that it was not among the earlier postglacial immigrants.

Poecilichthys exilis (Girard)

Iowa darter

The taking of this darter only in Chickenbone and Sargent lakes (by Koelz) is one of the many interesting results of the ichthyological investigation of the island. Its occurrence at this latitude is not unexpected, for Dymond (1947 : 28) reported it from much farther north. The surprising circumstances are: first, that a minute bottom-swimming fish without an air bladder and showing a decided preference for weedy situations should ever have swum across the deep channel to the island;

and, second, that, so far as known, after arriving on the island it should have survived only in two lakes, with outlets in close proximity.

CENTRARCHIDAE — SUNFISH FAMILY

Lepomis gibbosus (Linnaeus)

Pumpkinseed

The occurrence of this sunfish on Isle Royale was hardly to be expected, but Koelz took it in Lakes Richie and Mason, and Lagler found it in the outlet of Sargent Lake (L45 : 803). There is no reason to suspect that it was introduced. On Isle Royale it may represent a relict from a warm postglacial period, for it is not now known from waters on the adjacent mainland (Radforth, 1944 : 65–67; Dymond, 1947 : 29; Eddy and Surber, 1947 : 238), unless a record from Baptism River, eastern Minnesota (Smith and Moyle, 1944:123), represents a native population. Specimens reputedly from the Red River of the North, labeled as collected in the Saskatchewan River by S. H. Scudder (Museum of Comparative Zoölogy, No. 3502, seven specimens, received April 28, 1860, one now in the University of Michigan Museum of Zoology) suggests the occurrence of the species much farther north than has commonly been indicated. We understand that recent findings by Canadian ichthyologists confirm this suggestion.

COTTIDAE — SCULPIN FAMILY

Triglopsis thompsonii Girard

Deepwater sculpin

From Isle Royale this sculpin is known only on the basis of specimens found by Ruthven (1909 : 331) in the stomachs of lake trout caught off the "east coast." It is no doubt common, however, in deep water all around the island. It inhabits all the Great Lakes, including Lake Nipigon, and the same form, or a similar derivative of the Arctic marine *Triglopsis quadricornis*, occurs in rivers that flow into the Arctic Ocean (Hubbs, 1926:73–74; Hubbs and Lagler, 1947:97).

Cottus ricei Nelson

Spoonhead muddler

Koelz took this interesting species in three of the inland lakes of Isle Royale, namely, Siskiwit, Whittlesey, and Desor. Lagler found it in Siskiwit Lake outlet (L45 : 839) and in other stream stations as well as on the shore: L45 : 808, 811, 822, and 830 (pp. 77–79). It may be assumed to occur scatteringly about the entire island, since it is principally a fish of the shore habitat and is of wide range in Canada (Dymond, 1947 : 30). Its occurrence in three lakes and in streams on Isle Royale is an example of the tendency of fishes of the Great Lakes proper to enter smaller waters in the north. In other parts of Michigan *C. ricei* inhabits very few of the inland lakes. The records on Isle Royale confirm the view that it was one of the earliest of the postglacial immigrants. All specimens collected in 1945 were more or less covered with the dermal prickles that usually characterize this muddler.

Cottus bairdii kumlieni (Hoy)

Great Lakes muddler

As "*Cottus ictalops*" this muddler was recorded by Ruthven (1906 : 109; 1909 : 331) from Washington and Rock harbors. Koelz took it in Chickenbone Lake, one of the very few inland lakes known to be inhabited by this subspecies. In 1945 we collected it in stream mouths (including that of the Little Siskiwit River, where Stanley also found it) and at various shore stations more or less around the entire island. These collections were L45 : 798, 799, 805, 811, 830, 835, 843, 848, 850, and 852 (pp. 76–81).

Although the differences between the Great Lakes muddler and the common slimy muddler (*C. cognatus gracilis*) are reasonably trenchant, the characters are subject to much variation and, individually, to some overlap, and certain characters are not useful in small specimens. We have therefore prepared a summary, based on Isle Royale material, of the contrasting characters of the two species (Table XII).

Cottus cognatus gracilis Häckel

Common slimy muddler

Under the name *Uranidea franklini*, then current, Ruthven (1909: 331) reported this cold-water member of the sculpin family from Rock Harbor and from Benson Brook. Koelz took it in six inland lakes (Table IV). During our 1945 collecting in streams we found it more often than the Great Lakes muddler and also obtained it in stream mouths and at shore stations. It is, therefore, distributed all around the island. The station numbers are L45 : 803, 810, 811, 814, 819, 820, 830, 839 to 841, 843, and 852 (pp. 76–81). In Table XII are given distinctions between this species and the Great Lakes muddler (*C. bairdii kumlieni*).

TABLE XII

COMPARISON OF ISLE ROYALE SPECIMENS OF COTTUS BAIRDII KUMLIENI AND COTTUS COGNATUS GRACILIS COLLECTED IN 1945

Frequency of anal ray counts

	9	10	11	12	13	14	Mean
C. b. kumlieni	..	..	..	6	25	8	13.1
C. c. gracilis	3	18	22	5	..	..	10.4

Frequency of pelvic soft-ray counts

	Formula (left–right)				Each fin	
	3–3	3–4	4–3	4–4	3	4
C. b. kumlieni	2	..	4	33	8	70
C. c. gracilis	45	..	3*	..	93	3*

Frequency of sums of number of rays in anal and in both pelvic fins

	15	16	17	18	19	20	21	22	Mean
C. b. kumlieni	..	..	..	..	2	9	19	9	20.9
C. c. gracilis	3	19	22	2	2	..	..	..	16.6

Nonmeristic characters

Character	*C. b. kumlieni*	*C. c. gracilis*
Index of anus position in larger specimens†	Usually more than 0.5	Usually less than 0.5
Palatine teeth in larger specimens	Usually present (present on one or both sides in 15 out of 20 examined)	Usually lacking (absent in all six larger specimens)
Spots on anal fin	Darker	Fainter or lacking
Under side of chin	Conspicuously mottled (entirely dark in breeding males)	Not definitely mottled, nearly uniform, light or evenly dusky

* The innermost, fourth, ray was rudimentary in these three specimens.

† The index of anus position is the fraction in tenths of the caudal fin that is covered when the distance from the tip of the snout to the anus is stepped backward from the anus onto the caudal fin. In the smaller specimens the index is lower in each form, but the distinction between the species holds fairly well.

GASTEROSTEIDAE — STICKLEBACK FAMILY

Eucalia inconstans (Kirtland)

Brook stickleback

The northerly range of this species (Dymond, 1947 : 31) is in harmony with its occurrence on Isle Royale, though its usual bog-water habitat seems incongruous with the concept that it crossed the deep channel. Ruthven (1909 : 331) recorded it from tamarack and spruce swamps about Siskiwit Lake; Koelz found it in six other inland lakes (Table IV); and Lagler collected it in two additional ones. Our 1945 collecting showed this species to be one of the more common kinds on the island, occurring in ponds, including those formed by beaver dams, in streams, in stream mouths, and, as strays in one collection, along the Lake Superior shore. Boggy habitats appear to be preferred. The 1945 collecting stations were L45 : 798, 799, 807, 809, 810, 813, 815, 817, 820, 821, 823, 824, 826 to 828, 846, 850, 851, and 852 (pp. 76–81). Several specimens taken during the latter half of July and early August were in breeding condition. The females were ripe, and the males showed the characteristic black breeding color.

Pungitius pungitius (Linnaeus)

Ninespine stickleback

In addition to the many localities, principally stream mouth and shore, in which we collected this Arctic and Subarctic stickleback, several other records attest a general though chiefly marginal distribution about the island. Our stations are L45 : 799, 805, 811, 814, 815, 821, 835, 843, 846, 848, 849, and 851 (pp. 76–81). Previous records are those of Ruthven (1909 : 331) for Rock and Tobin harbors; of Koelz for three inland lakes (Siskiwit, Hatchet, and Desor); of Ellsworth for the mouth of Washington River; and of Stanley for the mouth of Little Siskiwit River. Throughout Michigan it is essentially confined to the shores of the Great Lakes and occurs in very few of the inland lakes. Its somewhat wider distribution on Isle Royale is in harmony with the northern latitude of the island, for in the far north this species, like several other fishes, occurs commonly in the smaller waters.

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PLATES I–II



FIG. 1. Harvey Lake and surroundings, Isle Royale



FIG. 2. Harvey Lake, north shoreline, looking east from outlet

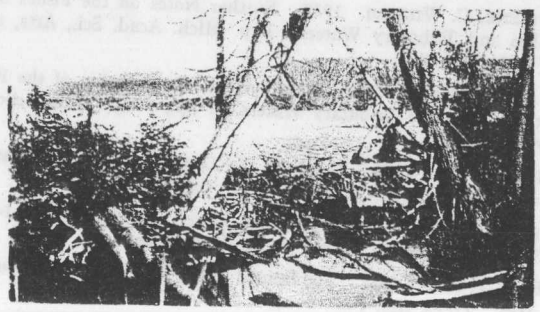


FIG. 3. Beaver dam, Harvey Lake outlet (most of Fig. 1 may be seen in background)

(All photographs by Karl F. Lagler, July, 1945)

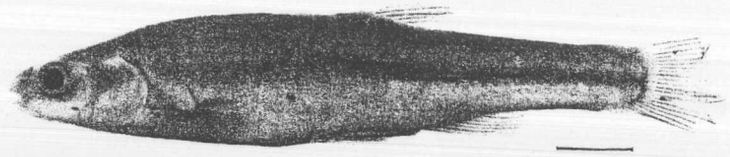


FIG. 1. *Margariscus margarita koelzi:* the holotype, 84 mm. in standard length, from Harvey Lake, Isle Royale, Michigan

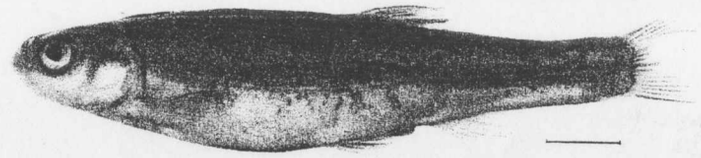


FIG. 2. *Margariscus margarita nachtriebi:* an adult, 80.5 mm. long, collected in Lake Desor, Isle Royale, by Walter Koelz, September 10, 1929

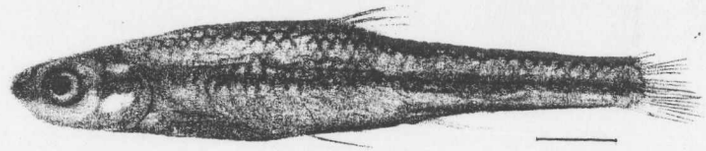


FIG. 3. *Notropis heterolepis regalis:* the holotype, 81 mm. long, from Harvey Lake, Isle Royale, Michigan

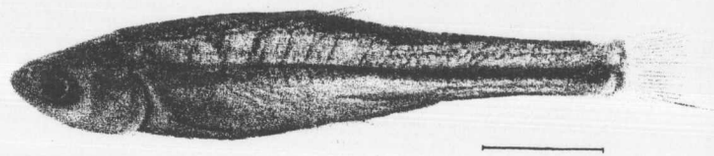


FIG. 4. *Pimephales promelas harveyensis:* the holotype, 51 mm. long, from Harvey Lake, Isle Royale, Michigan

(The scale bar equals one centimeter.)