A Comparison of Fish Communities from 32 Inland Lakes in Isle Royale National Park, 1929 and 1995–1997

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Cover graphic is an aerial photo of Angleworm and Benson Lakes in Isle Royale National Park.

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by

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Contents

Figures

Tables

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Abstract. Fish communities in 32 of Isle Royale National Park's inland lakes were surveyed in 1995–97 to determine if their composition had changed significantly since 1929 when the last complete survey was conducted. Gill nets, seines, and minnow traps were used for sampling the lakes, the surface areas of which were 1.2–1,635 ha and maximum depths of which were 1.5–46.3 m. The 1995–97 collections contained 28 of the 30 fish species reported in 1929. No new fish species were collected. Observed changes in the fish communities included no change (14 lakes), additional species (11 lakes), and undetected species (12 lakes). In five lakes, both species gains and losses were observed. Most gains seemed to be because of upstream dispersal from a downstream lake or a Lake Superior cove at the outlet of the watershed. Sculpins (*Cottus* sp.) and other small, demersal species accounted for most of the incidences where species were not detected. Species richness was 2–15 species per lake with 24 lakes having 5 or fewer species. Significant positive relations existed between the number of species and lake area and maximum depth. Isle Royale lakes contained moderate to high densities of northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), the two most widespread species. The average mercury concentration in standard-sized (550 mm) northern pike from 25 Isle Royale lakes was 304 ng/g (n = 135, range 74–693 ng/g). Compared to those of mainland lakes and adjacent Lake Superior, the fish communities in Isle Royale's inland lakes have changed relatively little since 1929. As a result, continued conservation of these native fish communities will provide further opportunities for understanding issues such as dispersal, isolation, and speciation.

Key words: Ecological contaminants, fish communities, fish populations, Isle Royale, limnology, national parks.

Surveys and studies of the fish communities of the inland waters of Isle Royale National Park, Michigan, date back to 1904–05 when Ruthven (1906, 1909) conducted cursory surveys of a few streams and inland lakes. No comprehensive investigation of the inland lakes was conducted until 1929 when Walter Koelz, as part of a University of Michigan scientific survey team, sampled 38 inland lakes. His investigation included detailed observations of shoreline and substrate types, aquatic vegetation, surrounding landforms and vegetation, and more than 3,600 hand-line measurements of water depths. Fish were sampled with linen gill nets and "common sense" seines. Koelz reported finding 30 fish species in the inland lakes (National Park Service File No. 714-01, "A survey of the lakes of Isle Royale, with an account of the fishes occurring in them," Isle Royale National Park Library, Mott Island, Michigan). He identified subspecies for five species, three of which were present in Harvey Lake.

Studies of the inland lakes since Koelz completed his work have been limited. Only four inland lakes were included in a 1945 survey, the emphasis of which was on short stream segments just upstream from Lake Superior (Hubbs and Lagler 1949). Hubbs and Lagler (1949), drawing heavily on

Koelz's work and the 1945 survey results, conducted a comprehensive analysis of the fish communities in the inland lakes and Lake Superior portions of the park. Counting subspecies, they listed 49 fish taxa as present in the park waters, 35 of which were in the inland lakes. They considered all the species in the inland lakes native species. The nonnatives they reported—sea lamprey (*Petromyzon marinus*), rainbow smelt (*Osmerus mordax*), and rainbow trout (*Oncorhynchus mykiss*)—were present only in Lake Superior. Using the data available at that time, they addressed issues such as faunal origin, postglacial reinvasion, dispersal, isolation, and speciation.

In 1960, a limited gill net survey was conducted by the U.S. Fish and Wildlife Service of the fish populations in the seven largest lakes and Hatchet Lake, which was believed to contain brook trout (*Salvelinus fontinalis*). Sharp and Nord (1960) indicated that some changes may have occurred in these fish populations because they failed to capture all of the species previously reported by Koelz. They suggested a diligent research project would be required to accurately assess the distribution of fishes on Isle Royale.

Baseline information on limnological characteristics and contaminant levels in Isle Royale's inland lakes was also limited. The deposition of organic contaminants and mercury from the atmosphere into the aquatic environment in the Lake Superior region is well documented (Eisenreich et al. 1981; Glass et al. 1986; Sorensen et al. 1990). Isle Royale's Siskiwit Lake, because it is isolated from any point sources, has been used by several researchers to assess the atmospheric input of organic contaminants. The lake's remoteness has obviously not protected it from atmospheric pollution, as organic contaminants have been found in water, sediment, and fish samples (Swain 1978; Czuczwa et al. 1984; McVeety 1986; Swackhamer and Hites 1988). Mercury levels in walleye (*Stizostedion vitreum*) from three park lakes were considered unusually high, averaging just more than 0.5 µmg/g and in some cases exceeding 1.0 µmg/g (Kelly et al. 1975). No comparable data existed for the other inland lakes.

This study was designed to assess long-term changes in the fish communities of the inland lakes by comparing present distributions to the results of previous surveys. Standardized sampling methods were used, particularly for larger fish, to establish a baseline for future monitoring and management programs. General life history characteristics, particularly those related to growth and size structure, were also investigated. Environmental data were collected that could be used to better define the major lake types and to explore relations with the observed fish distributions. This database on the fish communities of Isle Royale National Park will be used to effectively manage these resources for future generations. Additionally, fish collected as part of the study, particularly the ubiquitous northern pike (*Esux lucius*), were used to assess mercury contamination. This information can be used to determine if fish consumption advisories for park visitors are necessary and also to assess whether mercury poses any threat to other members of the aquatic food web, including piscivorous birds and furbearers.

Study Area

The study lakes are located in Isle Royale National Park, Michigan, a remote, wilderness archipelago surrounded by the cold, deep waters of Lake Superior (Figure 1). The archipelago, which has a northeast-to-southwest orientation, consists of Isle Royale, which is about 72 km long and 14 km wide, and about 400 smaller, adjoining islands. Isle Royale is 24 km from the Ontario shoreline, 35 km from Grand Portage, Minnesota, and 80 km from the Keweenaw Peninsula of Michigan. The highest point on Isle Royale, Mt. Desor, is 242 m above Lake Superior.

Isle Royale National Park lies in the Superior Upland physical province, which occupies the Precambrian areas of Minnesota, Michigan, and Wisconsin (Harris and Kiver 1985). Topographically, Isle Royale is characterized by a series of ridges and valleys and variable thicknesses of glacial drift deposits. This landscape is the result of glaciation modified by bedrock, with glacial

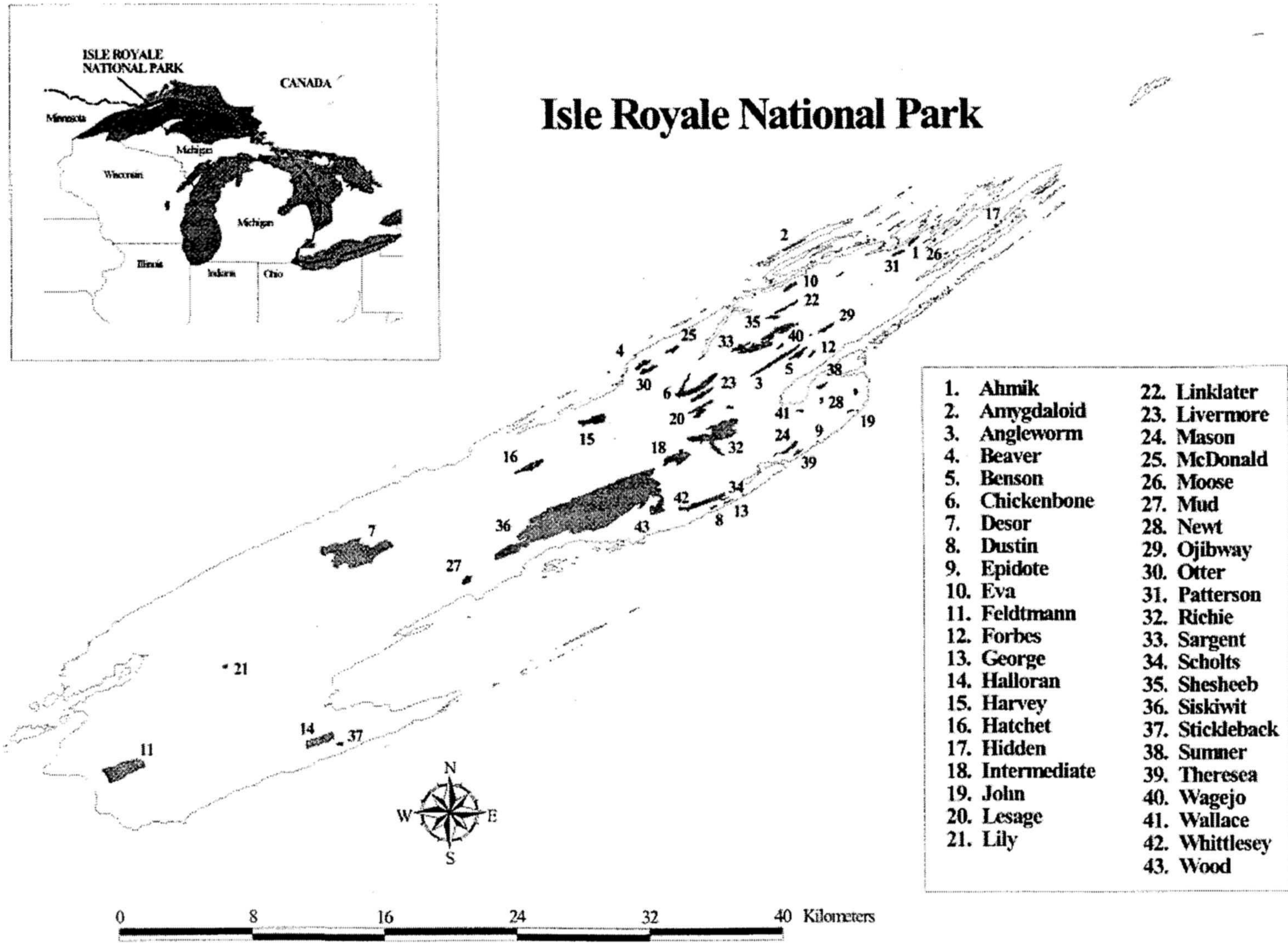

Figure 1. Inland lakes of Isle Royale National Park, Michigan.

erosion accentuating the asymmetry of the ridges and valleys that had originally been formed by stream erosion (Huber 1983). Glacial quarrying, which was probably the most important process of glacial erosion on Isle Royale (Zumberge 1955), was responsible for the creation of most of the inland lakes (Type 26, Hutchinson 1957). Two exceptions were Feldtman and Halloran Lakes, created when barrier beach bars isolated embayments from postglacial lakes Minong and Nipissing (Type 66, Hutchinson 1957).

Research of the glacial history of the Great Lakes region, while not changing the ordering of events, has changed the times attributed to major events that are of significance to the origins and distribution of the fish fauna of the Great Lakes (Underhill 1986). The final retreat of the Wisconsin glacier and the initial exposure of Isle Royale is now believed to have occurred from about 9,800 to 9,500 years before present (B.P.; Saarnisto 1975; Drexler et al. 1983; Huber 1983), or about 5,000 years later than was suggested by Hubbs and Lagler (1949) in their discussion of speciation of fish in Harvey Lake. Radiocarbon dating of a sediment core from Lily Lake, the highest lake on Isle Royale, indicates deglaciation occurred about 9,600 to 9,400 B.P. (Flakne 1997). The first inland lakes, including Lily Lake, seemingly appeared during the Lake Minong postglacial lake phase. Lake Minong, which was the first postglacial lake in the Superior basin to be free of an ice border along any portion of its border, ended between 9,500 and 9,300 B.P. (Wayne and Zumberge 1965; Saarnisto 1975). Lake Minong actually existed at an elevation 45 m below the present level of Lake Superior but, because of isostatic rebound, the remnants of its water plane currently rise from 24 m above Lake Superior at the southwest end of Isle Royale to about 52 m at the northeast end (Huber 1983). The present lake elevations of Angleworm, Benson, Desor, Forbes, Harvey, Hatchet, and Feldtman Lakes are at or above the Minong water plane, suggesting the lakes would have appeared before or during this phase. Analysis of sediment cores from Feldtman, Angleworm, and Harvey Lakes, however, provided contradictory evidence (Raymond et al. 1975). Sediment cores from the first two lakes only contained the basal reddish-brown clay layer indicating neither had been submerged by Lake Minong. A similar core from Harvey Lake contained an overlying gray clay layer that indicated the lake had been submerged despite the lake's lying 10 m above the Minong plane. Unfortunately, the cores were not dated so there is no obvious explanation for this contradiction.

Raymond et al. (1975) also used the sediment cores to differentiate two other groups of lakes, a group that was submerged by Lake Minong and a second group that was submerged by both Lakes Minong and Nipissing. The first group included Siskiwit, Harvey, and Otter Lakes, whereas Chickenbone, Eva, and Ahmik Lakes were included in the second group. Sediment cores from the first three lakes had only one gray clay layer overlying the basal reddish-brown clay, whereas cores from the last three lakes had two overlying gray clay layers. Conceivably, lakes in both groups could have first appeared in the Houghton or low-water phase that followed Lake Minong. However, the lower lying of these lakes were subsequently submerged by the higher waters of Lake Nipissing, which existed from 4,000 to 3,000 B.P. (Wayne and Zumberge 1965). On the basis of present lake elevations and profiles of water planes for the Minong and Nipissing phases for Isle Royale (Farrand 1960), it seems that 13 inland lakes could have appeared in the interval between the two phases and 12 during or after the Nipissing phase. Lakes from the first group could be from 9,000 to 4,000 years old, whereas those in the second group would be about 3,000 years old.

The following account of the geology of Isle Royale is compiled primarily from Huber (1973a, 1973b, 1983) and (Wolff and Huber 1973). The bedrock of Isle Royale is composed of two formations, the Portage Lake Lava Series and the overlying Copper Harbor Conglomerate—both of Late Precambrian age. The Lava Series consists of basaltic and andestic lava flows with minor interbedded layers of sedimentary and pyroclastic rocks. The linear ridges of the island are the eroded edges of these thick layers of lava and sedimentary rocks, which have been tilted southeastward. There is little variation in the chemical composition of the basalt rocks of Isle Royale, with most having a silica content of about 50%. The Copper Harbor Conglomerate, which consists primarily of conglomerates but does contain some sandstone, is primarily exposed along 32 km of the southwestern shore of Isle Royale. The three major rock types in the Conglomerate are sandstone, pebble conglomerate, and boulder and cobble conglomerate. The last two categories consist chiefly of volcanic rocks cemented together with calcite, which in coarse-grained sandstones composes about 15% and in pebble conglomerate about 20% of the material.

Soils on Isle Royale are the product of materials deposited by glaciers that have been subsequently reworked and redeposited by water, wind, and postglacial Great Lakes shoreline wave action (Shetron and Stottlemyer 1991). The thickness of glacial till deposits generally decreases from the southwest to the northeast end of the island. In the northeast, soils are thin and organic, whereas at the southwest end of the island they are deeper, better developed, and less organic. The glacial till is dominantly acidic, although carbonates were found in some locations by Shetron and Stottlemyer (1991). They suggested that, because most of Isle Royale's bedrock lacks carbonates from outcrops such as limestone, the carbonates either originated from calcite from the bedrock on the island or were from sources located further north in Canada.

Isle Royale, which is almost completely forested, contains representatives of two forest biomes (Linn 1966). The boreal coniferous forest is present primarily in those areas most directly affected by the cool, moist air of Lake Superior, whereas the northern hardwood forest is found in dryer, upland areas (Shelton 1975). Wetlands, including beaver ponds, bogs, and marshes, are concentrated in the island's many valleys.

Lake Superior has a major effect on Isle Royale's climate, moderating temperatures in both summer and winter. Summer temperatures along the shoreline typically range from about 5°C at night to 20°C during the day, while at higher elevations along the ridges daytime highs may exceed 30°C. Although no average annual precipitation data for Isle Royale exists, it is thought to be similar to that of nearby northeastern Minnesota where the average is about 700 mm per year (J. Oelfke, Isle Royale National Park, personal communication). Snow falls 6 months of the year. The inland lakes are typically covered with ice from late November to mid-April.

Methods

Surveys

Thirty-two of Isle Royale National Park's 42 named inland lakes were sampled—19 lakes between June 15 and September 10 in 1995 and 13 between June 12 and September 8 in 1996. All the lakes are on the main island of Isle Royale except one that lies on an adjoining small island, Amygdaloid Island. In 1997, sampling for four water chemistry parameters was repeated on all 32 lakes; the sampling was done on approximately the same date as the lakes were sampled in 1995 or 1996. Also, nine lakes were resampled in 1997 to collect fish species previously reported by Hubbs and Lagler (1949), but not found in 1995 or 1996. Because most of Isle Royale National Park is a designated wilderness area, all sampling was done from an unmotorized canoe. The canoe and all sampling equipment and resulting samples were portaged to the inland lakes from trail heads on Lake Superior. Portages ranged in length from 0.2 to 17.7 km.

Physical–chemical Variables

Limnological field measurements were made at one station near the location identified by Koelz in 1929 as the deepest point in each lake. Depths were measured with an electronic depth sonar. Profile measurements of water temperature and dissolved oxygen were made at 1-m intervals with a YSI Model 55 dissolved oxygen meter. Water transparency was measured with a standard 20-cm Secchi disk. Water samples for chemical and chlorophyll analyses were collected from about 10 cm below the surface using polyethylene cubitainers. All samples were transported to the park seasonal headquarters on Mott Island within 8 to 12 h.

At park headquarters, water samples were split for analysis on site or prepared and preserved for shipping to the Natural Resources Research Institute (NRRI), University of Minnesota–Duluth, for additional analyses. Raw water was analyzed on site for pH (Corning Model 340 pH meter), conductivity and total dissolved solids (Hach CO150 Conductivity meter), and alkalinity, which was determined by a ten-end point Gran Plot titration. An aliquot of raw water was frozen for total nitrogen and total phosphorus analysis at NRRI.

Water samples also were filtered through a 0.45 µm HAWP Millipore filter and analyzed on site for true color (Hach DR2000 spectrophotometer). Additional filtered water was preserved by freezing for analysis of the anions, chloride (Cl), nitrate (NO_3-N), and sulfate (SO_4; ion chromatography). Filtered water was also preserved with nitric acid (0.1 mL/100mL sample) for cation analysis (sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), and dissolved aluminum (Al) by atomic absorption spectrometry and with sulfuric acid (0.1 mL/100 mL sample) for dissolved organic carbon (DOC) and ammonia (NH_4-N) analysis. Between 0.5 and 1.0 L of raw water was filtered through a Whatman GF/C glass fiber filter for analysis of chlorophyll *a*. Three drops of saturated $MgCO_3$ were added to the last 10 mL of the water sample remaining on the filter. After filtration was completed, the filters were folded in quarters, placed in an aluminum envelope, and frozen until they could be transported to NRRI for analysis.

Fish Sampling

As recommended by Jackson and Harvey (1997), multiple fish sampling methods were used to detect the presence of species in the inland lakes. The standard fish sampling methods used were unbaited Gee minnow traps, a beach seine, and multifilament nylon experimental gill nets. The Gee minnow traps, which were 419 mm long, 229 mm in diameter, with 3.2 mm bar mesh wire screen, were set in nearshore areas where water depths were less than 1 m. They were used to sample areas typically not considered seinable, such as heavily vegetated areas, boulders, rock outcrops, and areas with fallen timber. A standard catch per unit of effort (CPUE) for the minnow traps was one trap fished overnight. A 6.1- × 1.2-m beach seine (bar mesh, 6 mm) was also used to sample nearshore waters but its effectiveness was limited by the lack of smooth, unimpeded substrates in shallow water. Because of this, no standardized unit of effort was established for seine hauls and the catches, even though counted, were only used to qualitatively document the presence of species. Fish collected in minnow traps and by seining were identified and enumerated, after which most were released. A small number of fish were preserved in 10% buffered formalin to confirm identifications and for use in taxonomic studies.

Experimental gill nets containing panels of different mesh sizes are commonly used to sample fish, particularly in lakes or rivers with low current velocities (Hubert 1996). As a passive gear, gill nets do have several known disadvantages, including dependence on fish movement and behavior, which in turn can be influenced by a variety of factors (Craig et al. 1986). Their catching ability is known to be affected by mesh size and color, the length of the net, and set time (Jester 1973; Hamley 1975; Davis and Schupp 1987; Minns and Hurley 1988). Their use also results in some fish mortality. Despite these limitations, gill nets, because of their versatility and suitability for sampling a wide range of habitats, continue to be used to obtain estimates of the relative abundance of numerous species. They are commonly used in remote wilderness areas like Isle Royale because they can be transported in a backpack and set from an unmotorized canoe or small boat (Hubert 1996). Some of the variability in gill net catches, which has been found to be less than that in several other commonly used fish sampling gears (Bagenal 1972; Craig et al. 1986), can be overcome by using a standardized sampling program (Hubert 1996).

Fish were sampled in 30 lakes with experimental gill nets like those that have been used in Minnesota lake surveys for more than 40 years. The gill nets were 76.2 m long and 1.8 m high, consisting of five 15.2-m panels with 19.1-, 25.4-, 31.8-, 38.1-, and 50.8-mm bar mesh. Twine used in the three smaller meshes was number 69 nylon, whereas number 104 nylon was used in the two larger meshes. Nets were fished on the bottom, but in no instance were sets made where dissolved oxygen concentrations were <2.0 mg/L. The number of gill net sets was stratified on the basis of lake area. The number of gill net sets per lake ranged from 1 in lakes with surface areas of 3–5 ha ($n = 3$ lakes), 2 sets 5.1–15 ha ($n = 8$ lakes), 4 sets 15.1–40 ha ($n = 6$ lakes), 6 sets 40.1–121 ha ($n = 7$ lakes), 9 sets 121–242 ha ($n = 3$ lakes), and 16 sets 1635 ha ($n = 1$). Exceptions to this sampling protocol were Hatchet Lake (49.6 ha) where the number of sets was reduced from six to five, and Desor Lake (427.9 ha) where the number was reduced from 12 to 6. In both instances, the reductions were because of exceptionally large fish catches. No gill net sets were made in Epidote (1.3 ha) and Scholts (2.3 ha) lakes because of their small areas. Instead, angling was used to collect northern pike for mercury analysis. The standard catch per unit of effort (CPUE) for gill nets was one net fished overnight. The average soak time for the 139 gill net sets made during the study was 19.3 h (SD = 2.9 h).

Total length (mm), weight (g), and sex were recorded for fish caught in experimental gill nets. Scale samples were taken for age determination along with cleithra from northern pike, pectoral fin rays from white sucker (*Catostomus commersoni*), and otoliths from burbot (*Lota lota*). Observations of food habits were made in the field because of the difficulties associated with the preservation and portaging of samples to Mott Island. Ocular estimates were made of the percentage by volume of stomach contents of fish collected in gill nets. If subsampling became necessary because of exceptionally large catches, scales or other structures and stomach analyses were taken from fish that encompassed the entire length range of the catch.

The 1997 attempts to verify previously reported fish presence in nine lakes were made with the standard minnow traps and seine. Overnight bottom sets also were made with a 30.5- × 1.5-m nylon-gill net with 9.5-mm bar mesh. The latter piece of equipment was used in an attempt to collect sculpins (*Cottus* sp.), trout-perch (*Percopsis omiscomaycus*), and other small, demersal fish species.

Creel Survey

Other than an unpublished 1960 creel survey conducted by a park ranger of the Siskiwit Lake fishery, no survey of the inland lakes fishery had ever been conducted. This most likely was because of the remoteness and relatively light use of the lakes which would tend to make on-site sampling impractical if not logistically impossible. Voluntary creel cards are frequently used in this type of situation, despite their known weaknesses (Pollock et al. 1994). Characteristic biases include higher reporting rates by successful anglers, exaggeration of catches, misidentification of fish, and misreporting of sizes of fish (Fraidenburg and Bargmann 1982; Essig and Holliday 1991). Even with these limitations, a voluntary creel card survey was conducted in 1997. Anglers were asked how many hours they fished, what species they caught, and how many were caught and kept. Other questions included whether anglers fished from shore or a canoe; whether they had previously fished the inland lakes and, if so, how many times; and whether they were satisfied with the number or size of fish they caught. Creel cards were issued when backpackers picked up their required camping permits. They were asked to return both items to park staff before they left the island. The primary objectives of the survey were to identify (1) which inland lakes were fished the most, (2) what species were being caught, and (3) what species were being harvested. Population parameters were not estimated because of the known limitations of the survey method.

Analysis

Morphometric and Geographic Variables

A Geographic Information System (GIS) was used to measure six geomorphic variables on 1:24,000 U. S. Geological Survey 7.5-min topographic quadrangle maps. The variables determined for each lake were surface area, maximum length, maximum width, shore line length, watershed area, and elevation above Lake Superior. The GIS analysis was done with PC ARC/INFO 7.1 and ArcView 3.0 (Environmental Systems Research Institute, Inc. 1994) at the School of Forestry and Wood Products, Michigan Technological University, Houghton. An electronic depth sonar was used to measure water depths and to confirm the maximum depths reported by Koelz in 1929. Formulas presented by Wetzel (1983) were used to calculate shoreline development (D_L) and relative depth (z_r) values for the inland lakes. D_L is the ratio of the length of the shore line (L) to the circumference of a circle of an area equal to that of the lake, whereas the z_r is the ratio of the maximum depth as a percentage of the mean diameter of the lake.

Trophic State

Trophic status for each lake was assessed by using Carlson's Trophic State Index (TSI; Carlson 1977) and classifications based on concentrations of total phosphorus (Bachmann 1980) and total nitrogen (Vollenweider 1968). Carlson's TSI numerical scale is based on interrelations between Secchi disk readings and chlorophyll and total phosphorus concentrations. The index values can range from zero to 100 with values less than 35 representing oligotrophic conditions; from 35 to 50, mesotrophic conditions; and higher values, eutrophic conditions (Walker 1988).

Age and Growth

Ages of most fish species were determined from impressions of three to five scales made in cellulose acetate plastic. Magnified impressions (×40) were examined with a microfiche reader, annuli were identified, and scale radii and distances from the focus were measured. Scales and other structures used for aging were independently examined to reduce reader bias, and ages assigned by two readers were compared. The Fraser-Lee method (DISBCAL software) was used to back-calculate lengths (Frie 1982). Standard intercept values proposed by Carlander (1982) for walleye and yellow perch (*Perca flavescens*) were used in the back-calculations. Intercept values of 33, 35, and 38 mm were used for northern pike (Franklin and Smith 1960), cisco (*Coregonus artedi*; Van Oosten 1929), and lake whitefish (*Coregonus clupeaformis*; Edsall 1960) back calculations, respectively. Scale ages of northern pike were compared with ages determined from cleithra examined at ×6.4 magnification against a black background. This comparison, though not validating the age assessments, provides some measure of confidence in the interpretation of northern pike ages (Casselman 1983; Laine et al. 1991). Although both scales and cross-sections of pectoral fin rays were examined from white suckers, ages were ultimately based on the fin cross-sections because scales have been found to underestimate the true age of older individuals by as much as 5 years (Beamish 1973). Annuli in fin rays were identified using a microscope. Growth rates of white suckers and burbot, ages of which were determined from otoliths, were based on lengths-at-age rather than back-calculated lengths. In those instances when subsampling was used, age distributions were generated with an age-length key (Ketchen 1949).

Size Structure

Size structures of northern pike, yellow perch, walleye, lake trout (*Salvelinus namaycush*), lake whitefish, and burbot were evaluated using proportional stock density (PSD; Anderson 1976) and relative stock density (RSD; Wege and Anderson 1978; Gabelhouse 1984). Proportional stock density is the proportion of quality or larger fish in a sample of fish equal to or larger than stock size (Anderson 1976). For relative stock density, the relation is the proportion of fish of any designated length-group in the sample of fish equal to or larger than stock size (Wege and Anderson 1978). Minimum lengths for stock (S), quality (Q), preferred (P), memorable (M), and trophy (T) size categories were taken from Gabelhouse (1984).

Body condition of northern pike, walleye, yellow perch, lake trout, white sucker, and burbot was evaluated with the relative weight (W_r) index (Wege and Anderson 1978). Relative weight (W_r) is the percentage resulting from a comparison of the actual weight (W) of a fish to W_s, a length-specific standard weight predicted by a weight–length regression constructed to represent the species (Wege and Anderson 1978). Standard weight (W_s) equations used were those developed by D. W. Willis (published in Anderson and Neumann 1996) for northern pike, Murphy et al. (1990) for walleye, Willis et al. (1991) for yellow perch, Piccolo et al. (1993) for lake trout, Murphy et al. (1991) for white sucker, and Fisher et al. (1996) for burbot. Weight–length regressions were developed for lake whitefish because no standard weight equation has been developed.

Mercury and Selenium Levels in Fish

Fish used for mercury (Hg) and selenium (Se) analyses were taken from gill net catches or were collected by angling. Five fish of representative sizes were typically collected from each lake, but in five of the 28 lakes, 10 fish were collected. Fillets were removed from the fish, individually packaged, and transported to Mott Island (transport time and distance 8–12 h, 5–58 km) where the samples were frozen until they could be transported to the University of Minnesota–Duluth for analysis.

Northern pike from 25 lakes, walleye from 2 lakes, and lake trout, yellow perch, lake whitefish, and white suckers from 1 lake each were analyzed for total mercury. U.S. Environmental Protection Agency Method 245.6 (U.S. Environmental Protection Agency 1991), which utilizes acid digestion followed by cold vapor atomic absorption spectrometry (CVAA), was used to determine total Hg levels in all the fish from each lake. All Hg levels are reported as wet-tissue weight for scaled, skin-on fillets. To facilitate comparisons between lakes, Hg concentrations in standard-length northern pike (550 mm) and walleye (390 mm) were determined from regressions of $\log_{10}$ transformed total length and mercury concentrations for each lake (Sorensen et al. 1990). The same regressions were used to determine Hg concentrations in 610 mm northern pike, which is the minimum legal angling length in Michigan.

Quality assurance included analyses of duplicate fish samples, spiked-fish samples, and reference material from the National Research Council of Canada (DORM-1 dogfish muscle, certified value 798 ppb). Mean relative precision values from the duplicates were 7.1% (n = 21) in 1995 and 6.8% (n = 9) in 1996. The average recovery of Hg from spiked samples was 101% (SE = 4%, n = 12) in 1995 and 110% (SE = 4%, n = 5) in 1996). Recovery of the reference material was 97% in both years (1995, SE = 2%, n = 12); 1996, SE = 2%, n = 10).

Selenium (Se) concentrations were determined because of its potential for reducing mercury uptake (Cuvin-Aralar and Furness 1991). For the Se analysis, which was restricted to one northern pike or walleye of about standard length per lake, tissue samples were digested with an HNO_3 and $HClO_4$ acid mixture in a sand bath. The resulting samples were diluted with HCl and deionized water and then reduced with $NH_{2x}OH.HCl$ and microwave heating. Samples were analyzed by hydride generation with $NaBH_4$, cryogenic trap collection, H_2/air flame quartz furnace decomposition, followed by atomic absorption detection (Liang et al. 1994).

Data Analyses

Statistics. Standard summary statistics, correlation and regression analyses, and cluster analyses were done on a microcomputer with the software package SYSTAT (Wilkinson 1990). With the exception of pH, chemical concentrations (including Hg and Se concentrations) and lake morphometry data were $\log_{10}$ transformed to meet assumptions of normality.

Relative Abundance. Whereas CPUE in standard gill nets is commonly used as an index of fish population density (Hubert 1996), the earlier surveys of Isle Royale's inland lakes did not provide CPUE data that would allow comparisons with the results of the current survey. In the 1929 survey, no standardized system was used in the gill netting program so it was impossible to calculate CPUE values. Sharp and Nord's (1960) results, although presented as a gill net ratio that indicated the number of fish taken in 100 feet of standard experimental gill net in 24 h, were of limited value because, in most instances, only one or two net sets were made per lake.

To overcome this lack of comparable information from earlier surveys, I compared the gill net CPUE values from Isle Royale with CPUE data collected from Minnesota lakes using the same nets and similar sampling procedures. To do this, the Isle Royale lakes were initially assigned to a lake class using an ecological classification system developed by Schupp (1992) from data from 3,029 Minnesota lakes. Parameters used to classify the lakes are lake area, maximum depth, shoreline length, percent littoral area (area of lake with depth <4.6 m), Secchi disk transparency, and total alkalinity. After Isle Royale lakes were classified using these morphoedaphic characteristics, their gill net CPUE results could be compared with summarized fish catch data from Minnesota lakes of the same lake classes.

The Isle Royale CPUE values were compared to intraclass quartiles developed for Minnesota lakes and values falling within the interquartile range were viewed as normal for that lake class. Values that fall above the third quartile or below the first quartile may be considered unusual, meriting more detailed examination (Schupp 1992). This approach, though statistically conservative, is particularly applicable when lakes are assessed infrequently or, as in the case at Isle Royale, there was no previous basis for comparison.

Results and Discussion

Lake Morphometry

The 32 inland lakes range in area (A) from 1.3 ha (Epidote) to 1,635.2 ha (Siskiwit; Table 1). Twenty-one (65%) lakes have areas of less than 50 ha, whereas six have areas between 50 and 100 ha. Areas of the five largest lakes range from 143 to 1,635 ha. Watershed areas (A_w) range from 18.1 ha for George Lake to 7,287.1 ha for Siskiwit Lake (Table 1). The watershed area:lake surface area ratios range from 2.4 to 204.0, with an arithmetic mean of 19.6 (Table 1). Dustin (113.1) and Scholts (204.0)—two small lakes—have unusually high ratios because they lie downstream of much larger Lake Whittlesey. On the basis of a linear regression analysis of logarithmically transformed lake and watershed area data, a significant positive relation exists between the two parameters ($r^2 = 0.597$, $P = 0.000$, $N = 32$).

The height of the lakes above Lake Superior ranges from 77.1 m (Lake Desor) to 3.8 m (Amygdaloid Lake; Table 1). Twenty-two of the lakes lie less than 30 m above Lake Superior. There was no significant relation between lake elevation and area.

Maximum depths (z_m)—other than Siskiwit Lake's 46 m—are all less than 15 m. The z_m is less than 5 m in 12 lakes, between five and 10 m in 16 lakes, and between 10 and 15 m in three lakes (Table 1). Significant positive relations exist between log transformed z_m and both lake and watershed area. The relations are $\log_{10}z_m = 0.370 + 0.263 \log_{10}A$ ($r^2 = 0.427$, $P = 0.000$, $N = 32$), and $\log_{10}z_m = 0.114 + 0.264 \log_{10}A_w$ ($r^2 = 0.348$, $P = 0.000$, $N = 32$).

For the Isle Royale lakes, shore development (D_L) values range from 1.4 to 3.6, and average 2.1 (Table 1). The majority (75%) of the inland lakes are long and narrow, having ratios of maximum lake length (l) to maximum width or breadth (b) that are greater than three (Table 1). Elongation, which has a disproportionate effect on D_L, is an important characteristic because it favors wind-induced water circulation that tends to enhance productivity (Hutchinson 1957; Koshinsky 1970).

Twenty-eight of Isle Royale's inland lakes have z_r values of less than 2% ,which is typical of most lakes (Table 1; Wetzel 1983). Also characteristically, the four exceptions, Amygdaloid, Dustin, Epidote, and John Lakes, are small lakes with relatively large z_m values.

Fourteen of the inland lakes contain islands that range in size from small, bare rock outcrops to relatively large forested islands such as Ryan Island in Siskiwit Lake. The number of islands per lake is from 1 to 12, with 10 lakes having three or less.

Table 1. Morphometric characteristics of 32 inland lakes in Isle Royale National Park, Michigan

Lake	Lake Code	Lake elevation (m)	Lake area (A) (ha)	Watershed area (A_w) (ha)	Maximum length (l) (km)	Maximum breadth (b) (km)	Shore development (D_L)	Maximum depth (z_m) (m)	Relative depth (z_r) (%)
Ahmik	AHM	192.7	10.3	35.4	0.89	0.16	2.1	3.35	0.98
Amygdaloid	AMY	187.0	10.8	26.1	1.53	0.10	2.7	8.84	2.38
Angleworm	ANG	240.5	50.4	495.6	3.51	0.20	3.0	8.40	1.05
Beaver	BEA	207.0	20.1	258.3	1.09	0.31	1.9	5.18	1.02
Benson	BEN	239.9	24.1	83.0	1.38	0.33	1.8	3.80	0.69
Chickenbone	CHI	1.2	92.6	1556.4	2.84	0.36	2.6	6.40	0.59
Desor	DES	260.3	427.8	1436.7	4.45	1.91	1.8	14.02	0.60
Dustin	DUS	198.0	4.4	497.8	0.49	0.16	1.7	6.10	2.58
Epidote	EPI	189.0	1.3	55.8	0.19	0.09	1.2	3.96	3.08
Eva	EVA	187.2	17.6	231.1	0.97	0.23	1.6	6.40	1.35
Feldtman	FEL	201.2	185.8	886.6	2.66	1.02	1.4	2.74	0.18
Forbes	FOR	236.0	6.8	40.8	0.54	0.17	3.0	5.80	1.97
George	GEO	203.9	3.8	18.1	0.61	0.10	2.0	2.70	1.23
Halloran	HAL	200.0	77.4	230.7	1.82	0.42	1.4	2.70	0.27
Harvey	HAR	232.3	55.4	292.8	1.75	0.46	1.7	4.00	0.48
Hatchet	HAT	229.9	49.6	502.2	1.90	0.41	1.7	5.20	0.65
Intermediate	INT	206.0	70.8	481.7	1.77	1.01	2.2	6.70	0.71
John	JOH	196.0	3.3	126.4	0.47	0.16	1.8	5.49	2.68
Lesage	LES	223.4	45.0	933.0	1.66	0.48	2.4	6.40	0.85
Linklater	LIN	222.2	17.3	99.4	1.56	0.17	2.4	6.00	1.28
Livermore	LIV	213.1	30.1	168.8	1.57	0.30	2.0	5.50	0.89
Mason	MAS	186.0	22.8	492.8	1.73	0.24	2.3	8.50	1.58
McDonald	MCD	213.0	14.8	104.9	0.93	0.31	1.8	4.00	0.92
Otter	OTT	213.0	20.2	96.3	1.19	0.28	1.8	4.27	0.98
Patterson	PAT	190.0	10.1	43.3	0.76	0.19	1.8	3.60	1.00
Richie	RIC	191.4	216.2	2080.2	3.20	1.99	2.4	10.67	0.64
Sargent	SAR	212.0	143.4	1089.3	4.37	0.86	3.6	13.72	0.57
Scholts	SCH	204.0	2.3	469.3	0.52	0.08	2.1	1.52	0.89
Shesheeb	SHE	222.0	11.5	155.1	0.88	0.35	1.9	5.49	1.43
Siskiit	SIS	201.0	1635.2	7287.1	11.06	2.30	2.2	46.00	1.01
Wagejo	WAG	228.9	6.1	58.2	0.49	0.22	1.4	2.19	0.79
Whittlesey	WHI	208.0	65.0	450.5	2.97	0.27	2.4	7.62	0.84

Physical, Chemical, and Trophic State Observations

In regard to thermal mixing, the Isle Royale lakes may be classified as continuous cold polymictic, discontinuous cold polymictic, or dimictic (Lewis 1983). The difference between the polymictic classifications is that continuous lakes are not stratified during the summer, whereas discontinuous lakes may be stratified for several days or weeks but mixing may occur at irregular intervals. Dimictic lakes are characterized by stable stratification throughout the warm season with mixing only occurring before and after the period of seasonal ice cover. To accurately classify the lakes, particularly according to the polymictic categories, would require monitoring temperatures throughout the open-water season rather than a one-time sampling, as was done in this study.

The summer sampling, however, found 11 unstratified and 21 stratified Isle Royale lakes. Nine of the unstratified lakes had z_m values of <5 m, whereas 18 of the stratified lakes had z_m values >5m. Thermoclines typically exist at depths of 3 to 5 m except in the larger, deeper lakes such as Siskiwit and Desor, where they existed at 9 to 10 m. The field observations agreed for 25 lakes, with predictions of lake stratification obtained with a Wisconsin model that uses z_m and A to predict lake stratification (Lathrop and Lillie 1980). Four lakes were stratified when the model indicated they should not be, whereas the opposite was true for three other lakes. Five of the seven disagreements were for small (<20 ha) lakes with z_m values <5 m. Small, relatively shallow lakes such as these may stratify by heating during the day, then mix completely during nighttime cooling (Schindler 1971).

Maximum surface temperatures ranged from 16.8 to 24.2°C, whereas mean epilimnetic or water column temperatures in unstratified lakes ranged from 16.7 to 23.9°C. The mean hypolimnetic temperature for the 21 stratified lakes was 12.6°C (range 6.6–17.9°C). Mean hypolimnion temperatures in Siskiwit, Sargent, Desor, and Richie—the four deepest lakes—were 6.6, 9.2, 10.7, and 15.4°C, respectively. Siskiwit Lake, the largest and deepest lake, had temperatures <10°C from a depth of 13 m to the bottom at 46 m.

Dissolved oxygen levels in the hypolimnion of all the stratified lakes except Siskiwit Lake were below 4 mg/L, an oxygen level below which many members of freshwater fish communities start to exhibit symptoms of distress (Davis 1975). In Siskiwit Lake, the dissolved oxygen concentration at the bottom, or 46 m, was 8.8 mg/L. Dissolved oxygen concentrations of <4 mg/L usually were confined to the bottom 1–2 m of lakes with z_m values <10 m and to the bottom 3–4 m in lakes with z_m values >10 m.

The depth of the euphotic zone of the 32 lakes, as determined by Secchi disk visibility, ranged from 1.3 to 9.0 m, with a mean of 2.9 m (Table 2). Only Angleworm, Sargent, and Siskiwit Lakes had Secchi readings >4.0 m. Secchi disk visibilities were inversely correlated with color (range, 9–110 platinum-cobalt units; r = -0.702, P = 0.000) and dissolved organic carbon (DOC; range, 5.0–15.3 mg/L; r = -0.647, P = 0.000). The relation with chlorophyll *a* concentrations (range, 0–7.68 mg/m^3) was also negative and approached significance (r = -0.344, P = 0.058).

The 32 lakes had pH values ranging from 7.3 to 8.9; both the mean and median values were 7.6 (Table 2). The 8.9 pH, which came from Harvey Lake, was the only reading that exceeded 8.0. Higher pH and alkalinity values generally corresponded, but the correlation was weak (r = 0.356, P = 0.045). There was an inverse relation between pH and color, but again the correlation was relatively weak (r = -0.346, P = 0.052).

Conductivity values ranged from 50.7 to 99.5 µmhos/cm, whereas total dissolved solids concentrations (TDS) ranged from 24.0 to 52.0 mg/L (Table 2). These parameters were highly correlated (r = 0.969, P = 0.000). They both were also positively correlated with alkalinity (conductivity r = 0.960, P = 0.000; TDS r = 0.975, P = 0.000). The observed values for TDS and alkalinity were similar to those reported for lakes in the western portion of the Upper Peninsula of Michigan

Table 2. Water chemistry, chlorophyll *a*, and transparency data for 32 inland lakes in Isle Royale National Park, Michigan.

Lake code	Chl *a* (mg/m^3)	TP (µg/L)	TN (mg/L)	NO_3-N (µg/L)	NH_4-N (µg/L)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	K (mg/L)	Al (µg/L)	SO_4 (mg/L)	SiO_2 (mg/L)	Cl (mg/L)	ANC (µeq/L)	Conductance µmhos/cm	TDS (mg/L)	DOC (mg/L
AHM	1.27	12	0.65	<5	27	10.4	4.38	1.92	0.32	14	2.01	4.8	0.21	943	91.5	48	13.5
AMY	0.67	10	0.35	<5	<10	8.2	3.45	1.53	0.34	15	2.52	3.1	0.37	645	64.5	34	9.7
ANG	1.27	7	0.28	12	6	5.8	2.13	1.32	0.51	11	3.11	4.0	0.23	414	50.7	24	6.2
BEA	0.53	10	0.61	<5	11	8.4	4.08	2.16	0.29	14	3.22	8.0	0.26	908	93.9	45	12.2
BEN	5.46	18	0.44	8	<10	7.7	2.80	1.30	0.47	13	2.19	2.3	0.27	576	57.4	30	9.8
CHI	2.00	13	0.54	16	13	9.6	3.66	2.08	0.39	10	2.94	8.5	0.57	817	79.3	42	9.9
DES	3.80	7	0.61	13	19	11.7	3.47	1.83	0.72	10	2.55	1.6	0.87	928	88.1	47	7.3
DUS	1.34	11	0.40	<5	7	8.7	2.09	1.17	0.24	21	2.99	2.0	0.20	560	56.8	30	7.5
EPI	0.47	5	0.47	<5	11	11.6	2.29	0.86	0.11	71	1.48	4.4	0.14	676	68.3	36	15.3
EVA	7.68	14	0.64	12	15	10.1	4.23	2.71	0.28	17	2.10	8.6	1.43	893	91.1	48	14.7
FEL	0.27	13	0.49	<5	9	8.4	1.85	1.08	0.20	26	3.18	1.5	0.35	473	58.4	28	12.4
FOR	2.27	11	0.30	ND	<10	9.4	2.69	1.43	0.46	18	1.44	3.9	0.25	646	66.5	35	8.6
GEO	1.00	9	0.41	<5	<10	17.5	1.56	0.96	0.15	65	2.29	3.0	0.29	1038	91.6	48	10.3
HAL	1.07	10	0.46	19	11	7.5	0.92	0.99	0.39	22	1.76	0.9	0.75	446	50.7	24	9.8
HAR	2.32	10	0.40	11	<10	9.6	3.82	1.87	0.81	23	2.72	1.7	0.26	778	66.0	34	8.9
HAT	3.62	7	0.41	<5	<10	9.9	3.44	1.75	0.54	10	2.29	10.7	0.31	764	75.5	39	11.7
INT	3.35	14	0.47	<5	<10	8.2	2.32	1.08	0.76	16	2.95	2.3	0.27	510	55.3	28	10.1
JOH	0.67	6	0.43	<5	10	13.2	2.16	0.95	0.17	37	1.81	6.3	0.17	1062	99.5	52	13.9
LES	3.19	10	0.34	<5	<10	8.9	2.80	1.39	0.53	11	2.84	4.5	0.21	606	61.7	32	9.6
LIN	6.24	11	0.38	11	<10	10.5	4.72	2.05	0.40	8	2.68	8.2	0.61	919	99.5	47	10.1
LIV	1.48	10	0.32	5	<10	10.6	3.46	2.09	0.42	9	3.00	8.8	0.29	798	79.9	42	7.8
MAS	4.67	8	0.41	9	<10	10.4	2.27	1.24	0.54	31	3.18	5.7	1.30	522	58.6	31	15.2
MCD	0.87	12	0.52	<5	11	8.4	4.26	2.24	0.25	14	3.33	6.7	0.29	875	88.7	41	12.1
OTT	0.93	10	0.35	11	12	8.0	3.21	1.74	0.26	11	2.83	6.3	0.25	648	69.8	33	8.3
PAT	2.90	12	0.51	ND	<10	14.0	5.27	2.05	0.68	6	1.19	9.8	0.23	961	93.1	49	15.1
RIC	2.86	10	0.45	<5	<10	9.8	2.90	1.49	ND	36	3.24	6.4	1.03	646	68.2	36	9.6
SAR	0.07	12	0.40	<5	<10	5.8	2.32	1.21	0.34	5	3.26	7.9	0.56	788	84.5	38	8.7
SCH	0.00	8	0.52	12	<10	11.1	1.98	1.05	0.28	39	2.69	ND	0.21	680	68.2	36	12.5
SHE	5.68	11	0.36	ND	<10	10.4	4.34	1.84	0.42	6	1.74	6.2	0.42	896	96.7	45	9.9
SIS	1.07	14	0.27	27	14	8.6	2.24	1.16	0.36	5	4.49	2.7	0.37	598	65.0	34	5.0
WAG	7.09	17	0.35	11	<10	9.1	3.00	1.95	0.40	17	3.34	5.9	0.41	605	68.4	32	10.0
WHI	2.51	7	0.25	21	<10	8.6	1.98	1.18	0.41	13	2.66	2.9	0.24	540	54.1	28	8.3

(Schneider 1975), and for Ontario lakes lying to the north and west of Lake Superior (Ryder 1964).

Ionic composition of the water in Isle Royale's inland lakes is characteristic of lakes in the temperate zone (Wetzel 1983). The order of concentration for the major cations in all the lakes was Ca>Mg>Na>K, with concentrations (mg/L) ranging from 5.8 to 17.5 for Ca, 0.9 to 5.3 for Mg, 0.9 to 2.7 for Na, and 0.1 to 0.8 for K (Table 2). Proportions of Ca and Mg—known to be closely related to bedrock geology (Hem 1971)—varied, with higher proportions of Ca present in lakes associated with the Copper Harbor Conglomerate and sandstone and conglomerate outcrops. These lakes are located primarily in the southwest half of Isle Royale.

The order of concentration for the dominant anions was HCO_3>SO_4>Cl. Alkalinity levels (HCO_3) ranged from 20.8 to 53.5 mg/L (Table 2). According to Hooper's (1956) classification for Michigan Lakes, water in 19 Isle Royale lakes would be considered soft (alkalinity 20–39 mg/L) and medium (alkalinity 40–104 mg/L) in the other 13 lakes. Concentrations of sulfate ranged from 1.19 to 4.49 mg/L and chloride from 0.14 to 1.43 mg/L.

Total nitrogen concentrations ranged from 0.25 to 0.65 mg/L, with a mean of 0.43 mg/L. Both NO_3-N and NH_4-N had concentrations ranging from 3 to 27 mg/L, but in about 50% of the lakes they were both below detection level (Table 2). Total phosphorus concentrations ranged from 5 to 18 mg/L. Total nitrogen:total phosphorus ratios, which are often suggested as limiting to phytoplankton growth (Schindler 1978; Harris 1986), all exceeded the 15:1 ratio considered to indicate phosphorus limitation (Lillie and Mason 1983).

Twenty-four of the 96 TSI values were <35, 68 were in the 35 to 50 range, and four were >50. The proportions assigned to the various trophic levels, however, varied; chlorophyll *a* TSI had the highest proportion of oligotrophic lakes and the Secchi TSI the lowest (Figure 2). The Secchi TSI was most likely influenced by the negative relation between transparency and color and DOC. Based on total phosphorus concentrations, Carlson's TSI indicated

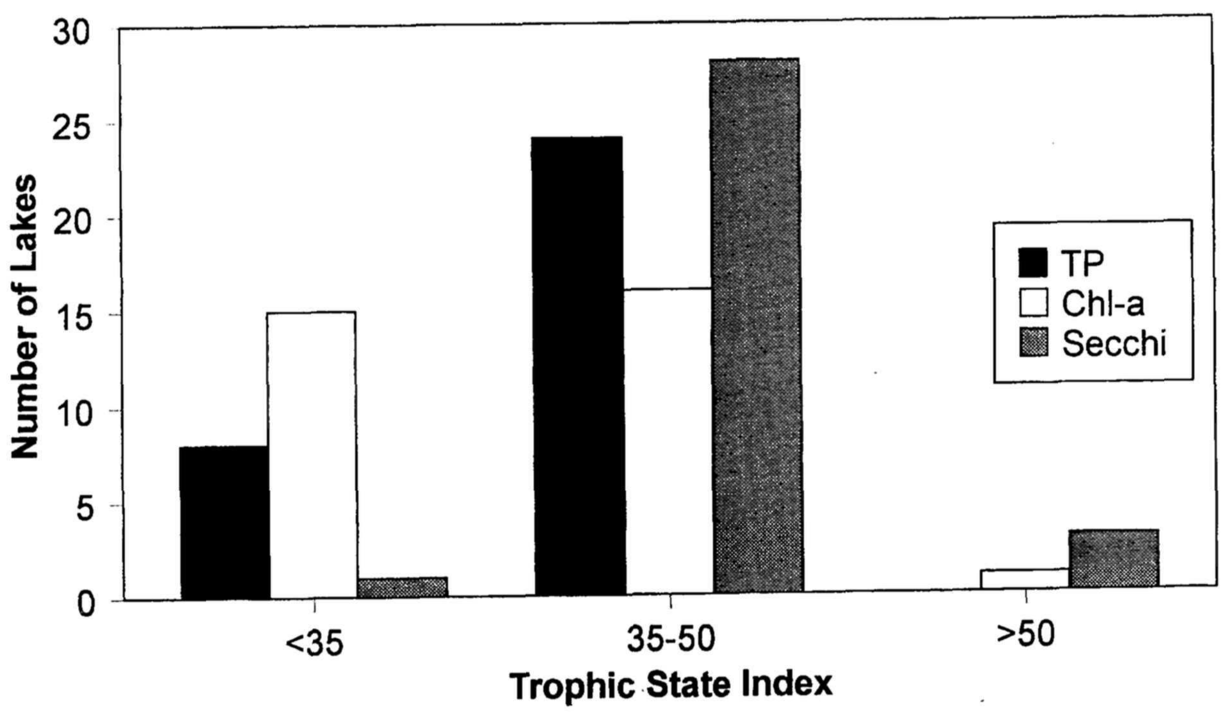

Figure 2. Distribution of trophic state indexes for 32 inland lakes in Isle Royale National Park, 1995–1996. Indexes are based on total phosphorus (TP), chlorophyll *a* (chl *a*), and Secchi disk (Secchi) readings.

Table 3. Comparison of the distribution of fish in inland lakes in Isle Royale National Park, Michigan in 1995–1997 to distributions reported by Hubbs and Lagler (1949). NC = present in both time periods; KA = present only in 1995–1997; and, HL = reported only by Hubbs and Lagler (1949). Dashes indicate fish was not present in that lake.

	Lakes																															
Species	**AHM**	**AMY**	**ANG**	**BEA**	**BEN**	**CHI**	**DES**	**DUS**	**EPI**	**EVA**	**FEL**	**FOR**	**GEO**	**HAL**	**HAR**	**HAT**	**INT**	**JOH**	**LES**	**LIN**	**LIV**	**MAS**	**MCD**	**OTT**	**PAT**	**RIC**	**SAR**	**SCH**	**SHE**	**SIS**	**WAG**	**WHI**
Cisco	--	--	--	--	--	--	NC		--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	NC	--	--	NC	--	--
Lake whitefish	--	--	--	--	--		NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--
Brook trout	--	--	--	--	--		HL	--	--	--	--	--	--	--	--	HL	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Lake trout	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--
Northern pike	NC	NC	NC	NC	--	NC	--	NC	NC	NC	NC	--	NC	NC	--	--	NC	HL	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
Lake chub	--	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Pearl dace	--	--	--	--	--	--	NC	--	--	--	--	NC	--	--	NC	NC	--	KA	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Golden shiner	--	--	--	NC	--	--	--	--	--	NC	--	--	--	NC	--	--	NC	--	--	NC	--	NC	--	HL	--	NC	NC	--	NC	--	--	--
Emerald shiner	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--
Blackchin shiner	--	--	--	--	--	KA	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	KA	--	--	--	--	--
Blacknose shiner	--	--	--	NC	NC	KA	--	NC	--	NC	--	NC	--	NC	NC	--	NC	NC	--	NC	NC	NC	--	NC	--	NC	NC	NC	NC	NC	--	KA
Spottail shiner	--	NC	--	HL	--	NC	--	--	--	NC	--	--	--	--	--	--	NC	--	--	--	--	--	--	NC	--	NC	NC	--	--	NC-	--	NC
Mimic shiner	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--	--	--	--	--
N. redbelly dace	--	--	--	--	--	KA	KA	--	--	--	--	--	--	--	--	KA	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Finescale dace	--	--	--	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	KA	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fathead minnow	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Creek chub	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
White sucker	--	--	KA	--	--	NC	NC	NC	--	--	NC	--	--	--	NC	NC	NC	NC	--	--	--	--	--	--	--	NC	NC	HL	--	NC	--	NC
Trout-perch	--	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	NC	HL	--	--	--	--	--	--	--	--	NC	--	--	--	NC	--	NC
Burbot	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--
Brook stickleback	--	--	--	--	KA	--	NC	--	--	--	--	--	--	--	NC	NC	--	--	--	--	--	--	--	--	--	KA	--	--	--	HL	--	--
Ninespine stickleback	--	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	HL	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--
Pumpkinseed	--	--	--	--	--	KA	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--	--	NC	KA	--	--	--	--	--
Iowa darter	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	--	--	--	--
Yellow perch	NC	NC	NC	NC	NC	NC	--	NC	NC	KA	NC	NC	NC	NC	NC	--	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	KA	NC
Logperch	--	--	--	--	--	--	--	HL	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	NC
Walleye	--	--	--	--	--	NC	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC
Mottled sculpin	--	--	--	--	--	HL	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Slimy sculpin	--	--	--	--	--	HL	HL	--	--	--	--	--	--	--	--	--	--	--	--	--	--	HL	--	--	--	NC	NC	--	--	NC	--	--
Spoonhead sculpin	--	--	--	--	--	--	NC	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	NC	--	HL

that 24 lakes would be classified as mesotrophic and eight as oligotrophic. Bachmann's (1980) lake classification model yielded 26 as mesotrophic and six as oligotrophic. Based on total nitrogen levels (Vollenweider 1968), three would be oligotrophic and the remainder mesotrophic. Thus, on the basis of these three methods, most of the inland lakes would be classed as mesotrophic with a few exhibiting oligotrophy.

Fish

Species Composition

Through the use of multiple sampling methods, 28 of the 30 fish species previously collected by Koelz in 1929 and reported by Hubbs and Lagler (1949) as present in the inland lakes were collected in this survey (Table 3; Appendix A). The two species not collected were brook trout and the mottled sculpin, *Cottus bairdi*. In accordance with Bailey and Smith (1981), I have for this paper chosen not to recognize the subspecies listed by Hubbs and Lagler (1949) for five of the species found in the inland lakes. Bailey and Smith (1981) concluded that the available data did not support subspecific partition. The beach seine produced 21 species, the gill nets 11 species, and the minnow traps 10 species. Eight species were caught exclusively in the seine and six species only in the gill nets. All of the species captured in the minnow traps also were captured in at least one of the other sampling gears.

No fish species new to the Isle Royale archipelago were collected from the inland lakes. None of the additional 36 fish species identified by Bailey and Smith (1981) and Underhill (1986) as native to Lake Superior and its tributaries have invaded the inland lakes since 1929. This is also true for the many introduced and exotic species, including the ruffe (*Gymnocephalus cernuus*) and round goby (*Neogobius melanostomus*) that have become established in Lake Superior during this period (Bailey and Smith 1981; Underhill 1986; Mills et al. 1993). The 28 species that were collected include representatives of 10 families. The best-represented family is the Cyprinidae, which is represented by 12 of the 20 cyprinid species present in Lake Superior. Other families and the number of species from each present in the inland lakes are Catostomidae (1), Esocidae (1), Salmonidae (3), Percopsidae (1), Gadidae (1), Gasterostidae (2), Cottidae (3), Centrarchidae (1), and Percidae (4).

Nine species were collected in 16 new locations, whereas 12 species were not collected in the 15 locations reported by Hubbs and Lagler (1949; Table 3). The northern redbelly dace (*Phoxinus eos*) was found in three new lakes and blackchin shiner (*Notropis heterodon*), blacknose shiner (*N. heterolepsis*), brook stickleback (*Culaea inconstans*), pumpkinseed (*Lepomis gibbosus*), and yellow perch were each found in two additional lakes. In all instances, the presence of species in new locations could be attributed to upstream dispersal. As determined from the 1929 distributions, dispersal in nine instances was apparently from adjoining downstream inland lakes or major coves in Lake Superior; in seven instances dispersal was directly from Lake Superior.

The failure to detect species where they were previously reported could conceivably be because of sampling deficiencies or the species was no longer present. The absence of brook trout from samples from Desor and Hatchet Lakes and northern pike from John Lake suggests they are no longer present; both species can be sampled effectively with gill nets. Sharp and Nord (1960), who also failed to collect brook trout from Desor and Hatchet Lakes, and Koelz commented that neither lake seemed well-suited to brook trout. Temperatures and dissolved oxygen concentrations during this survey also seemed marginal for brook trout survival. Though water temperatures in the hypolimnion of Desor Lake were below the 18°C preferred temperature of brook trout (Coutant 1977), dissolved oxygen concentrations were <1 mg/L. In Hatchet Lake, temperatures were higher than 23°C throughout the water column except in the bottom meter where the temperature was 16.6°C. The oxygen concentration at that depth, however, was only 0.25 mg/L. This combination of relatively high temperatures and low dissolved oxygen concentration may also explain why ninespine stickleback (*Pungitius pungitius*) were not detected in Hatchet Lake. The ninespine stickleback is usually considered a cool- to cold-water species (Becker 1983).

There is no apparent explanation for the disappearance of northern pike from John Lake because there were no barriers on the lake's outlet stream that would prevent northern pike from moving upstream from Lake Superior. In fact, a large beaver dam that historically was present on the outlet stream, and that conceivably could have served as a barrier, no longer exists.

The failure to detect the three sculpin species, which accounted for 5 of the 15 instances where species were not relocated, would seem to be because of inappropriate or inadequate sampling. Despite the use of multiple sampling methods, the presence of slimy sculpin, *Cottus cognatus*, and spoonhead sculpin, *C. ricei*, was primarily determined from the examination of stomach contents of large piscivores. The only sculpins collected by any of the other sampling methods were five slimy sculpins caught by seining in Richie Lake.

Three additional instances where species reported by Koelz in 1929 were not detected involved the demersal species, trout-perch, logperch (*Percina caprodes*), and the white sucker. Increased sampling effort with gear types specifically designed to sample such species will be needed to determine whether or not these species are still present.

Some uncertainty exists regarding the final three instances of nonrelocation because none of the three species were originally reported by Koelz. Hubbs and Lagler (1949) concluded that brook sticklebacks were present in Siskiwit Lake on the basis of Ruthven's (1909) report that they were present in tamarack and spruce swamps about the lake. The presence of golden shiners (*Notemigonus crysoleucas*) in Otter Lake and spottail shiners (*Notropis hudsonius*) in Beaver Lake was based on specimens found by Hubbs while he was confirming the shiners collected by Koelz. Because only single specimens were found it is conceivable they had mistakenly been mixed in from a fish collection from one of the other inland lakes. Given this uncertainty, further collections will need to be made to verify whether or not these species are present in these particular lakes.

Fish Communities

Fish communities in 18 of the 32 inland lakes were affected by the changes in species distributions. Eleven lakes gained species, 12 lakes lost species, and 5 lakes experienced both gains and losses (Table 3). Changes in the majority of the lakes were either a gain or loss of one species. The biggest exception was Chickenbone Lake, which gained three species and lost two. The only other lakes that gained or lost more than one species were John and Sargent, which each gained two, and Desor and Hatchet, which each lost two.

Clustering the lakes by fish species present yielded five major groups of lakes (Figure 3). Seven of the nine lakes in Group I contained only yellow perch and northern pike, the other two lakes also contained white suckers. In Group II, which contained 11 lakes, the average number of species per lake was 4.1. Lakes in this group, in addition to containing yellow perch and northern pike, typically had one or more of the three most widespread shiner species—blacknose, spottail, and golden. Yellow perch and the blacknose shiner were also present in the four lakes in Group III, which contained an average of 4.25 species per lake. The primary features that distinguished the Group III lakes from those in Group II were the complete absence of northern pike and the presence of pearl dace (*Margariscus margarita*) in three of the lakes. Group IV contained six lakes including three of the four largest lakes. The number of species per lake in this group ranged from 6 to 15 and averaged 10.1. In addition to containing the most ubiquitous species, lakes in this group included all three that contained walleye and three of the four with cisco. Group V consisted of only Desor and Hatchet Lakes, which contained 10 and 7 species, respectively. The characteristic that distinguished them from all of the other lakes was that neither contained yellow perch or northern pike.

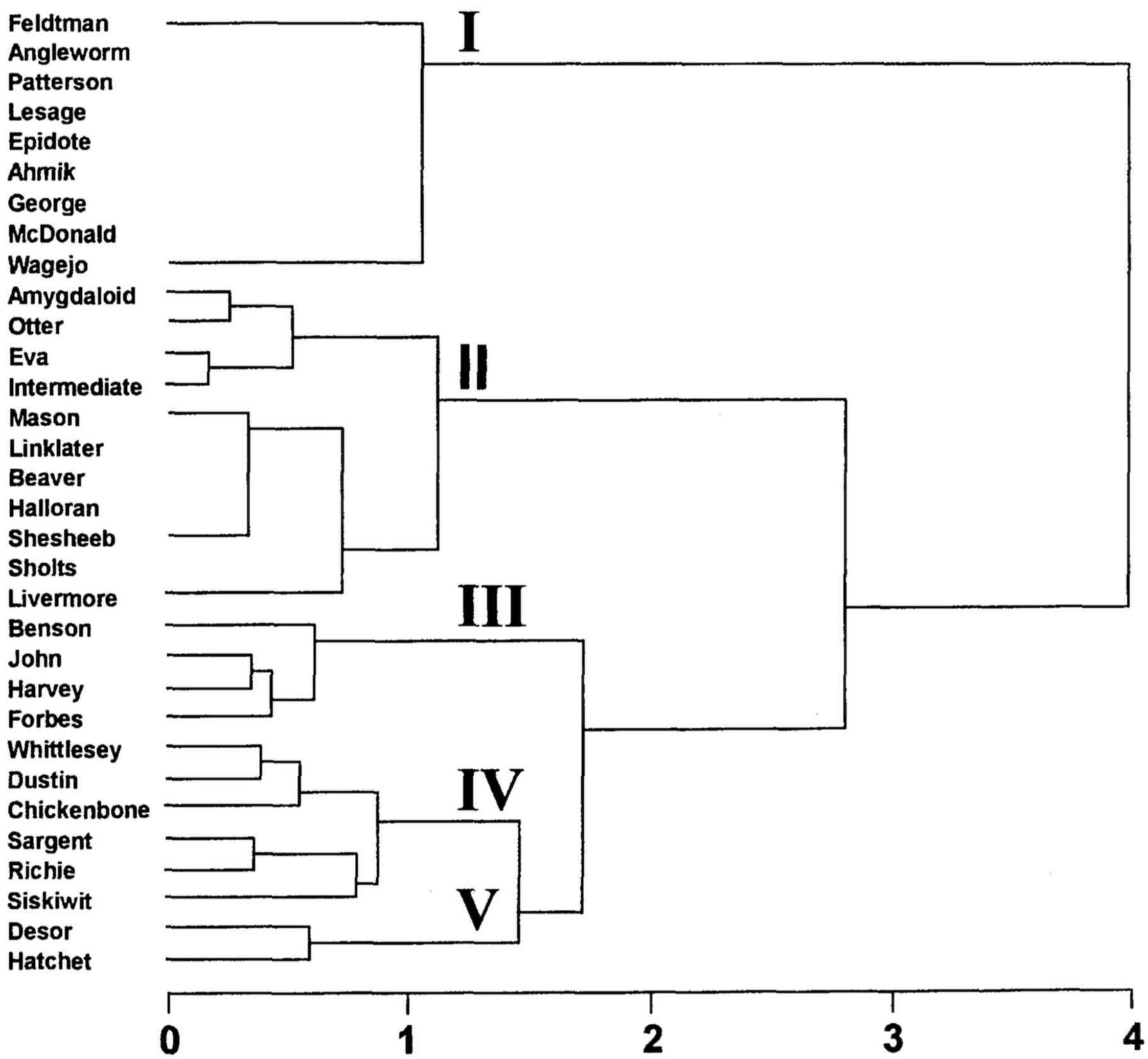

Figure 3. Dendrogram representing similarities in the fish communities of Isle Royale National Park inland lakes, based on the presence or absence of fish species.

Species Richness

The majority of the fish species had limited distributions with 22 species present in five or fewer lakes (Table 3). Emerald shiner (*Notropis atherinoides*), lake trout and burbot are present only in Siskiwit Lake, whereas lake chubs (*Couesius plumbeus*) are restricted to Desor Lake, mimic shiners (*Notropis volucellus*) to Richie Lake, and creek chubs (*Semotilus atromaculatus*) to Hatchet Lake. Although restricted to single lakes, all these species except the creek chub have been collected either from small streams on the island or from adjoining Lake Superior waters (Hubbs and Lagler 1949). Hubbs and Lagler (1949), in discussing the unusual presence of the creek chub, dismissed the idea that the population may have resulted from the release of bait minnows. They indicated that the remoteness of the island would most likely preclude such an event. Instead, they suggested the creek chub may have been an early postglacial migrant and thus was probably a native species. Such an event is certainly conceivable because the creek chub is widely distributed in tributaries to Lake Superior (Becker 1983; Underhill 1986) and has been found in the Great Lakes to depths of 13 m (Hubbs and Lagler 1964). The apparently unresolvable question remains: Why did they become established in this lake but not the other lakes?

The two most ubiquitous species were yellow perch and northern pike, present in 30 and 26 lakes, respectively. The only lakes yellow perch have not successfully colonized are Desor and Hatchet, both of which lie above the Minong plane. Also, northern pike were not found in five of the seven lakes that lie above the Minong plane, the exceptions were Feldtman and Angleworm Lakes. The blacknose shiner, which was found in 20 lakes, was also absent from four of those lakes that lie above the Minong plane. The absence of these otherwise relatively widespread species from these older lakes may suggest they were not early postglacial migrants and that their presence now was the result of upstream migration at some later date. Small barrier falls on the outlets of this group of lakes may prevent any further incursions of these species as well as any others that exist in the Lake Superior drainage.

Since Hubbs and Lagler (1949) completed their analysis of the Isle Royale fishes, numerous studies have applied the theory of island biogeography (MacArthur and Wilson 1967) to the analysis of fish species richness in lakes (Barbour and Brown 1974; Magnuson 1976; Browne 1981; Harvey 1981; Eadie et al. 1986). Fish species richness is the result of both regional and local processes, the former involving geographic dispersal and speciation with the latter including those biotic and abiotic factors that determine the success or failure of a fish species in a lake or group of lakes (Ricklefs 1987; Jackson and Harvey 1989; Minns 1989). Additionally, fish species richness may be affected by human alteration of fish assemblages or habitats in lakes (Magnuson 1976; Minns 1989). Fish stocking, habitat modification, pollution, and even angling have all contributed to changes in numerous fish communities, particularly those in more accessible mainland lakes and rivers. Fortunately, the inland lakes of Isle Royale have not been subjected to most of these activities and, as a result, their fish communities remain relatively intact.

The regional processes—postglacial dispersion and speciation—were major components of Hubbs and Lagler's (1949) discussion of the origin of the fish fauna of Isle Royale. In regard to postglacial dispersion, they suggested the lake trout, lake whitefish, cisco, northern pike, burbot, ninespine stickleback, and sculpins invaded Lake Superior from the northwest after the last glaciers receded. They indicated, however, that some of these species also may have invaded from the unglaciated Upper Mississippi drainage in Ohio, Indiana, Illinois, and Wisconsin, which formed the Mississippian Refugium during the Wisconsian glacial period. This refugium they considered the source of all the remaining species at Isle Royale.

Contrary to those of Hubbs and Lagler (1949), more recent studies generally support the idea that all of the species found on Isle Royale came from the Mississippian Refugium (Bailey and Smith 1981; Underhill 1986; Mandrak and Crossman 1992). Bailey and Smith (1981) and Underhill (1986) concluded that none of the species in the Great Lakes were derived from a western source. Underhill (1986) suggested that immigration from the Nelson River basin (which included Lake Agassiz) into Lake Superior, though historically possible, was not required to explain the origin of the Lake Superior fish fauna. Evidence for possible Mississippian origins for the species that Hubbs and Lagler (1949) indicated may have come from the northwest was provided by McPhail and Lindsey (1970), and more specifically for lake whitefish (Franzin and Clayton 1977; Bernatchez and Dodson 1990), ninespine stickleback (Nelson 1968; Lyons 1984), and northern pike (Reist 1983; Senanan 1997).

Recent research using mitochondrial DNA (mtDNA) analysis of walleye (Ward et al. 1989) and lake trout (Grewe and Hebert 1988; Wilson and Hebert 1996), however, suggests that populations of the two species in the Great Lakes may have derived from three glacial refugia. Three dominant mtDNA haplotypes were identified for each of the species. Walleye haplotype A, which was most common in the eastern Great Lakes, is thought to have arisen from the Atlantic Refugium, whereas haplotype B, which was present most frequently in the central Great Lakes and adjoining areas, is attributed to the Mississippian Refugium. Ward et al. (1989) suggested that a haplotype C, present most frequently in samples from western Lake Superior and lakes in Manitoba, supported the possibility of a Missourian Refugium. Haplotype C was also represented in walleye from Lake Nipigon, which drains into Lake Superior north of Isle Royale (Billington et al. 1992). Genetic analysis is being conducted by U.S. Geological Survey–Biological Resources Division (USGS–BRD) researchers in an attempt to resolve the origin of the walleye in Chickenbone and Whittlesey Lakes on Isle Royale. Hubbs and Lagler (1949) considered walleye to be a native species despite Koelz's footnote reference stating that walleye fry had been planted in Richie Lake in 1925.

The presence of three mtDNA haplotype groups in lake trout brood stocks and natural populations indicated that the lake trout populations in the Great Lakes may have also derived from three separate glacial refugia (Grewe and Hebert 1988; Wilson and Hebert 1996). The predominant haplotype (A) apparently came from a refugia located south of the glaciers, whereas the other two haplotypes (B, C) came from eastern and western refugia.

All three haplotypes were present in lake trout from Isle Royale's Siskiwit Lake and from Lake Superior (Burnham-Curtis et al. 1997). Haplotype A composed 83% of the Siskiwit Lake samples, with the B and C types composing 15% and 2%, respectively. Frequencies of the different haplotypes in the three lake trout phenotypes in Lake Superior varied and the frequencies of A, B, and C were 56%, 15%, 29% for siscowets; 68%, 7%, 25% for leans, and 31%, 21%, 47% for humpers. The frequencies for the humpers were similar to the 33%, 19%, and 48% values reported for lake trout from Hare Island in Lake Superior (Grewe and Hebert 1988).

Whereas Hubbs and Lagler (1949) concluded that some speciation had occurred in the inland lakes, Bailey and Smith (1981) questioned their findings and chose not to recognize the subspecific status that had been assigned. As previously mentioned, I have for this paper chosen not to recognize the subspecies listed by Hubbs and Lagler (1949) for five of the species found in the inland lakes. However, USGS-BRD and University of North Dakota scientists are conducting a separate taxonomic study to determine whether the subspecific status given to three cyprinid species from the park's inland waters, particularly Harvey Lake, has merit.

Local factors that may have affected species richness addressed by Hubbs and Lagler (1949) included the suggestion that it was improbable that all the early fish immigrants had survived, particularly those that required cold, clear-water conditions. They cited as evidence the fact that the coregonids had vanished from all but the four deepest lakes. The apparent loss of brook trout from Desor and Hatchet Lakes and the low densities of cisco in Sargent and Richie Lakes suggests this process may be continuing. Another local factor was an apparent decrease in species richness with elevation, which they attributed to those species arriving late in the postglacial redispersal and unable to ascend the small, intermittent streams of Isle Royale. My results, however, do not support this. In the recent survey, there was no significant correlation between lake elevation and number of species ($r = 0.026$, $P = 0.886$) and there was evidence of species moving upstream and colonizing additional lakes.

Hubbs and Lagler's (1949) observation of a positive relation between the size of the lakes and fish species richness preceded the better known citations of this now relatively well-documented relation (Barbour and Brown 1974; Browne 1981; Harvey 1981; Eadie et al. 1986). Based on the 1990s fish distributions, the number of fish species in the Isle Royale lakes is strongly correlated with the logarithms of the lake area ($r = 0.752$, $P = 0.000$), maximum depth ($r = 0.767$, $P = 0.000$), and watershed area ($r = 0.776$, $P = 0.000$). The relation between species richness and the shore development factor was also positive and approached significance ($r = 0.317$, $P = 0.077$). Positive relations such as these have generally been attributed to the increased habitat diversity in larger, deeper lakes with more complex shorelines (Tonn and Magnuson 1982; Eadie and Keast 1984; Eadie et al. 1986).

The slope of a species richness-area regression for the 32 Isle Royale lakes (0.26) was similar to values reported from lake assemblages in New York (0.24, Browne 1981), Ontario (0.24, Eadie et al. 1986), and Wisconsin (0.32, Tonn et al. 1990).

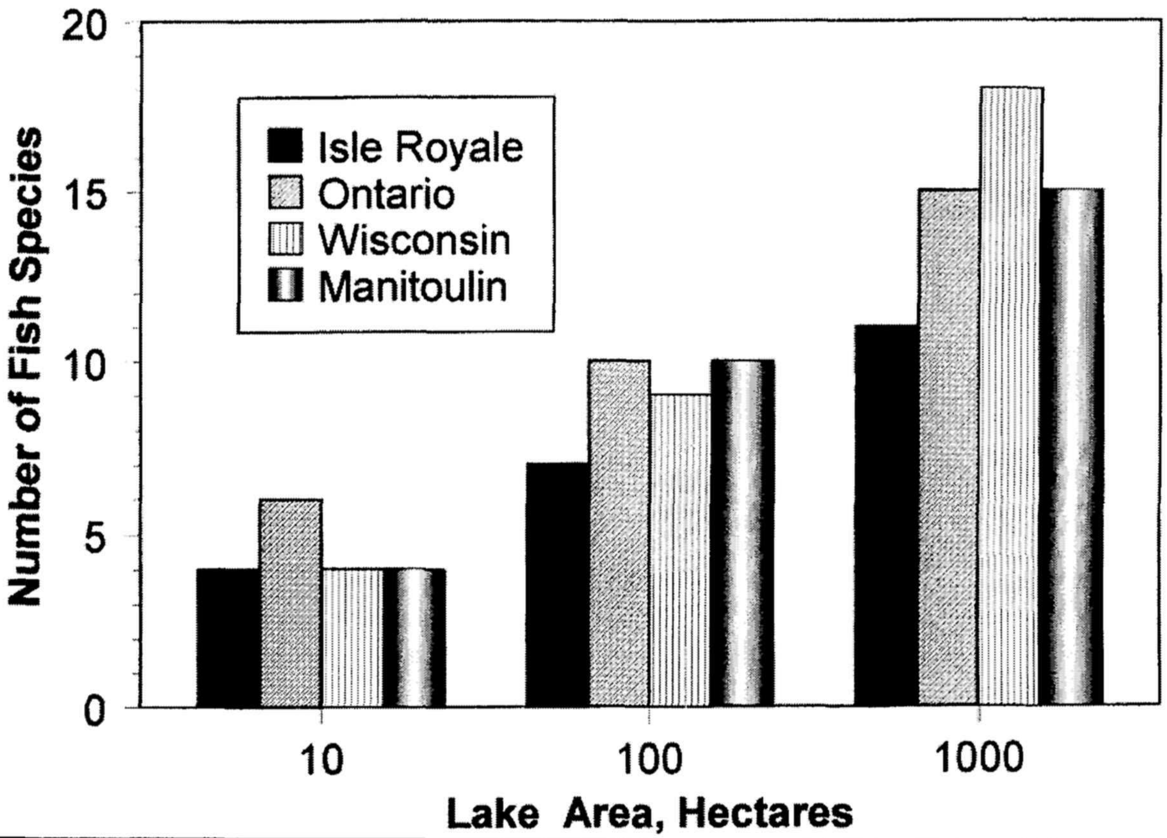

Figure 4. Fish species richness in inland lakes in Isle Royale National Park compared to species richness in lakes in Ontario (Matuszek et al. 1990), Wisconsin (Tonn et al. 1990), and on Manitoulin Island in Lake Huron (Harvey 1978).

However, the number of fish species in Isle Royale lakes is generally less than in comparable-sized lakes in the north-central states and Ontario (Figure 4). Hubbs and Lagler (1949) attributed the sparsity of fish species on Isle Royale more to the depauperate fauna of Lake Superior than to the barrier of the cold, deep water that surrounded the archipelago. It seems, however, that the lake has served as a barrier to warmwater fish because no new species from the centrarchid and catostomid families have invaded since 1929. Other species may have reached Isle Royale since then but were unable to establish self-sustaining populations because of unfavorable habitat conditions in the inland lakes. A survey of the waters surrounding the island, particularly the larger embayments, could conceivably provide evidence of whether or not that has occurred.

Another local factor that apparently affects species richness in some of the Isle Royale lakes is predation by northern pike. Northern redbelly dace, finescale dace (*Phoxinus neogaeus*), brook stickleback, fathead minnows (*Pimephales promelas*), and pearl dace seldom coexisted with northern pike. Predatory exclusion of cyprinids and other small-bodied species by northern pike has also been reported as an important regulatory process in small, forested lakes in Ontario, Wisconsin, and Alberta (Harvey 1978, 1981; Tonn and Magnuson 1982; Robinson and Tonn 1989; Magnuson et al. 1998). In a laboratory study of the survival of four prey in the presence of northern pike, yellow perch—which commonly coexist with pike—had the highest survival rate, whereas brook sticklebacks, finescale dace, and fathead minnows had significantly lower survival rates (Robinson 1988).

Relative Abundance

The gill net CPUE results must be interpreted cautiously because in 11 lakes only one or two sets

Table 4. Catch per unit of effort for experimental gill nets in inland lakes in Isle Royale National Park, Michigan, 1995–1996.

Lake code	Lifts	NOP	YEP	WAE	WTS	LAT	LKW	TLC	BUB	CYP[1]
AHM	2	5.50	1.50	--	--	--	--	--	--	--
AMY	2	3.50	3.50	--	--	--	--	--	--	--
ANG	6	4.17	6.00	--	1.50	--	--	--	--	--
BEA	4	8.50	5.00	--	--	--	--	--	--	--
BEN	4	--	120.75	--	--	--	--	--	--	--
CHI	6	6.00	21.33	18.17	1.33	--	--	--	--	--
DES	6	--	--	--	83.50	--	13.00	1.33	--	1.17
DUS	1	2.00	2.00	1.00	4.00	--	--	--	--	--
EVA	2	3.50	0.50	--	--	--	--	--	--	--
FEL	9	11.56	8.89	--	2.56	--	--	--	--	--
FOR	2	--	62.00	--	--	--	--	--	--	--
GEO	1	3.00	3.00	--	--	--	--	--	--	--
HAL	6	15.17	0.00	--	--	--	--	--	--	--
HAR	6	--	30.67	--	41.33	--	--	--	--	--
HAT	5	--	--	--	53.00	--	--	--	--	3.00
INT	6	8.67	7.83	--	1.33	--	--	--	--	--
JOH	1	--	2.00	--	2.00	--	--	--	--	--
LES	6	7.00	8.17	--	--	--	--	--	--	--
LIN	4	4.50	2.50	--	--	--	--	--	--	--
LIV	4	6.25	34.25	--	--	--	--	--	--	--
MAS	4	3.75	2.75	--	--	--	--	--	--	--
MCD	2	23.00	17.00	--	--	--	--	--	--	--
OTT	4	7.50	0.25	--	--	--	--	--	--	--
PAT	2	3.00	2.00	--	--	--	--	--	--	--
RIC	9	6.78	4.78	--	8.89	--	--	0.00	--	--
SAR	9	8.67	0.11	--	1.00	--	--	0.67	--	--
SHE	2	2.00	0.00	--	--	--	--	--	--	--
SIS	16	0.31	3.56	--	4.69	5.31	2.94	0.44	1.19	--
WAG	2	8.50	5.50	--	--	--	--	--	--	--
WHI	6	3.17	17.83	14.00	9.67	--	--	--	--	--

[1] CYP = cyprinids, which includes creek chubs in Hatchet Lake and pearl dace and lake chubs in Desor Lake.

were made. Additional sets, which would have been preferable from the statistical perspective, were not made in these small lakes (areas, < 15 ha) because of concerns that they might result in mortality levels that could severely affect the existing fish populations.

Eleven species were collected by gill netting (Table 4). Northern pike and yellow perch were dominant species (those that composed more than 30% of the catch by number) in 19 lakes each. Walleye was a dominant species in two lakes and white suckers in five lakes. In Siskiwit Lake, no species of the seven caught was dominant.

In the 18 small, relatively homogeneous lake basins where four or more gill net sets were made, the variance in CPUE was comparatively small. Coefficents of variation in northern pike, yellow perch, and white sucker catches in 30 of 36 possible catches were less than 76.5%—Craig et al (1986) concluded this to be an appropriate value for gillnet catches in freshwaters. As might be expected, coefficents of variation in catches from Siskiwit Lake's large, complex basin were much higher, ranging from 96.7 to 286.8% for the seven species caught in gill nets.

The Isle Royale lakes were assigned to 10 lake classes through application of Schupp's (1992) Minnesota classification system. In Minnesota these classes are centered in the three most northeastern counties, an area similar to Isle Royale geologically and climatically. Fifteen Isle Royale lakes were

Table 5. Interquartile ranges for gill net catch per unit effort for Minnesota lake classes represented in Isle Royale National Park, Michigan.

Lake class	NOP	YEP	WTS	LAT	LKW	TLC	BUB	WAE
1	0.27–1.02	0.28–2.83	1.67–5.00	0.85–4.25	1.07–9.28	1.40–17.38	0.31–1.33	NA
3	0.56–2.38	0.39–3.69	0.83–5.31	NA	NA	3.18–20.20	NA	NA
5	1.77–5.50	1.71–14.12	2.33–8.69	NA	9.50–43.00	1.40–13.05	NA	NA
8	2.27–5.10	1.25–10.25	1.67–12.50	NA	NA	NA	NA	1.00–7.06
9	NA	1.12–12.42	1.00–8.92	NA	NA	NA	NA	NA
12	NA	2.18–14.58	3.62–14.05	NA	NA	NA	NA	NA
14	3.92–9.38	2.00–23.00	NA	NA	NA	NA	NA	NA
16	2.00–6.04	4.71–15.83	2.96–11.00	NA	NA	NA	NA	NA
17	3.00–9.00	3.33–18.33	NA	NA	NA	NA	NA	NA
18	4.00–15.00	2.00–15.00	NA	NA	NA	NA	NA	NA

assigned to Class 8 and seven to Class 14. The other lake classes and the number of Isle Royale lakes assigned to each were as follows: Classes 1, 3, 9, 12, 16, and 17—one lake each, and Classes 5 and 18—two lakes each. White suckers, northern pike, and yellow perch were primary or secondary components of all the lake classes except the two in which white suckers were the only component (Schupp 1992). Lake trout were a primary component in only Class 1 of which Siskiwit Lake is the only representative on Isle Royale.

Interquartile CPUE ranges for the species present in the lake classes that Isle Royale lakes were assigned to are presented in Table 5 (Minnesota Department of Natural Resources, unpublished data). In comparison to these ranges, 42% of the northern pike CPUE values from the Isle Royale lakes were within the ranges, 42% were above the ranges, and 16% were below. If only the lakes with four or more gill net sets are considered, northern pike CPUEs were within the ranges in 40% of the lakes and above in 60%. For yellow perch, 54% of the CPUEs were within the interquartile ranges, whereas 25% were above and 21% below for all lakes. For those lakes with ≥4 gill net sets, the comparable percentages were 47, 35, and 18. White sucker CPUE values were evenly distributed with 38% within the ranges and 31% both above and below. In lakes with ≥4 gill net sets, the values were 28%, 36%, and 36%, respectively. Walleye CPUEs in Chickenbone and Whittlesey Lakes were considerably above the interquartile range for Class 8, to which they both were assigned. In Siskiwit Lake, the lake trout CPUE was above the range for Class 1 lakes, whereas lake whitefish and burbot CPUEs were within their respective ranges. The CPUE of lake whitefish in Desor Lake was also within the applicable range. Cisco CPUEs were below the interquartile range in all four lakes where they occur.

Comparison with the quartile values not only helps identify unusual values, but also provides a framework for evaluating the catches and considering potential management actions (Schupp 1992). The results of the interquartile comparison for northern pike and yellow perch tend to concur with Koelz's (1931) and Sharp and Nord's (1960) earlier qualitative observations that the Isle Royale lakes contained moderate to high densities of these species. This suggests that this is probably the normal long-term situation for this group of lakes and that, at any specific time, densities in some lakes will be "normal," whereas in other lakes they may be either above or below average. Because fish populations fluctuate because of variations in year class strength and other factors, more frequent and intensive sampling would be needed to determine the timing and magnitude of these fluctuations and to identify factors that might be causing them.

The interquartile comparisons were used to assess possible interactions between northern pike and yellow perch and white suckers, two of their primary prey species (Becker 1983). In the eight lakes where all three species were present sympatrically, yellow perch and white sucker

CPUEs were within the interquartile range in four and three lakes, above in three and one, and below in one and four, respectively. In those lakes where only northern pike and yellow perch were caught in the gillnets, CPUEs of perch were within the interquartile range in nine lakes, below in five, and above in only one. If only the lakes with ≥4 gillnet sets are considered, the comparable values were three, two, and one. In five of the six lakes where northern pike were not present, CPUEs of white sucker and yellow perch were 2 to 10 times the upper quartile level. In Harvey Lake, the only lake where the two species were present sympatrically without northern pike, the CPUEs were 2.9 and 2.1 times the upper quartile level, respectively. Thus, it seems that in these relatively small lakes predation by northern pike does affect the abundance of these prey species, particularly of white sucker. Similar conclusions have been reached from studies of other north-temperate lakes (Colby et al. 1987; Hinch et al. 1991). Colby et al. (1987), from an analysis of management case histories, observed that northern pike introductions typically resulted in reductions in yellow perch and white sucker abundance, whereas removals had the opposite effect. The degree to which northern pike regulated the abundance of perch and suckers seemed to depend on the size of the northern pike population and the size of the lake, with the interactions between the species more intense in smaller lakes (Colby et al. 1987). In a group of Ontario lakes, white suckers were more abundant in lakes without pike than they were in lakes where the two species were present sympatrically (Hinch et al. 1991).

Whereas walleye are commonly present in small (<100 ha) lakes, they are abundant in relatively few (Kitchell et al. 1977). This is generally thought to be related to the lack of sufficient wave action to expose boulder and gravel substrates for spawning. Higher densities, such as those in Chickenbone and Whittlesey Lakes, may occur if an inlet (or, as in these lakes, an outlet) stream provides satisfactory spawning habitat. Relatively low fishing pressure may also contribute to the comparatively high CPUEs in Chickenbone and Whittlesey Lakes. Many visitors to Isle Royale are backpackers so angling is typically done from shore. As a result, their fishing efficiency for walleye is limited other than possibly in May before the fish move into deeper water. Low effective fishing pressure may also contribute to the higher than normal CPUE of lake trout in Siskiwit Lake.

The significance of the low CPUEs of cisco is difficult to interpret. They may actually be the result of low fish densities or because the fish are not susceptible to the gill nets either because of their size or distribution. As was mentioned earlier, the limited amount of cold water habitat may be the reason for the low densities in Sargent and Richie Lakes. A similar situation seems to exist in Desor Lake, although the CPUE of lake whitefish, a congener of the cisco, was within the comparable interquartile range. Siskiwit Lake, with its deep, well-oxygenated hypolimnion, provides excellent habitat for cisco and other cold water species. Given the lake's depth, however, it is conceivable that the bottom gill net sets did not effectively sample the cisco population. A much better understanding of the distribution and abundance of cisco could be obtained by sampling with vertical gill nets and portable hydroacoustic equipment (Chadwick et al. 1987; Brandt 1996).

Initially, I had planned to collect relative abundance data on small and juvenile fish from the catches in the unbaited minnow traps. Unfortunately, the traps proved so ineffective that in 1996 they were not used in all the lakes. In 5 of the 21 lakes where the traps were set, no fish were captured. Of the 10 species caught in the traps, yellow perch and pumpkinseed were the only species caught regularly. Yellow perch were caught in 15 lakes, whereas pumpkinseed were caught in 4 lakes. The CPUEs of yellow perch ranged from 0 to 13.17, and were <1.0 in 10 of the 15 lakes where they were caught. Pumpkinseed CPUEs ranged from 0.11 to 2.13. These results would seem to support Jackson and Harvey's (1997) recommendation that because of the difficulties associated with estimating relative abundance it is better to focus on the capture and detection of species and restrict the data to a simple presence–absence format. This would especially seem to be true when dealing with relatively difficult to catch small-bodied species.

Species Characteristics

Northern pike. In all, 739 northern pike were collected by gillnetting from 24 lakes. The majority of the female northern pike were from 510 to 670 mm long, whereas most males were between 490 and 630 mm long (Figure 5). Only six pike more than 700 mm long were captured, with four of them coming from Siskiwit Lake. Thirteen percent of the males and 25% of the female pike exceeded the Michigan minimum legal length of 610 mm. No legal-sized pike were caught in six lakes. The sex ratio in the gill net catches was 1.6 females per male, a ratio similar to that observed by Casselman (1975) in Ontario lakes. Casselman (1975) attributed this to the females, which are typically faster

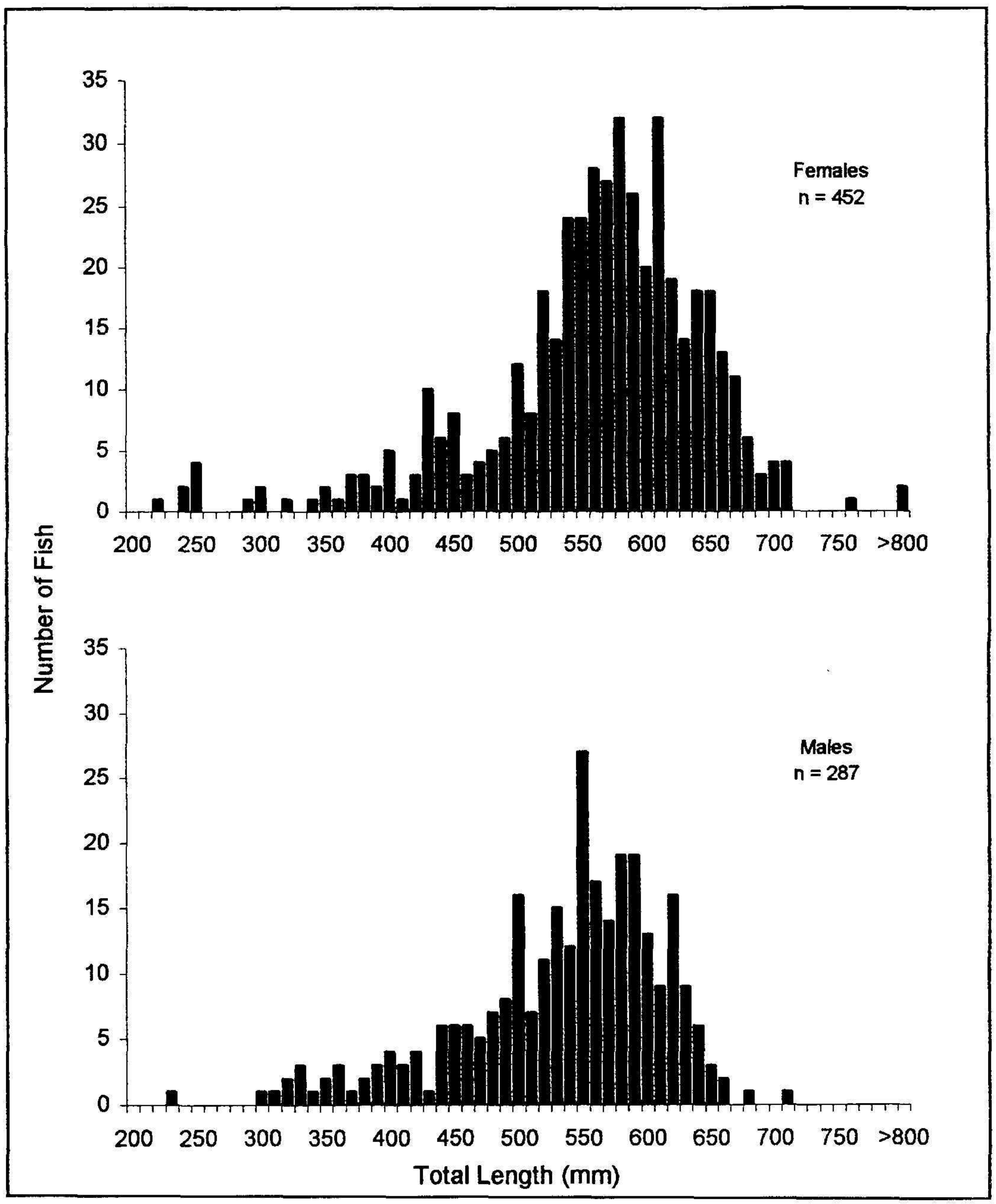

Figure 5. Length distribution of northern pike (*Esox lucius*) captured in experimental gill nets in 24 inland lakes in Isle Royale National Park, 1995–1996.

growing and thus requiring more food for somatic growth, being more active and thus more susceptible to capture.

The northern pike populations had truncated age distributions; most pike were less than 6 years old. Age-4 and age-5 fish composed more than 51% of the gill net catches (Figure 6). Mean ages, which ranged from 2.5 to 6.2 years, were mostly between age 3 and age 5 (Table 6).

Of the 739 northern pike, 25 were less than stock length (<350 mm), 219 were stock length (350–529 mm), 492 quality length (530–709 mm), two preferred length (710–859 mm), and one memorable length (860–1,119 mm). PSD values in the 17 lakes where ≥10 northern pike were caught ranged from 10 to 95 (Table 6). PSD values in five lakes were within the 30 to 60 objective range identified by Anderson and Weithman (1978) as an acceptable stock density index for balanced northern pike populations. Three lakes were below and nine were above this range. A balanced population is one that lies between the extremes of a large number of small fish and a small number of large fish and indicates that the rates of recruitment, growth, and mortality may be satisfactory (Anderson and Weithman 1978). RSD-610 values, which represent the proportion of legal-sized northern pike, ranged from 0 to 53 in these 17 lakes (Table 6).

The mean relative weight (W_r) for all the northern pike was 82. Mean relative weights for individual lakes, which ranged from 74 to 100, were less than 90 in 19 lakes (Table 6). The mean W_r values for stock length pike were higher than the mean for quality length fish (Table 6). The mean W_r values for northern pike from the Isle Royale lakes were in or below the range in W_r values from northern pike populations classified by Willis (1989) as having high densities and slow growth. Relatively poor body condition is evidently not a new phenomenon in regard to northern pike in Isle Royale's inland lakes. In his report on the 1929 survey, Koelz commented

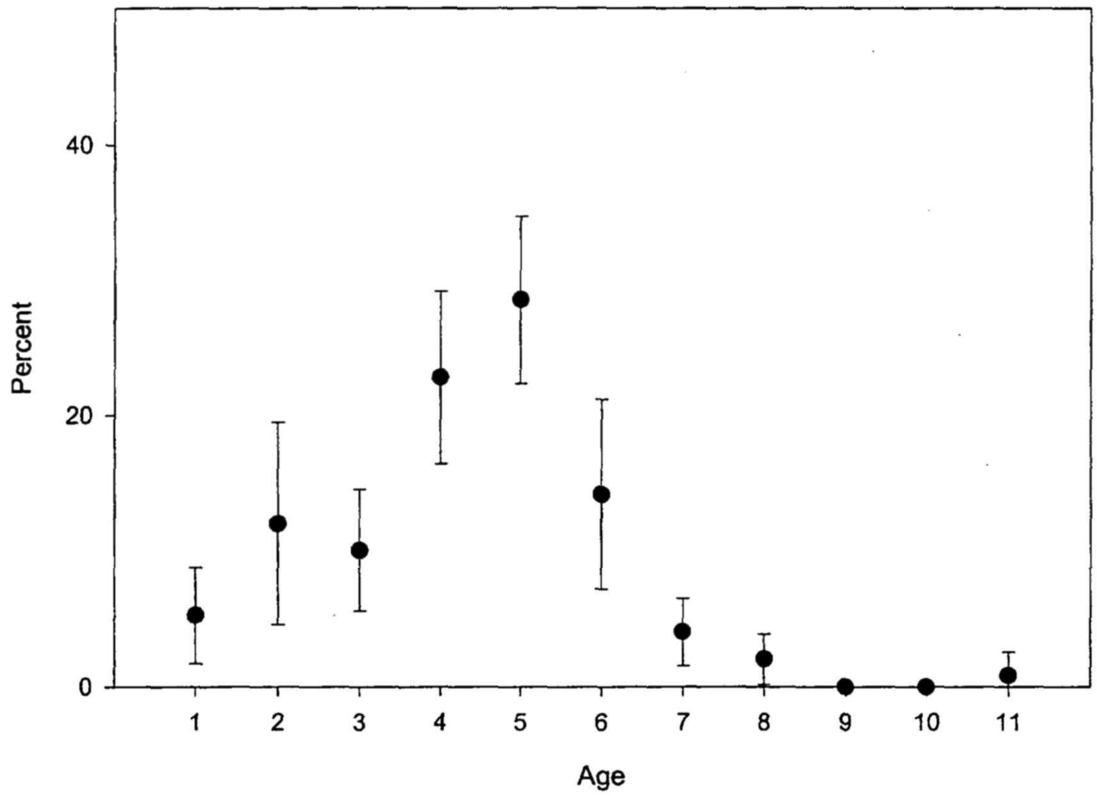

Figure 6. Age distribution of northern pike (*Esox lucius*) captured in experimental gill nets in 24 inland lakes in Isle Royale National Park, 1995–1996. Vertical bars represent ±95% confidence interval of the mean.

Table 6. Mean ages and size-related structural indices for northern pike populations in Isle Royale National Park inland lakes, 1995–1996. N = fish from all size categories. Standard errors are given in parentheses.

Lake	N	Mean age (years)	PSD	RSD 610	Stock n	Stock W_r	Quality n	Quality W_r	Mean W_r
AHM	11	2.5	18	10	9	97(2.7)	2	100(22.0)	98(3.7)
AMY	7	4.7	100	14	--	--	7	84(2.4)	84(2.4)
ANG	25	5.4	92	16	2	86(3.0)	23	77(2.1)	78(2.0)
BEA	34	4.6	70	6	10	84(2.5)	23	77(1.3)	79(1.3)
CHI	36	3.7	40	9	21	86(1.5)	14	85(1.2)	85(1.0)
DUS	2	5.0	100	0	--	--	2	87(6.8)	87(6.8)
EVA	7	4.1	43	0	4	90(3.4)	3	84(1.5)	87(2.1)
FEL	104	4.6	83	42	17	91(4.9)	86	82(0.8)	84(1.1)
GEO	3	3.0	33	33	2	98(1.5)	1	104(--)	100(2.0)
HAL	91	5.3	95	53	5	87(1.1)	86	73(0.8)	74(0.9)
INT	52	4.4	67	2	17	93(1.7)	34	81(1.5)	85(1.4)
LES	42	4.2	59	5	16	96(2.3)	23	84(2.1)	89(1.6)
LIN	18	4.9	59	0	7	78(2.7)	10	72(2.0)	75(1.8)
LIV	25	4.0	68	32	8	91(1.7)	17	81(2.8)	84(2.2)
MAS	15	2.6	10	0	9	86(1.3)	1	86(---)	85(2.3)
MCD	46	4.6	93	43	3	89(5.2)	43	82(1.3)	83(1.2)
OTT	30	4.2	35	0	17	76(1.8)	9	71(2.2)	75(1.4)
PAT	6	3.3	60	20	2	90(3.5)	3	84(4.2)	86(2.5)
RIC	62	3.1	32	7	40	91(1.3)	19	88(1.7)	90(1.0)
SAR	78	5.3	85	6	12	87(1.6)	66	75(1.0)	77(1.0)
SHE	4	5.5	75	0	1	83	3	74(6.7)	76(5.3)
SIS	5	6.2	100	100	--	--	1	99(---)	100(2.5)
WAG	17	5.4	27	0	11	86(2.9)	4	80(3.1)	85(5.4)
WHI	19	3.4	61	17	7	91(3.7)	11	85(2.7)	87(2.1)

that "the pike were thin, often extremely emaciated with no infestation of parasites to account for the loss of flesh".

In the 17 lakes where ≥10 pike were caught, there was a significant inverse relation between PSD and W_r (r = -0.529, P = 0.029, N = 17). As the proportion of quality or larger fish increased, body condition decreased. All of the PSD-W_r combinations fell outside the management objective ranges of 95–105 for W_r and 40–70 for PSD suggested by Anderson (1980). A factor that may contribute to the relatively low W_r values is limited prey abundance, particularly of appropriate sizes of prey. Higher W_r values for less than stock-length and stock-length pike indicates their energy requirements are better met than those of quality-length pike by invertebrates and smaller prey fish, which are likely to be more abundant than larger prey. Although larger pike may continue to eat small prey (Hart and Connellan 1984; Chapman et al. 1989), their need for larger prey such as white suckers increases as they grow (Diana 1987). Intraspecific competition is apparently more intense in those lakes with higher densities of quality-sized pike (higher PSDs) and results in lower W_r values.

Another factor that might have contributed to the size structure and low W_r values of northern pike in Isle Royale's inland lakes is the limited quantity of vegetative habitats. Numerous factors can limit aquatic vegetation (Casselman and Lewis 1996), and, on Isle Royale, grazing by moose (*Alces alces*) seems to be a major and rather unique limiting factor. In 1995, when moose densities were extremely high, exceeding four animals per km^2 (Peterson 1999), densities of aquatic vegetation seemed to be well below the 35 to 80% suggested by Casselman and Lewis (1996) as optimal for juvenile and adult northern pike. The lack of vegetative cover, making small pike more susceptible to cannibalism and thereby reducing the number of stock-sized fish, may have contributed to the high PSD values. It may also have contributed to the low W_r values by reducing the feeding efficiency of the larger pike, which typically ambush their prey from cover (Bry

1996). Conceivably, the large winter die-offs of moose that occurred in 1995–96 and 1996–97 (Peterson 1999) could translate into positive changes for northern pike populations as a result of reduced grazing pressure on the aquatic vegetation.

Northern pike growth was variable among lakes with ranges in lengths for age-2 to age-6 fish of about 140 mm for females and 120 mm for males (Table 7; Appendix B). Females grew faster than males; at age 6 the difference in the mean lengths of the two sexes was 40 mm (Table 7). Based on the mean growth rates, northern pike would reach stock length at age 2 and quality length at age 4. Both sexes would not reach the 610 mm minimum legal length until age 6 or older, and in many lakes they, particularly males, may never reach it. Exceptions to this are Siskiwit, Feldtman, Halloran, and Chickenbone Lakes where the legal length may be reached at age 4 or age 5.

Growth rates of northern pike in Isle Royale's inland lakes could be characterized as moderate to slow based on comparisons with a growth standard determined from 82 circumpolar water bodies (Casselman 1996) and Michigan statewide average lengths (Merna et al. 1981). The mean growth rate of Isle Royale northern pike to age 4 was similar to the circumpolar growth standard (Table 7). After age 4, however, growth increasingly became slower so that by age 8 the mean lengths of females and males were 91% and 80% of the standard, respectively. Mean lengths of Isle Royale pike were generally between 80 and 90% of the Michigan statewide average length at all ages (Table 7).

To assess relations between growth and size structure and body condition, back-calculated lengths of northern pike were correlated with PSD and W_r values. A positive relation was found between growth and PSD for pike from ages 2 to 5 but not for age 6 (Table 8). Willis and Scalet (1989), who found a similar relation between growth and PSD in eight northern pike populations from six states, suggested this was a cause and effect relation and contended that covariance with growth was likely for both PSD and W_r. Other investigators, however, have provided contradictory evidence regarding the relation between growth and W_r (Gutreuter and Childress 1990; Gabelhouse 1991; Liao et al. 1995). On the basis of this evidence, Liao et al. (1995) suggested that the common assumption that condition mirrors growth needs to be critically examined on a case-by-case basis. In the Isle Royale northern pike populations, there was no significant relation between growth and W_r (Table 8).

Fish were the predominant food item for northern pike, present in 64.8% of the 327 stomachs that contained food items. Yellow perch, present in 34.9% of the stomachs (Table 9), were prey in 23 lakes. Use of other fish species was relatively minor, with only spottail shiner and cisco present in more than 1% of the stomachs. Cannibalism was observed in three lakes. Insects were prey items in 16 lakes and were present in 29.1% of the stomachs. Of the identifiable insects, odonate naiads were most frequently observed, present in 8.3% of the stomachs. Leeches, which were consumed by northern pike in eight lakes, were present in 9.5% of the stomachs.

Table 7. Comparison of mean total lengths (mm) of male and female northern pike from Isle Royale National Park inland lakes to the Michigan statewide average (Merna et al. 1981) and an average from 82 circumpolar water bodies (Casselman 1996).[a]

Age (years)	ISRO Males	ISRO Females	MI Average	Circumpolar
1	193 (182–204)	199 (187–210)	297	196
2	350 (334–366)	356 (339–373)	450	337
3	462 (442–483)	468 (451–485)	528	441
4	523 (502–545)	535 (515–555)	594	520
5	549 (525–573)	568 (547–590)	648	588
6	560 (537–582)	600 (571–629)	693	653
7	569 (533–606)	613 (567–659)	744	671
8	577 (498–655)	657 (522–791)	792	719

[a]Confidence limits = 95%.

Table 8. Correlation analyses for proportional stock density (PSD) and relative weight (W_r) with mean back-calculated length-at-age for northern pike populations in Isle Royale National Park inland lakes, 1995–1996.

			PSD		W_r	
Age	**Sex**	***N***	***r***	***P***	***r***	***P***
2	m	17	0.502	0.040	0.181	0.487
2	f	17	0.689	0.002	0.331	0.195
3	m	16	0.759	0.001	0.314	0.236
3	f	17	0.755	0.000	0.312	0.222
4	m	16	0.734	0.001	0.235	0.382
4	f	17	0.623	0.008	0.116	0.658
5	m	15	0.760	0.001	0.168	0.550
5	f	17	0.654	0.004	0.173	0.507
6	m	10	0.318	0.370	0.008	0.982
6	f	14	0.292	0.312	0.001	0.997

Yellow perch. Yellow perch captured in gillnets ranged in length from 102 to 383 mm, with the majority of both males and females between 140 and 250 mm long (Figure 7). The gill net catches were dominated by yellow perch from age-groups 2–6 (Figure 8). The oldest fish taken was 14 years old. Mean ages of yellow perch were primarily between 2 and 6 years (Table 10).

Yellow perch growth was variable among lakes; the range of mean back-calculated lengths at age 4, in 95% confidence limits, was 30–40 mm (Table 11; Appendix C). Extreme differences in back-calculated lengths were evident; at age 4 the calculated length for females from Wagejo Lake was 272 mm, whereas from Amygdaloid Lake it was only 106 mm. For age-4 males, the calculated

Table 9. Summary of food habits of five fish species in Isle Royale inland lakes, showing the percentage frequency of presence of food items in stomachs containing food.

	NOP	YEP	WAE	LAT	LKW
Number examined	**744**	**1265**	**192**	**65**	**115**
Percent with food	**44.0**	**48.5**	**58.9**	**70.8**	**52.2**
Food item					
Unidentified fish	30.0	11.6	25.7	78.3	15.0
yellow perch	34.9	2.4	4.4	8.7	--
northern pike	0.9	--	--	--	--
walleye	0.3	--	--	--	--
white sucker	0.9	--	--	2.2	--
spottail shiner	1.5	--	--	--	--
cisco	1.2	--	--	6.5	--
sculpins	2.4	--	--	13.0	--
ninespine sticklebacks	--	--	--	4.4	36.7
logperch	--	0.2	--	--	--
Unidentified insects	15.0	53.2	69.9	--	--
Odonata	8.3	5.1	--	--	1.7
Ephemeroptera	3.4	3.1	--	2.2	--
Trichoptera	3.4	1.5	--	4.4	--
Plecoptera	--	0.3	--	--	--
Hemiptera	0.3	0.3	--	--	--
Diptera	--	--	--	2.2	16.7
Unidentified Invertebrates	1.5	7.0	15.9	--	--
Amphipoda	--	5.5	--	--	26.7
Pelecypoda	0.3	--	--	--	31.7
Gastropoda	0.3	0.9	--	--	1.7
Zooplankton	0.3	0.9	--	--	6.7
Hirudinea	9.5	6.7	--	--	5.0
Oligochaeta	0.3	2.5	--	--	--
Nematoda	--	6.9	--	--	--

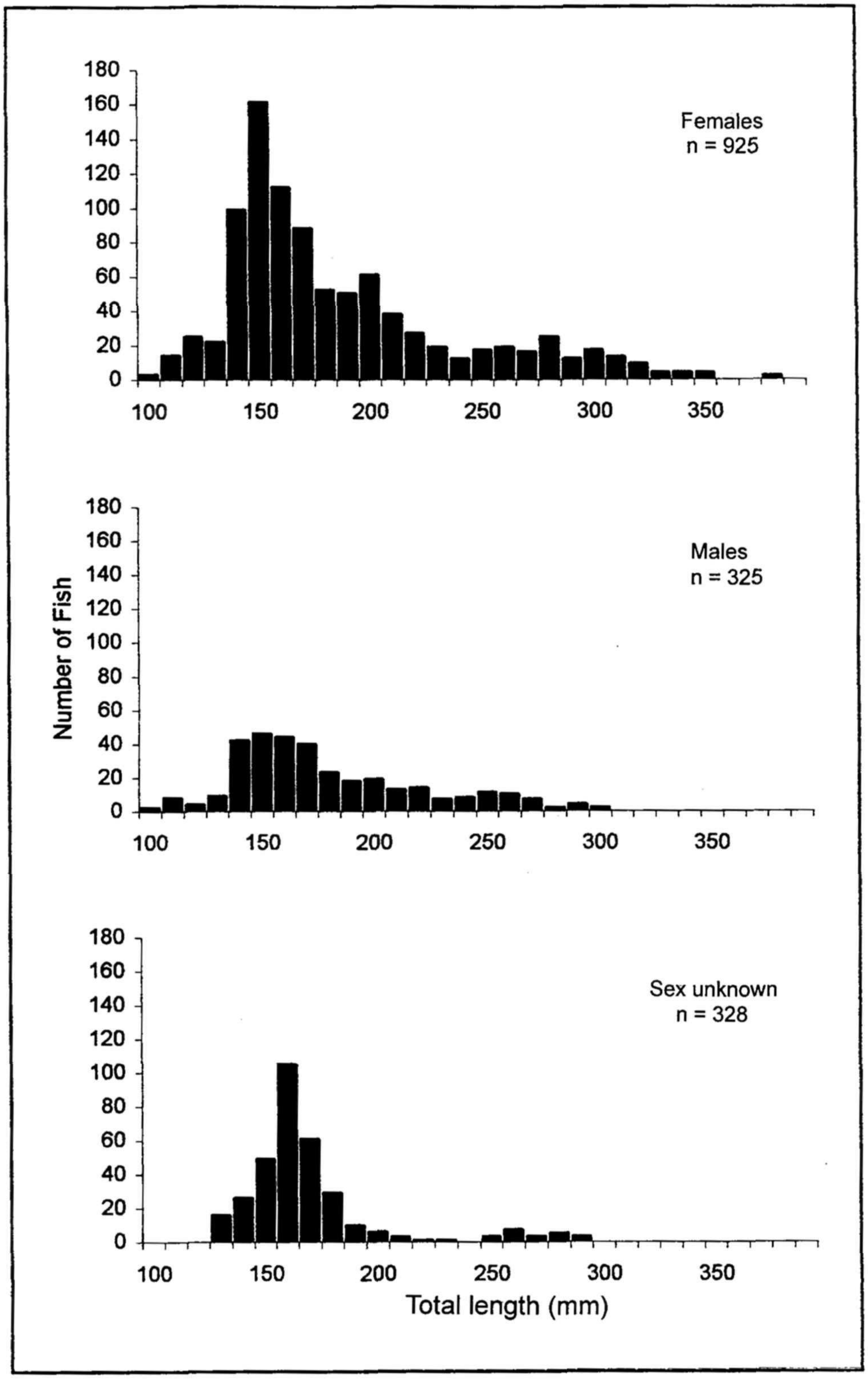

Figure 7. Length distribution of yellow perch (*Perca flavescens*) captured in experimental gill nets in 26 inland lakes in Isle Royale National Park, 1995–1996.

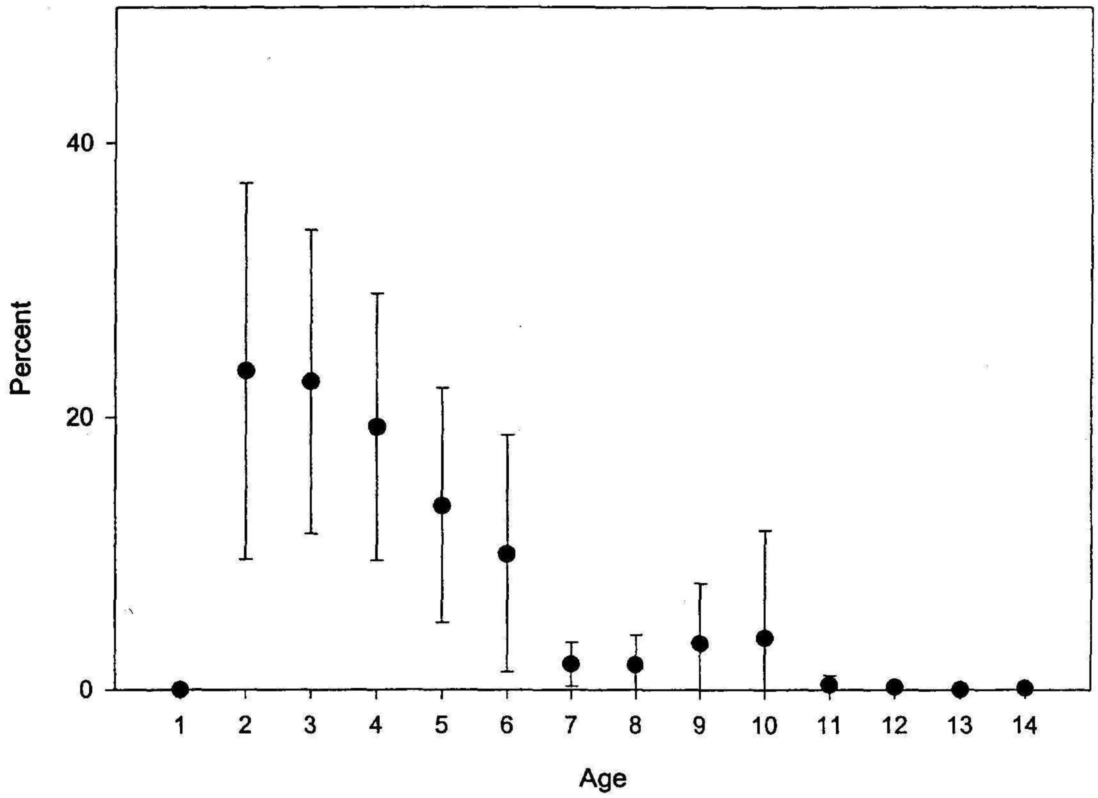

Figure 8. Age distribution of yellow perch (*Perca flavescens*) captured in experimental gill nets in 26 inland lakes in Isle Royale National Park, 1995–1996. Vertical bars represent ±95% confidence interval of the mean.

length was 207 mm for Benson Lake and 110 mm for Amygdaloid Lake. Females, as is typical, grew faster than males (Table 11). Up to age 5, the mean back-calculated lengths of Isle Royale yellow perch were between 70 and 90% of the Michigan statewide average (Merna et al.1981) and mean length-at-age values presented by Carlander (1997) for a region encompassing Michigan, Wisconsin, and Minnesota (Table 11). After age 5, the mean back-calculated lengths of the Isle Royale yellow perch were similar to the Michigan average and the values reported by Carlander (1997).

The overall PSD for the 1,586 yellow perch from the 26 lakes was 28. PSD values for the 17 lakes where ≥10 yellow perch were caught ranged from 0 to 100, with only four of the lakes having PSD values that were within the 30 to 50 objective range recommended for yellow perch (Table 10; Anderson and Weithman 1978). The PSD values were below this range in 12 lakes and above in 1: Wagejo Lake, where the catch consisted entirely of yellow perch from the preferred- and memorable-length categories. The large proportion of low PSD values in the Isle Royale lakes is probably associated with the slow growth rates of the yellow perch. In most of the lakes, yellow perch do not reach quality size (200 mm) until age 5 or older, a condition that can lead to low PSD values (Anderson and Weithman 1978).

The mean W_r for the 1,586 yellow perch was 78. Mean W_r values in the 17 lakes where ≥10 yellow perch were caught ranged from 65 to 93 (Table 10). In 10 lakes the mean W_r was less than 80. Mean W_r values were relatively consistent among length categories, ranging from 77 for quality-length yellow perch to 84 for memorable-length fish (Table 10). Mean W_r values of this magnitude, which would seem to suggest that Isle Royale yellow perch generally have below average body condition, are generally typical of yellow perch populations in Michigan and Wisconsin (Willis et al. 1991). Willis et al. (1991), who analyzed mean W_r values from yellow perch populations from throughout the species' range, concluded that geographic patterns

Table 10. Mean ages and size-related structural indices for yellow perch populations in Isle Royale National Park inland lakes, 1995–1996. N = fish from all size categories. Mean W_r does not include less then stock length yellow perch.[a]

Lake code	N	Mean age (years)	PSD	Stock n	Stock W_r	Quality n	Quality W_r	Preferred n	Preferred W_r	Memorable n	Memorable W_r	Mean W_r
AHM	3	3.0	100	--	--	1	91(---)	2	100(12.5)	--	--	97(7.8)
AMY	7	3.7	0	--	--	--	--	--	--	--	--	77(---)
ANG	36	4.6	3	35	65(3.2)	1	65(---)	--	--	--	--	65(3.1)
BEA	20	4.1	25	15	88(2.3)	1	87(---)	1	86(---)	1	93(---)	86(2.2)
BEN	482	3.3	31	331	77(0.6)	59	78(0.8)	79	72(0.6)	13	75(1.5)	76(0.5)
CHI	128	4.6	44	72	94(1.0)	34	91(1.0)	21	91(1.1)	1	87(---)	93(0.7)
DUS	2	3.0	0	2	87(5.0)	--	--	--	--	--	--	87(5.0)
EVA	1	5.0	0	1	81(---)	--	--	--	--	--	--	81(---)
FEL	80	4.7	26	59	75(0.9)	21	71(1.1)	--	--	--	--	74(0.8)
FOR	124	4.4	12	109	68(0.6)	14	63(2.0)	1	62(---)	--	--	68(0.6)
GEO	3	2.0	0	3	82(4.8)	--	--	--	--	--	--	82(4.8)
HAR	184	5.2	45	102	73(0.8)	31	73(1.2)	27	72(2.0)	24	71(1.6)	73(0.6)
INT	47	4.4	6	44	75(0.8)	3	80(3.8)	--	--	--	--	75(0.8)
JOH	2	7.5	0	2	68(1.0)	--	--	--	--	--	--	68(1.0)
LES	49	2.7	12	42	73(1.8)	6	71(2.0)	--	--	--	--	73(1.6)
LIN	10	3.6	0	9	85(2.5)	--	--	--	--	--	--	86(2.5)
LIV	137	3.6	32	93	84(0.6)	40	80(0.9)	4	82(1.8)	--	--	83(0.5)
MAS	11	4.2	0	11	69(3.3)	--	--	--	--	--	--	69(3.3)
MCD	34	3.4	15	29	76(0.9)	3	78(5.3)	2	69(5.0)	--	--	76(0.9)
OTT	1	10.0	100	--	--	--	--	--	--	--	--	90(---)
PAT	4	2.5	0	4	83(2.9)	--	--	--	--	--	--	83(2.9)
RIC	43	5.0	28	31	85(1.4)	3	81(1.8)	6	79(2.5)	3	84(0.7)	84(1.1)
SAR	1	6.0	0	1	85(---)	--	--	--	--	--	--	85(---)
SIS	57	2.2	0	10	72(1.7)	--	--	--	--	--	--	71(1.7)
WAG	11	8.0	100	--	--	--	--	1	94(---)	10	95(2.4)	95(2.2)
WHI	107	3.0	11	95	87(1.1)	12	89(1.2)	--	--	--	--	87(1.0)

[a]Standard errors are given in parentheses.

in W_r values might be associated with soil fertility. Based on this relation, they suggested that it is probably unrealistic for biologists from areas such as northern Michigan and Wisconsin to expect to find yellow perch populations with a mean W_r of 100 or more.

There was a significant positive correlation between PSD and mean W_r for the 17 lakes where ≥10 yellow perch were caught ($r = 0.611$, $P = 0.009$). Unlike the northern pike, increases in the proportion of quality or larger yellow perch coincided with increases in body condition. A similar relation

Table 11. Comparison of mean total lengths (mm)of male and female yellow perch from Isle Royale National Park inland lakes to the Michigan statewide average (Merna et al. 1981) and an average from lakes in Michigan, Wisconsin, and Minnesota (Carlander 1997).[a]

Age, years	ISRO Males	ISRO Females	MI Average	MI, WI, MN
1	56 (52–60)	58 (53–63)	84	71
2	91 (82–99)	98 (87–109)	133	115
3	119 (107–131)	138 (123–153)	165	158
4	148 (135–161)	171 (149–192)	191	187
5	177 (161–194)	196 (172–220)	216	209
6	198 (166–230)	232 (204–259)	240	234
7	228 (180–277)	262 (228–297)	262	251
8	-----	280 (237–322)	282	265

[a]Confidence limits = 95%.

was reported by Willis et al. (1991) for fall samples of yellow perch.

Both intra- and interspecific interactions have the potential to affect PSD and W_r. Intra- and interspecific competition for food has been observed to reduce growth rates and result in stunted yellow perch populations (Keast 1977; Hanson and Leggett 1985). Low PSD values may also be caused by too few game fish preying on young yellow perch or too many large predators feeding on adult perch (Anderson and Weithman 1978; Colby et al. 1987; Guy and Willis 1991). I attempted to determine whether such interactions were occurring in the Isle Royale lakes by correlating these indices with the abundance and biomass of yellow perch and northern pike and other piscivores in the 17 Isle Royale lakes. All the results, however, were nonsignificant ($P > 0.05$).

The relation between growth and size structure and body condition was assessed by correlating PSD and mean population W_r values with length at annuli for yellow perch from ages 2 to 6. Significant positive correlations were found between PSD and lengths at all ages, whereas for W_r significant correlations with length occurred for ages 4, 5, and 6 (Table 12). Willis et al. (1991), in an analysis involving 28 yellow perch populations from a large geographic range, found significant correlations between W_r and length at annuli for ages 2 to 6.

Insects were the primary food of yellow perch, present in more than 63% of the 614 stomachs that contained food items (Table 9). Whereas unidentified insect remains were the most frequently present food item, six insect orders were found in yellow perch stomachs. Fish were consumed by yellow perch in 13 of the 26 lakes and were present in about 14% of the stomachs. Other food items frequently present included nematodes, leeches, and amphipods.

Walleye. Whereas the overall size ranges of walleye in Chickenbone and Whittlesey Lakes were similar, gill net catches from Chickenbone Lake contained a larger proportion of smaller fish (Figure 9). Forty-two of the 109 walleyes from Chickenbone Lake were less than stock length (<250 mm), 47 were stock length (250–379 mm), 16 were quality length (380–509 mm), and four were preferred length (510–629 mm). Comparable values from Whittlesey Lake were 2, 41, 38, and 3. Eighteen percent of the Chickenbone Lake walleye and 49% of the walleyes from Whittlesey Lake exceeded the Michigan minimum legal length of 381 mm. The PSD values for Chickenbone and Whittlesey Lakes were 30 and 50, both of which were within the 30 to 60 range recommended for walleye by Anderson and Weithman (1978).

Walleyes from age groups 1 to 11 were collected in Chickenbone Lake, from age groups 3 to 12 in Whittlesey Lake (Figure 9). Age 1 was the dominant age class in Chickenbone Lake, composing about 34% of the gillnet catches. Ages 3, 4, and 5 composed an additional 44% of the catch. Catches in Whittlesey Lake were dominated by age-4 to

Table 12. Correlation analyses for proportional stock density (PSD), relative weight (W_r), and mean back-calculated length-at-age for yellow perch populations in Isle Royale National Park inland lakes, 1995–1996.

			PSD		W_r	
Age	Sex	N	r	P	r	P
2	m	14	0.349	0.222	0.004	0.990
2	f	17	0.784	0.000	0.357	0.159
3	m	13	0.567	0.042	0.111	0.718
3	f	17	0.820	0.000	0.506	0.038
4	m	13	0.628	0.022	0.090	0.771
4	f	16	0.817	0.000	0.584	0.018
5	m	10	0.582	0.077	0.318	0.371
5	f	15	0.795	0.000	0.671	0.006
6	m	6	0.546	0.262	0.177	0.737
6	f	13	0.707	0.007	0.680	0.011

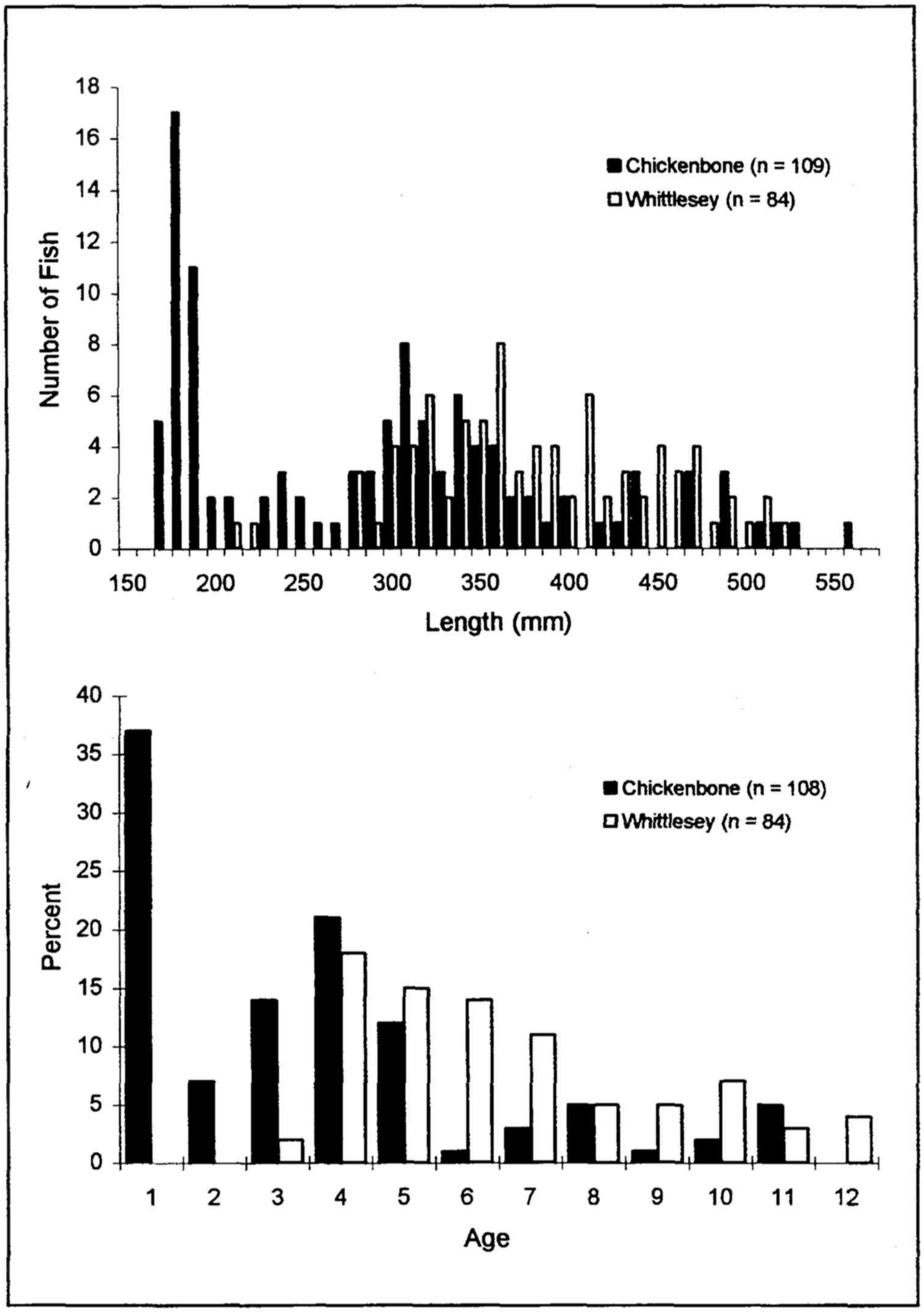

Figure 9. Length and age distribution of walleye (*Stizostedion vitreum*) from Chickenbone and Whittlesey Lakes, Isle Royale National Park, 1995.

age-7 walleyes, which composed 69% of the catch. The mean ages of the walleye were 3.6 years in Chickenbone Lake and 6.5 years in Whittlesey Lake. The one walleye caught in Dustin Lake was 5 years old.

There was relatively little variation in W_r values between length categories for walleye from either Chickenbone or Whittlesey Lakes. In Chickenbone Lake, which had an overall mean W_r of 89, the mean W_r values for less-than-stock-, stock-, quality-, and

Table 13. Comparison of mean back-calculated total lengths (mm) of walleye from Whittlesey and Chickenbone lakes with mean lengths reported by Carlander (1997) for walleye from Minnesota, Wisconsin, and Michigan lakes and Michigan statewide average lengths (Merna et al. 1981).

Age	WHI M	WHI F	CHI M	CHI F	MN, WI, MI M	MN, WI, MI F	MI Average
1	101	102	131	131	150	155	180
2	167	170	188	190	257	261	264
3	229	235	243	245	321	339	353
4	289	289	285	293	368	396	401
5	333	336	323	349	397	432	447
6	369	378	380	399	417	463	488
7	393	414	403	436	434	499	523
8	415	438	425	472	442	543	549
9	429	458	450	495	465	545	569
10	495	481	460	509	484	580	---
11	453	488	474	528	---	602	---
12	461	486	---	---	---	---	---

preferred-length fish were 87, 90, 91, and 89, respectively. Comparable values for Whittlesey Lake, which had a mean population W_r of 86, were 90, 85, 87, and 88. Although the Isle Royale W_r values for walleyes are below the target range of 100 ± 5 recommended by Anderson (1980), they are in the 85–89 range within which 24% of 114 walleye populations from throughout North America fell (Murphy et al. 1990).

Growth rates of walleye in Chickenbone and Whittlesey Lakes were similar, with females not reaching legal length until age 6 and males until age 7 (Table 13). Characteristically, females grew faster than males so that by age 7 there was about a 20- to 30-mm difference between the two sexes. Walleye growth is relatively slow in comparison with the Michigan statewide average for walleyes (Merna et al.1981) and with mean length-at-age values presented by Carlander (1997) for a region encompassing Michigan, Wisconsin, and Minnesota (Table 13). For ages 5–9, the mean lengths of Isle Royale walleyes were between 75 and 80% of the Michigan averages, which includes both males and females. Isle Royale male walleyes were about 81–97% of the values reported by Carlander (1997), whereas female lengths were 78–91% of those of their counterparts.

Insects were the most common food of walleye, present in 69.9% of the 113 stomachs that contained food items (Table 9). Insect remains were present in 83% of the walleye stomachs from Chickenbone Lake and in 56% of those from Whittlesey Lake. Most of the fish remains present in 30.1% of the walleye stomachs were partly digested and therefore unidentifiable. Yellow perch, the only fish species positively identified, was present in 3.4% and 5.5% of the walleyes from Chickenbone and Whittlesey Lakes, respectively.

Lake trout. Total lengths of the 85 lake trout in Siskiwit Lake gill net catches ranged from 264 to 702 mm; more than 61% were longer than 500 mm (Figure 10). Two fish were less than stock length (<300 mm), 31 were stock length (300–499 mm), 48 were quality length (500–649 mm), and 4 were preferred length (650–799 mm). The PSD was 63. The mean W_r values for the four length groups were 76, 74, 72, and 77, respectively.

To facilitate comparisons with length–weight relations for lake trout other than those included in the relative weight standard (W_s) developed by Piccolo et al. (1993), regression analysis was applied using the logarithms of the lengths and weights of the 85 trout from Siskiwit Lake. The resulting equation is:

$$\text{Log}_{10}\text{Weight(g)} = -5.6571 + 3.1860\ \text{Log}_{10}\ \text{Total length(mm)}$$

Based on this relation, predicted weights of Siskiwit Lake lake trout, in addition to being well below the W_s standard, are also less than those of comparable-sized lake trout in 23 Ontario lakes (Figure 11; Payne et al. 1990). Their weights are

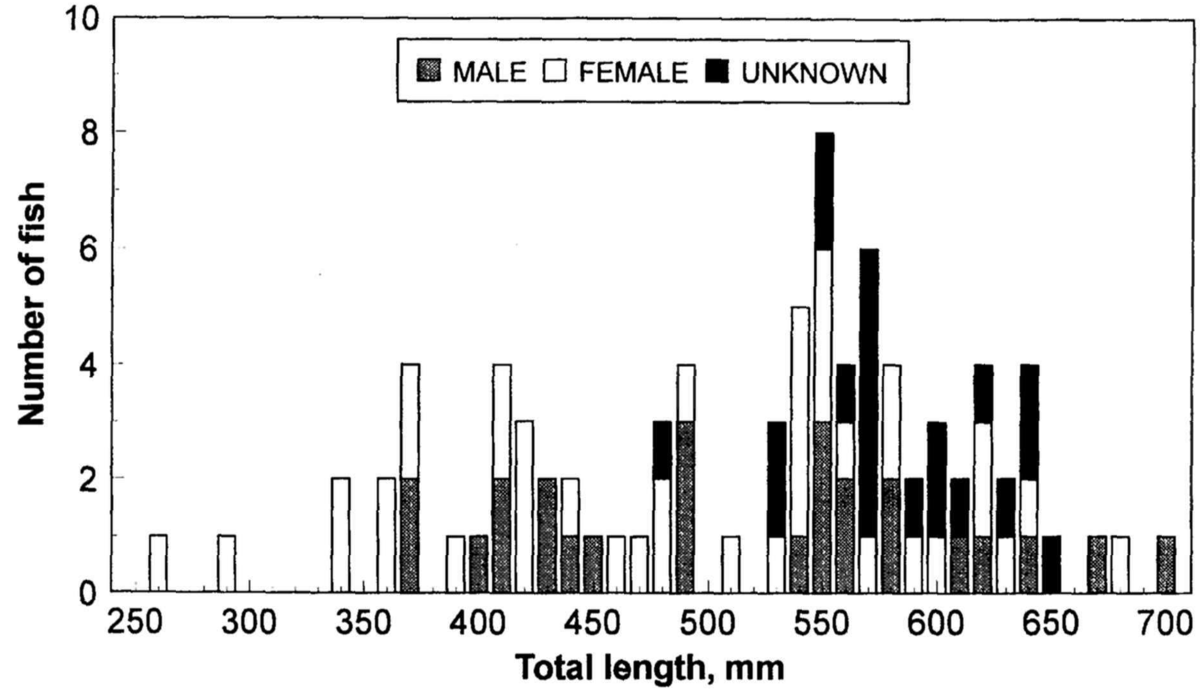

Figure 10. Length distribution of lake trout (*Salvelinus namaycush*) captured in experimental gill nets in Siskiwit Lake, Isle Royale National Park, 1996.

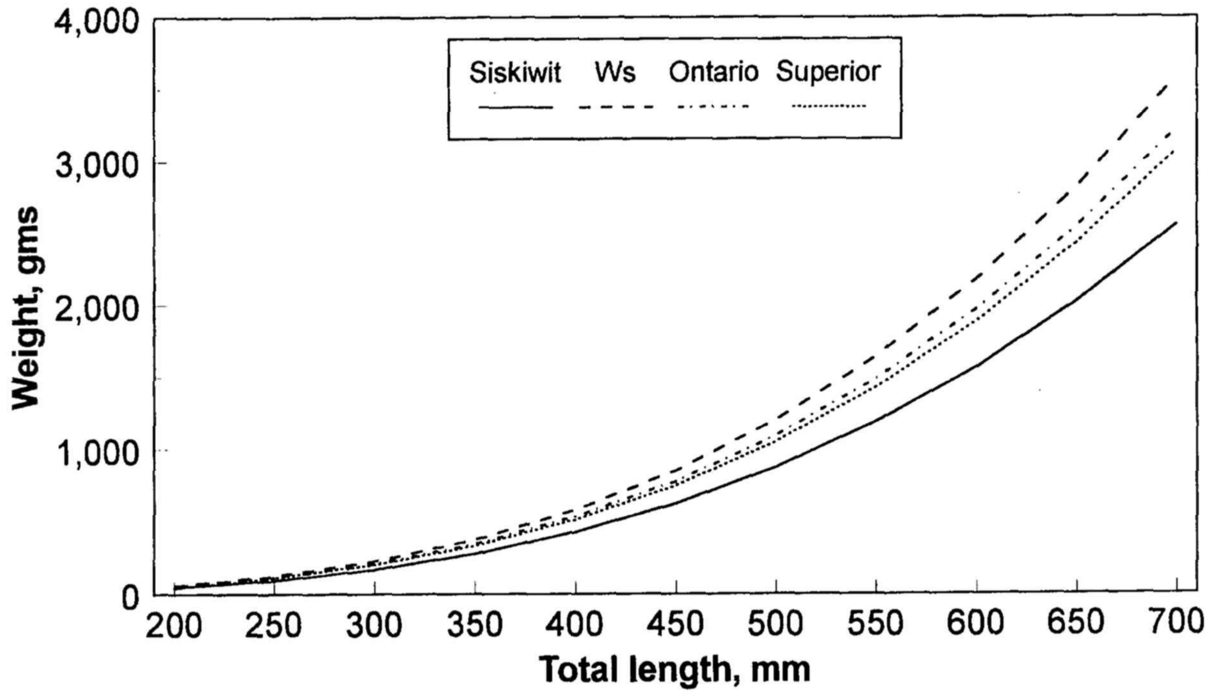

Figure 11. Length-weight relations of lake trout (*Salvelinus namaycush*) from Siskiwit Lake, Isle Royale National Park, 23 Ontario lakes (Payne et al. 1990), Lake Superior (Eschmeyer and Phillips 1965), and the lake trout standard weight equation (Piccolo et al. 1993).

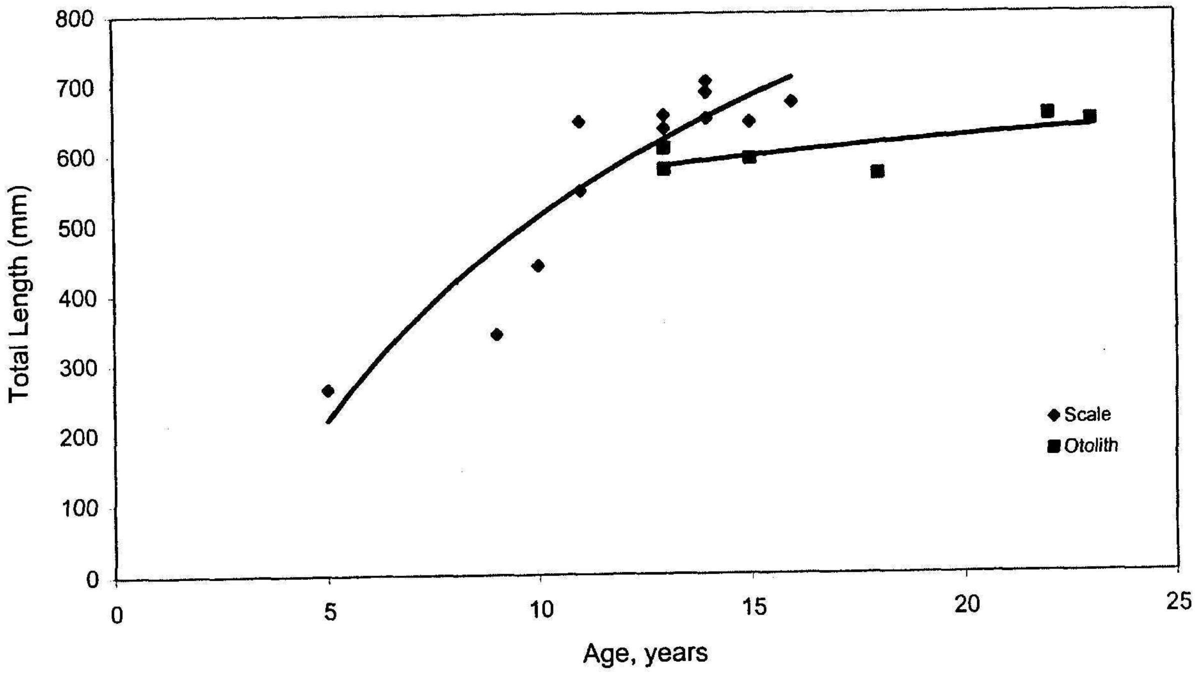

Figure 12. Age and growth determinations from scales and otoliths for lake trout (*Salvelinus namaycush*) from Siskiwit Lake, Isle Royale National Park. All values represent separate fish because both structures were not available for comparisons.

also less than those of lean lake trout from Lake Superior (Figure 11; Eschmeyer and Phillips 1965), to which they are most genetically similar (Burnham-Curtis et al. 1997). A 700-mm lake trout from Siskiwit Lake would weigh 500 gm less than a lean trout from Lake Superior.

The aging of slow-growing species such as lake trout is a problem. Although scales have been used in many instances, it is widely recognized they result in underestimates of age for mature lake trout (Casselman 1983; Sharp and Bernard 1988). Because of this, Lester et al. (1991) recommended that scales only be used for lake trout up to 7 years old. For older fish otoliths should be used. Otoliths, unfortunately, were only collected from six lake trout that were frozen whole for later contaminants analysis. A comparison of ages determined from these otoliths and scales from 12 other lake trout and the length-frequency distribution indicates the majority of the Siskiwit Lake lake trout were more than 7 years old (Figure 12). Both the otoliths and scales indicate the length at age 13 is about 600 mm, which suggests growth in Siskiwit Lake is similar to or slightly slower than that in 47 Ontario lakes (Payne et al. 1990).

Lester et al. (1991) developed a mean length statistic, ML400 (mean fork length above 400 mm), that would provide at low cost a growth-dependent index of mortality for lake trout in Ontario's district lakes. Use of the 400 mm (= 441 mm total length) length criterion presumes that all trout of this length or greater are fully represented in the gill net samples. Application of this model to the Siskiwit Lake lake trout catches resulted in an ML400 of 518 mm (569 mm total length). According to an analysis of the relation between ML400 and asymptotic fork length in Ontario lakes (Lester et al. 1991), this value suggests that annual mortality of lake trout in Siskiwit Lake is between 20 and 30%. Olver et al. (1991) recommended that total annual mortality for self-sustaining lake trout stocks in Ontario not be allowed to exceed 45%. Siesennop (1998) recommended a more conservative value of 30% for Minnesota lake trout stocks.

Fish was the predominant item in the lake trout diet, present in 44 of the 46 stomachs that contained food. Unidentifiable fish remains were the most frequently observed food (Table 9). Five fish species were identified from the stomachs, with sculpins and yellow perch present most frequently (Table 9).

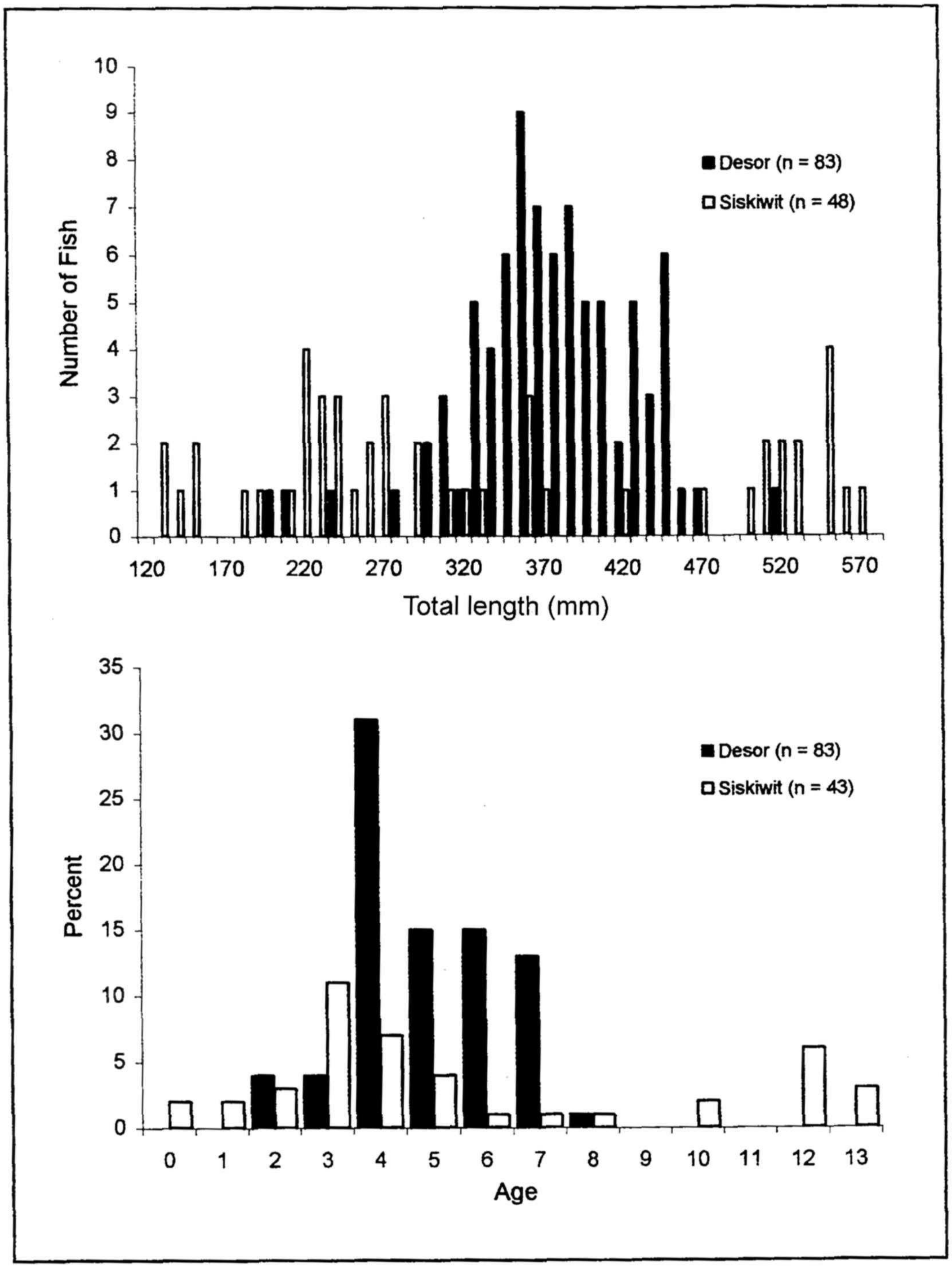

Figure 13. Length and age distribution of lake whitefish (*Coregonus clupeaformis*) from Desor and Siskiwit Lakes, Isle Royale National Park, 1996.

9). The only other food items were immature insects, which were found in four stomachs.

Lake whitefish and cisco. Lake whitefish 200–500-mm long composed 66% of the gillnet catch in Siskiwit Lake; in Desor Lake, 94% of the whitefish were between 300 and 500 mm long (Figure 13). The PSD values for Siskiwit and Desor Lakes were 55 and 95, respectively. Dominant age groups were ages 3, 4, and 12 in Siskiwit Lake and ages 4

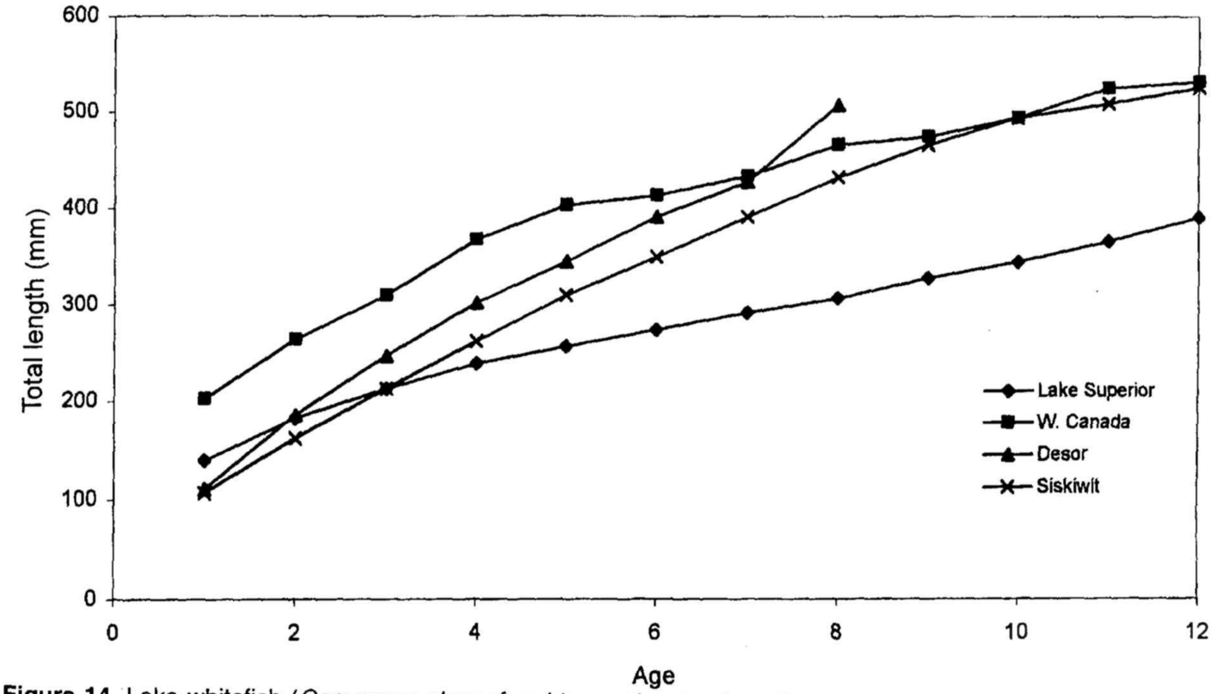

Figure 14. Lake whitefish (*Coregonus clupeaformis*) growth rates from Desor and Siskiwit lakes in Isle Royale National Park, Lake Superior (Edsall 1960), and western Canadian lakes (Carlander 1969).

through 7 in Desor Lake (Figure 13). Mean ages in the two lakes were 6.1 and 4.9 years, respectively.

Because the data showed no consistent differences for length by sex, back-calculated lengths from males and females were combined for the determination of growth rates. Growth of lake whitefish in Desor Lake was faster than in Siskiwit Lake; the difference in the back-calculated lengths was about 40 mm at ages 6 and 7 (Figure 14). Growth rates in both lakes are faster than those reported by Edsall (1960) for lake whitefish in Lake Superior, but are slower than those in western Canadian lakes (Figure 14; Carlander 1969). The weight–length relations for lake whitefish were $Log_{10}Weight(g) = -5.927 + 3.332Log_{10}$ Total length(mm) from Siskiwit Lake and $Log_{10}Weight(g) = -5.998 + 3.340Log_{10}$ Total length(mm) for Desor Lake. Based on these formulas, predicted weights of a 500-mm lake whitefish would be 1,164 g in Siskiwit Lake and 1,039 g in Desor Lake. A comparative weight from a Lake Superior lake whitefish would be 990 g (Edsall 1960).

Fish, amphipods, and fingernail clams were the food items most frequently present in lake whitefish (Table 9). Benthic organisms such as amphipods, chironomid larvae, and fingernail clams were present in 84% of the 25 lake whitefish stomachs from Siskiwit Lake that contained food items. Zooplankton was present in 16% and fish in only 4% of the Siskiwit Lake fish. In contrast, fish—primarily ninespine sticklebacks—were present in 94% of the 35 stomachs containing food in Desor Lake. Benthic organisms were present in only 6% and leeches in 9%. This high utilization of fish, which was also noted by Koelz in 1929 and Sharp and Nord (1960), is not typical for lake whitefish. Although fish have been found in whitefish stomachs, in most instances benthic organisms are the primary prey of lake whitefish (Scott and Crossman 1973). Hubbs and Lagler (1949) suggested that the large mouth and slender form of Desor Lake's endemic lake whitefish may be adaptations to its piscivorous food habits. All the lake whitefish from Siskiwit Lake that I examined had the normal or characteristic body morphology of the species and did not, as Hubbs and Lagler (1949) reported, superficially resemble the round whitefish, *Prosopium cylindraceum*.

Catches of cisco in experimental gill nets were small, with nine fish caught in Siskiwit Lake, eight in Desor Lake, and six in Sargent Lake. The 9.5-mm mesh gill nets produced 1 cisco in Richie Lake and 88 additional cisco in Desor Lake. Koelz (1931) and Hubbs and Lagler (1949) classified the cisco in Siskiwit Lake as a separate species, *Leucichthys bartletti*. Because of the continued debate over this classification, the specimens I collected, which ranged in length from 106 to 209 mm, were given to T. Todd (USGS, Great Lakes Science Center, Ann Arbor, Michigan) for use in his investigation of the origin and speciation of ciscoes. All except one of the 96 ciscoes from Desor Lake were from 130 to 150 mm long and 2 years old. The only exception was an age-4 cisco that was 225 mm long. Lengths and ages of the cisco from Sargent Lake ranged from 155 to 270 mm and from 2 to 4 years. The only cisco from Richie Lake was 115 mm long.

White sucker. Gillnet catches contained white suckers from 110 to 590 mm long, with modal size groups present at 170–180 mm and 230–240 mm (Figure 15). White suckers from 1 to 16 years old were captured; the dominant age groups were 2, 4, and 5 years (Figure 16). There were, however, large variations in age frequencies between lakes, with mean ages ranging from 3.5 to 11.7 years.

White suckers in the Isle Royale lakes, as is found throughout the range of the species (Beamish 1973), exhibited a wide range in growth (Figure 17; Appendix D). There was a 242-mm difference in total length of age-8 white suckers from Whittlesey and Hatchet Lakes. Growth was inversely related to density with significant negative correlations occurring between CPUE and mean lengths at ages 6, 7, and 8 ($r = 0.890$, $P = 0.007$; $r = 0.770$, $P = 0.043$; $r = 0.863$, $P = 0.006$). Growth was slowest in Hatchet, Desor, and Harvey Lakes, all of which had relatively high white sucker densities and no northern pike. Growth was considerably faster in lakes with relatively low CPUEs of white sucker, which were inversely correlated with the CPUE of northern pike ($r = 0.609$, $P = 0.047$).

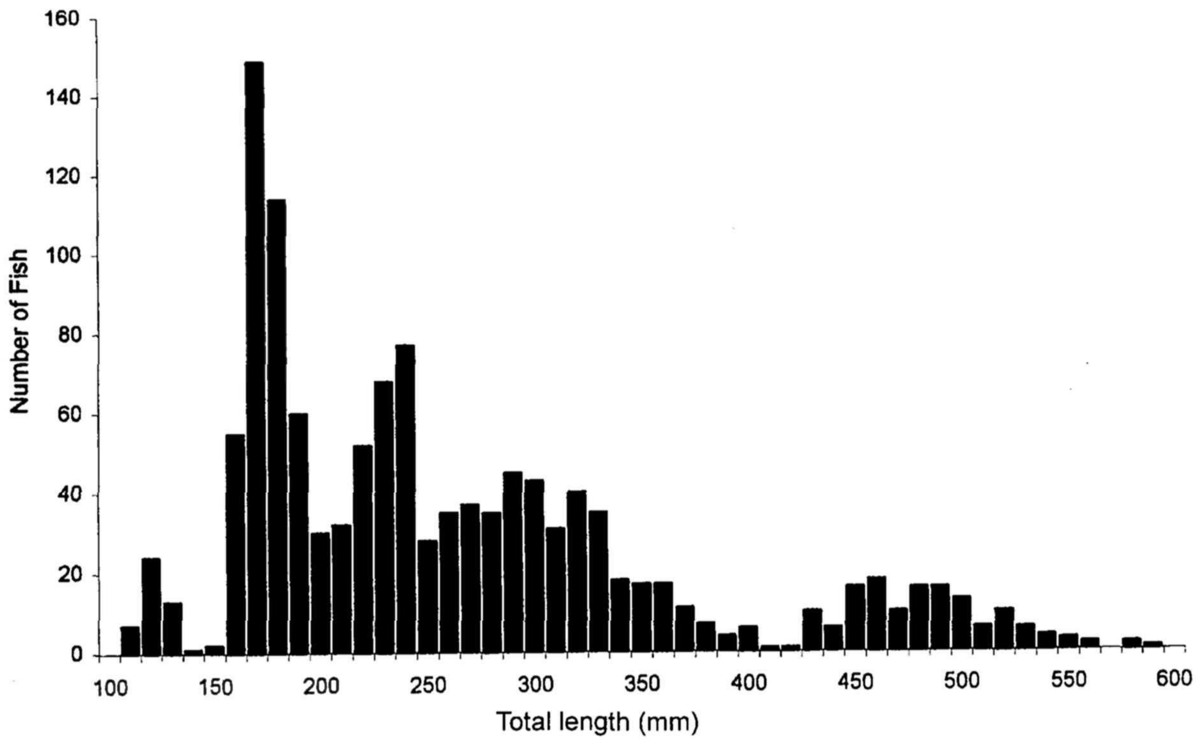

Figure 15. Length distribution of white sucker *(Catostomus commersoni)* captured in experimental gill nets in 13 inland lakes in Isle Royale National Park, 1995–1996.

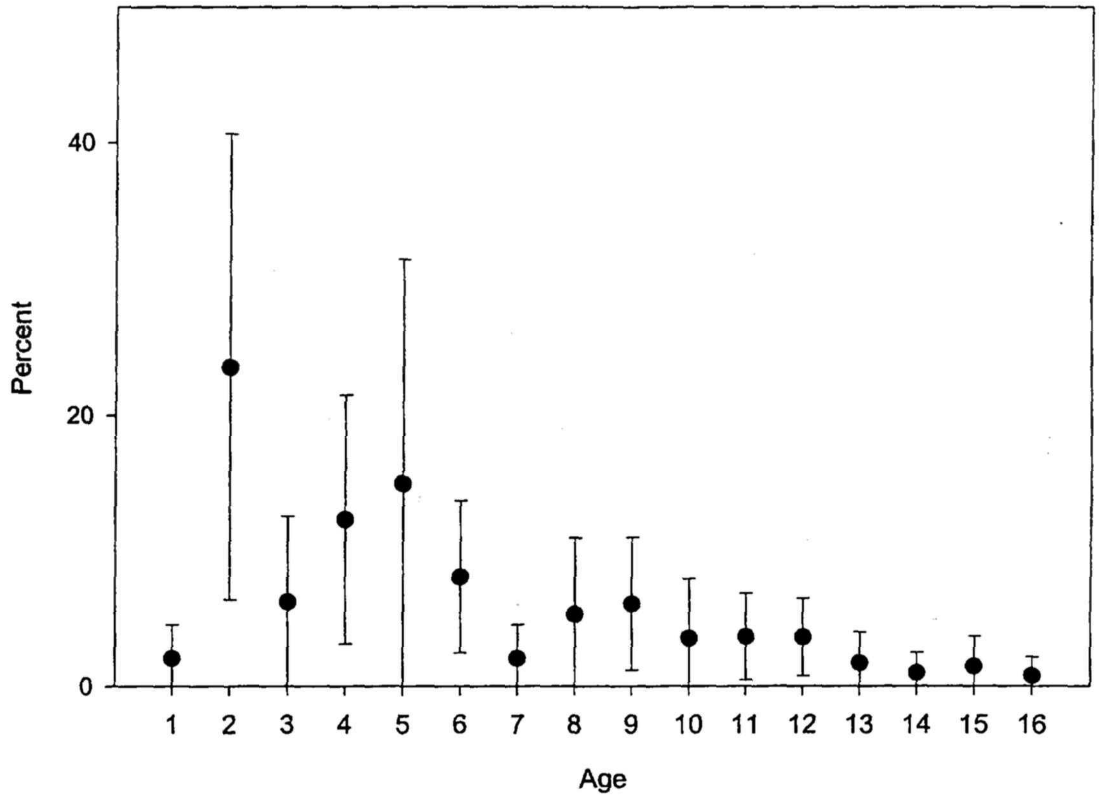

Figure 16. Age distribution of white sucker *(Catostomus commersoni)* captured in experimental gill nets in 13 inland lakes in Isle Royale National Park, 1995–1996. Vertical bars represent ±95% confidence interval of the mean.

Negative relations between white sucker growth and abundance have also been reported by Trippel and Harvey (1987) and Chen and Harvey (1995).

Mean population W_r values for the 13 lakes with white sucker ranged from 76 to 108 with seven lakes having W_r values between 80 and 89 and four between 90 and 99. The overall mean W_r for the 1,234 white suckers was 85. Body condition, like growth, was inversely correlated with abundance (r = 0.647, P = 0.032). There were significant positive correlations between W_r and lengths at ages 6, 7, and - (r = 0.883, P = 0.008; r = 0.946, P = 0.001; r = 0.799, P = 0.017). Limitations of food supply and accessible waters as well as increases in predation and disease were presented as possible contributors to the negative relation between density and growth and body condition (Chen and Harvey 1995). As determined from a study of 23 white sucker populations in Ontario, Chen and Harvey (1995) concluded that growth was probably constrained by both density and food supply, and in particular the abundance of chironomid larvae in the littoral zone.

Burbot. Total lengths and ages of the 19 burbot collected from Siskiwit Lake ranged from 376 to 608 mm and from 5 to 15 years. About 74% of the burbot were between 400 and 500 mm long and from 7 to 9 years old. The mean length at age 7 and age 8 were 415 and 442 mm, respectively. Based on these lengths, growth of burbot in Siskiwit Lake is slower than in Lake Superior (Bailey 1972) and in four Canadian lakes (Carlander 1969). The PSD was 94 and the mean W_r was 84. Comparable PSD and W_r values for burbot from northwestern Lake Superior were 100 and 114 (Fisher et al. 1996). No diet analysis was feasible because the burbot stomachs typically inverted as the nets were lifted.

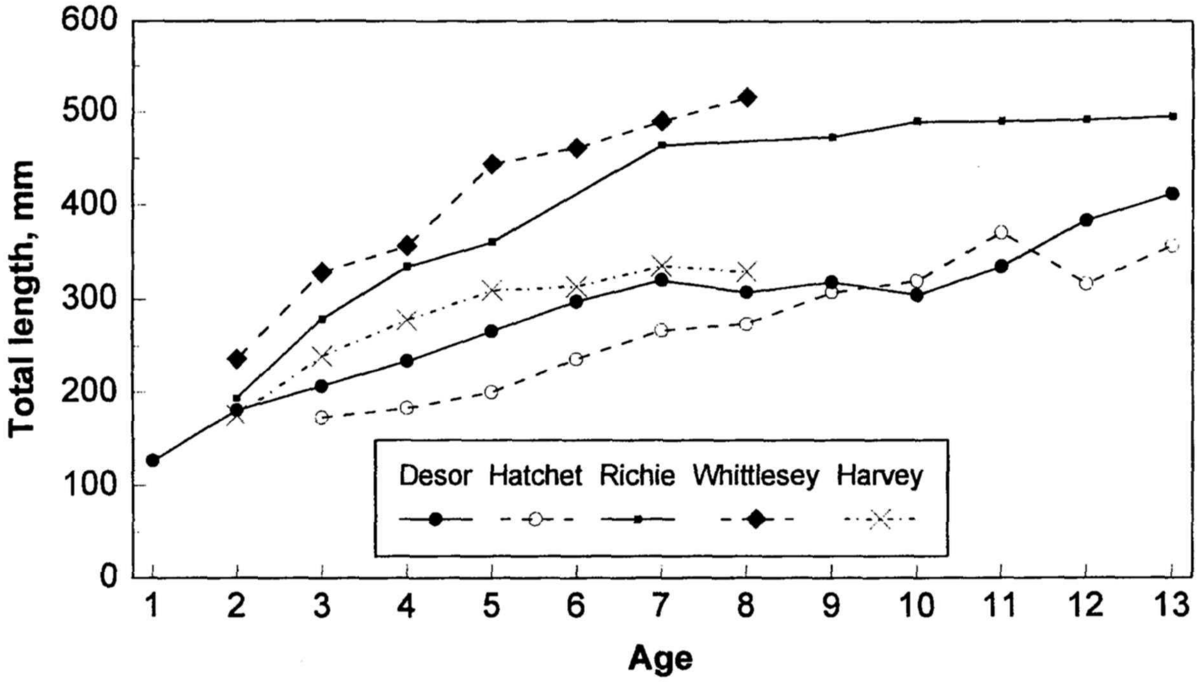

Figure 17. White sucker *(Catostomus commersoni)* growth rates in five inland lakes in Isle Royale National Park, 1995–1996.

Creel Survey

Of the 374 volunteer angler report cards issued in 1997, 117 (31.2%) were returned. Anglers reported fishing in 20 lakes but only one or two reports were received from eight lakes (Table 14). Ten of the 12 lakes from which no reports were received were not directly accessible from a developed trail. The most frequently fished lakes, Richie and Chickenbone, both lie along heavily used trails. The second most intensively fished group of lakes included Whittlesey, Siskiwit, and Intermediate Lakes, which lie on a loop commonly used by canoeists and kayakers. Fifty-two (44%) of the anglers indicated they had fished in more than one lake. The number of days anglers fished ranged from one to eight but 80% fished four or fewer days.

There were obvious differences in the reports received from 35 anglers who had previously fished in the park and from 82 for whom this was their first trip. In response to the question on whether fishing was the primary objective of their trip, 54% of the experienced anglers indicated yes, whereas only 15% of the new visitors replied in the affirmative. The proportions of the two groups that fished from boats were also noticeably different—57% for experienced anglers and 32% for newcomers. Of experienced anglers, 91% said they were satisfied with the number of fish, and 83% were satisfied with the size. In contrast, only 46% of the first time visitors were satisfied with the number of fish and only 41% with the size of the fish. This probably reflects differences in expectations and fishing methods of the two groups. Previous visitors had more realistic expectations as a result of their earlier experiences and thus came away satisfied. First time visitors, not having that basis for comparison, were disappointed when fishing didn't meet what were probably overly optimistic expectations for a wilderness area. The fact that a large proportion of these new people fished from shore rather than from a boat probably also contributed to their lack of satisfaction. Catch rates of northern pike from boats in Chickenbone and Richie Lakes were about 1.6 fish per hour, whereas from shore they were only 0.5 fish per hour. The catch rate for walleye by boat anglers in Chickenbone Lake was 0.2 per hour; for shore fishermen it was zero.

Table 14. Angler fishing methods and catches from inland lakes in Isle Royale National Park, Michigan, June–September, 1997.

Lake		Fished from			Hours	Hours per	NOP		YEP		WAE		LKT	
Code	Reports	Boat	Shore	Both	fished	hectare	Caught	Harvest	Caught	Harvest	Caught	Harvest	Caught	Harvest
ANG	7	--	7	--	35.5	0.70	65	4	--	--	--	--	--	--
BEN	2	--	2	--	3.0	0.12	--	--	--	--	--	--	--	--
CHI	30	12	16	2	109.0	1.17	132	17	2	0	13	8	--	--
DES	4	--	4	--	4.5	0.01	--	--	--	--	--	--	--	--
DUS	1	1	--	--	2.0	0.45	2	0	--	--	--	--	--	--
FEL	1	--	1	--	6.0	0.03	4	1	--	--	--	--	--	--
HAR	1	--	1	--	3.0	0.05	--	--	9	9	--	--	--	--
HAT	6	1	--	--	7.5	0.15	--	--	--	--	--	--	--	--
INT	17	15	5	2	115.5	1.63	212	17	--	--	--	--	--	--
LES	5	3	1	1	9.0	0.20	13	1	--	--	--	--	--	--
LIV	5	3	2	--	9.5	0.32	12	3	--	--	--	--	--	--
MAS	5	1	2	2	12.0	0.53	15	2	--	--	--	--	--	--
MCD	1	--	1	--	2.5	0.17	9	2	--	--	--	--	--	--
OTT	1	--	1	--	1.0	0.05	1	1	--	--	--	--	--	--
RIC	60	30	24	6	274.0	1.27	387	32	15	2	--	--	--	--
SAR	2	--	2	--	14.0	0.10	50	10	--	--	--	--	--	--
SIS[1]	30	26	--	4	181.0	0.11	32	12	--	--	--	--	55	23
WAG	2	--	2	--	3.0	0.49	10	0	--	--	--	--	--	--
WHI	19	15	--	4	109.5	1.68	66	7	18	2	76	27	--	--
TOTAL	199	107	71	21	901.5	--	1,010	109	44	13	89	35	55	23

[1]Includes portion of basin commonly designated as Wood Lake.

Northern pike was the predominant species in the fishery, composing more than 84% of the reported catch (Table 14). Catch rates of northern pike in the seven lakes with more than 30 reported hours of fishing pressure averaged 1.08 fish per hour and ranged from 0.18 in Siskiwit Lake to 1.84 in Intermediate Lake. Harvest rates, or the number of fish kept by anglers, in these lakes were much lower, ranging from 0.02 to 0.16 fish per hour and averaging 0.11 fish per hour. Yellow perch, despite being the most widespread species in the inland lakes, were reported by anglers from only four lakes (Table 14). In some instances, yellow perch may have been caught incidently while the angler was fishing for northern pike or walleye, except for Harvey Lake, where there are no large piscivores. Walleye catch and harvest rates in Chickenbone Lake were 0.12 and 0.07 fish per hour, whereas in Whittlesey Lake they were 0.69 and 0.25 fish per hour. Catch and harvest rates for lake trout in Siskiwit Lake were 0.55 and 0.23. In 1960, a catch rate for lake trout of 0.14 fish per hour was determined from a creel survey of 131 anglers who fished a total of 2,238 h on Siskiwit Lake (Isle Royale National Park, unpublished data). Whether the difference between the two surveys is real or just the result of the inherent biases of the creel card type survey is unknown.

The proportions of fish reportedly kept by anglers were 11% for northern pike, 30% for yellow perch, 43% for lake trout from Siskiwit Lake, and 62% and 36% for walleyes from Chickenbone and Whittlesey Lakes, respectively. The lower proportional harvest of northern pike is probably because of the limited number of legal-sized (610 mm) pike in many of the inland lakes. The higher harvest proportions for the other three species are probably because they are all highly sought-after food fish.

Mercury and Selenium Levels in Fish

The Hg concentrations found in fish in this study ranged from 30 to 1,720 ng/g (Table 15). Mercury concentrations in 32 (17.9%) of the 179 fish analyzed exceeded 500 ng/g (Figure 18), a level commonly used as a criteria in fish consumption advisories. As would be expected from feeding habits and food web structure (Wiener and Spry 1996), ranges in mercury concentrations in the three piscivores—northern pike, walleye, and lake trout—were similar and were higher than those of lake whitefish and white sucker, which are both customarily considered benthivores. Unexpectedly, the highest concentrations were in yellow perch from Harvey Lake. Yellow perch are normally considered omnivores and as such would be expected to have intermediate mercury concentrations. Stomach analysis of yellow perch from Harvey Lake, however, indicated the larger, older perch were functioning as piscivores—54% of the stomachs that contained food containing fish remains. Grieb et al. (1990), who found similar high Hg levels in older yellow perch from lakes from Michigan's Upper Peninsula, also suggested they may be explained by a change in dietary preference.

Mercury concentrations in Isle Royale northern pike, which ranged from 39 to 1,002 ng/g (Table 15), were similar to values for northern pike from mainland lakes in upper Michigan (Grieb et al. 1990) but were slightly lower than levels from northern Minnesota lakes (Heiskary and Helwig 1986; Sorensen et al. 1990). The average Hg level in standard-sized (550 mm) northern pike from the Isle Royale lakes was 304 ng/g (range 74–693 ng/g; Figure 19), whereas for 80 northern Minnesota lakes it was 450 ng/g (range 140–1500 ng/g; Sorensen et al. 1990). The average Hg level in legal-sized (610 mm) pike from Isle Royale was 414 ng/g (range 90–1,286 ng/g). Legal-sized pike from 5 of the 25 lakes had a Hg level exceeding 500 ng/g (Table 15).

Numerous investigations of the relations between Hg concentrations in fish and lake morphology and water chemistry have been conducted in the Great Lakes states and Ontario (Heiskary and Helwig 1986; McMurtry et al. 1989; Cope et al. 1990; Grieb et al. 1990; Sorensen et al. 1990; Suns and Hitchin 1990; Wiener et al. 1990; Bodaly et al. 1993). These studies have consistently shown that Hg concentrations in fish are typically higher in lakes with low pH and low buffering capacity. Relations between lake morphology and Hg concentrations have been less conclusive, with investigators

Table 15. Total lengths and Hg and Se content of fish from Isle Royale National Park's inland lakes, 1995–1996, including calculated Hg concentrations in 550 mm and 610 mm northern pike.

Lake Code	Species	N	Range: Length mm	Range: Hg ng/g	550 mm Hg ng/g	610 mm Hg ng/g	Se ng/g
AHM	NOP	5	417–702	113–338	213	256	180
AMY	NOP	5	531–591	95–206	124	234	246
ANG	NOP	5	525–656	487–877	555	673	414
BEA	NOP	5	515–600	178–396	274	332	270
CHI	NOP	5	441–635	150–538	280	370	397
DUS	NOP	5	474–634	140–478	285	464	290
EPI	NOP	5	360–689	104–642	281	369	362
EVA	NOP	5	485–552	319–851	693	1286	257
FEL	NOP	5	507–655	201–580	245	380	349
GEO	NOP	5	449–626	39–103	74	90	354
HAL	NOP	5	535–612	111–342	188	215	321
INT	NOP	5	343–595	87–584	352	454	301
LES	NOP	5	296–594	98–608	390	470	294
LIN	NOP	5	248–540	135–572	439	490	301
LIV	NOP	5	399–622	62–359	181	251	308
MAS	NOP	5	243–497	175–385	380	402	292
MCD	NOP	5	436–655	48–164	95	134	284
OTT	NOP	5	304–552	72–348	243	307	268
PAT	NOP	5	294–663	103–443	275	301	117
RIC	NOP	10	299–651	63–259	153	173	209
SAR	NOP	10	476–585	260–861	433	590	307
SHE	NOP	5	529–575	408–1,002	609	1081	214
SIS	NOP	5	325–1000	65–719	142	171	532
WAG	NOP	5	224–525	86–473	454	528	246
WHI	NOP	5	348–642	75–460	254	324	374
CHI	WAE	10	187–528	136–570	--	--	397
WHI	WAE	10	228–511	103–671	--	--	374
DES	LKW	5	371–479	150–363	--	--	--
HAR	YEP	5	269–335	649–1,720	--	--	317
HAT	WTS	5	268–401	30–75	--	--	--
SIS	LAT	9	264–702	152–617	--	--	462

reporting no relation (Cope et al. 1990), a positive relation (McMurtry et al. 1989), and negative or inverse relations (Sorensen et al. 1990; Bodaly et al. 1993). Suns and Hitchin (1990) found a positive relation between Hg concentrations in yearling yellow perch and drainage area:lake volume ratios.

For the Isle Royale lakes, pH was the only water quality variable that was significantly correlated with Hg concentrations in standard-sized northern pike (r = -0.42, P = 0.035). This relation is consistent with the findings that mercury methylation rates are much lower at circumneutral pH levels such as are present in the Isle Royale lakes (range 7.3–8.9; Xun et al. 1987). Given the relatively high pH values, mercury concentrations in northern pike from some of the Isle Royale lakes are surprisingly high. There was no correlation between the northern pike Hg concentrations and Se concentrations, which ranged from 117–532 ng/g (Table 15). Also, there were no apparent relations between mercury concentrations in northern pike and morphometric characteristics of the lakes.

The six lakes with the highest Hg concentrations in northern pike all lie along a 4.8-km-long N–S transect extending from Eva Lake to Angleworm Lake (Figures 1 and 19). At this time, I can only speculate on why the higher levels were concentrated in this area, particularly because the analysis showed little relation to internal lake processes and characteristics. Geologic sources may be one explanation. Kelly et al. (1975), after comparing Hg levels in walleye from Isle Royale

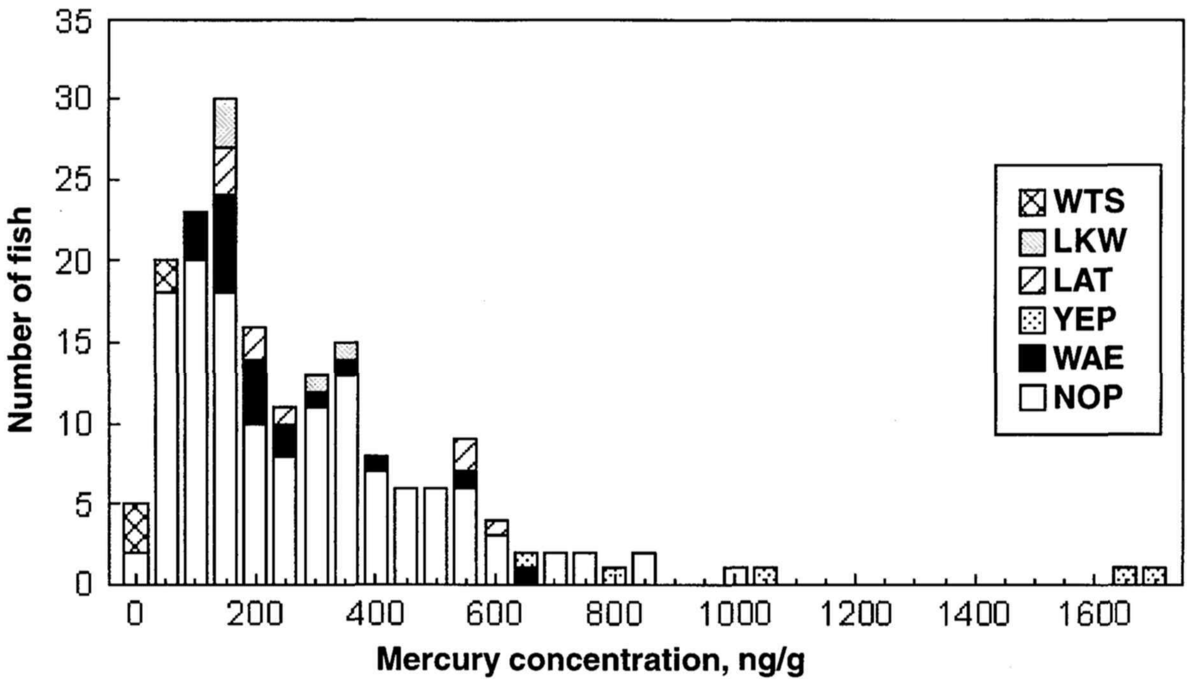

Figure 18. Distribution of mercury concentrations in fish from inland lakes in Isle Royale National Park, 1995–1996.

and six mainland Michigan populations, suggested that higher levels in Isle Royale fish were probably because of the Keweenawan basalt, conglomerate, sandstone, and associated copper deposits containing more mercury than the glacial drift at the other localities. Recent geochemical surveys by Cannon and Woodruff (1999), however, indicated that, whereas there are elevated Hg levels in the soils in the affected area, they are not caused by local bedrock enrichment or concealed copper deposits. Their data show that there is a general lack of Hg in the most common rocks of the island. Native copper deposits on the island contain some Hg but the affected area lacks any geochemical indication of native copper mineralization. They concluded that the high levels in the soils are probably caused by airborne deposition.

Atmospheric deposition has been identified as a source of Hg in remote areas such as Isle Royale (Fitzgerald et al. 1998). Whereas atmospheric transport of mercury is primarily considered to be long-range, higher concentrations are present in precipitation near industrialized or polluted areas (Lindqvist et al. 1991). Industrial activities that occur in northeastern Minnesota and Ontario that have been identified as sources of Hg include coal combustion, mining, pulp and paper production, waste incineration, and the dumping of sewage sludge (Mitra 1986). Mercury pollution has been identified as an issue in Thunder Bay, Ontario (Glass et al. 1990), which is one of the 42 areas of concern identified by the International Joint Commission around the Great Lakes. Thunder Bay, which lies 56 km NNW of Isle Royale, is one of six of such areas associated with Lake Superior. The monitoring of atmospheric deposition of Hg at a number of sites on Isle Royale could be used to determine whether deposition rates are uniform or are focused in particular areas.

Mercury concentrations in walleye from Chickenbone and Whittlesey Lakes were similar, with concentrations of 278 and 279 ng/g, respectively, in standard-sized (390 mm total length) walleye (Figure 20). Hg concentrations exceeded 500 ng/g for lengths greater than 500 mm. Concentrations were lower than those reported by Kelly et al. (1975) for walleye taken from the two lakes in 1929 and 1971. Mean concentrations for the 280-mm standard-length walleyes used by Kelly et al (1975) were about 420 ng/g in 1929 and

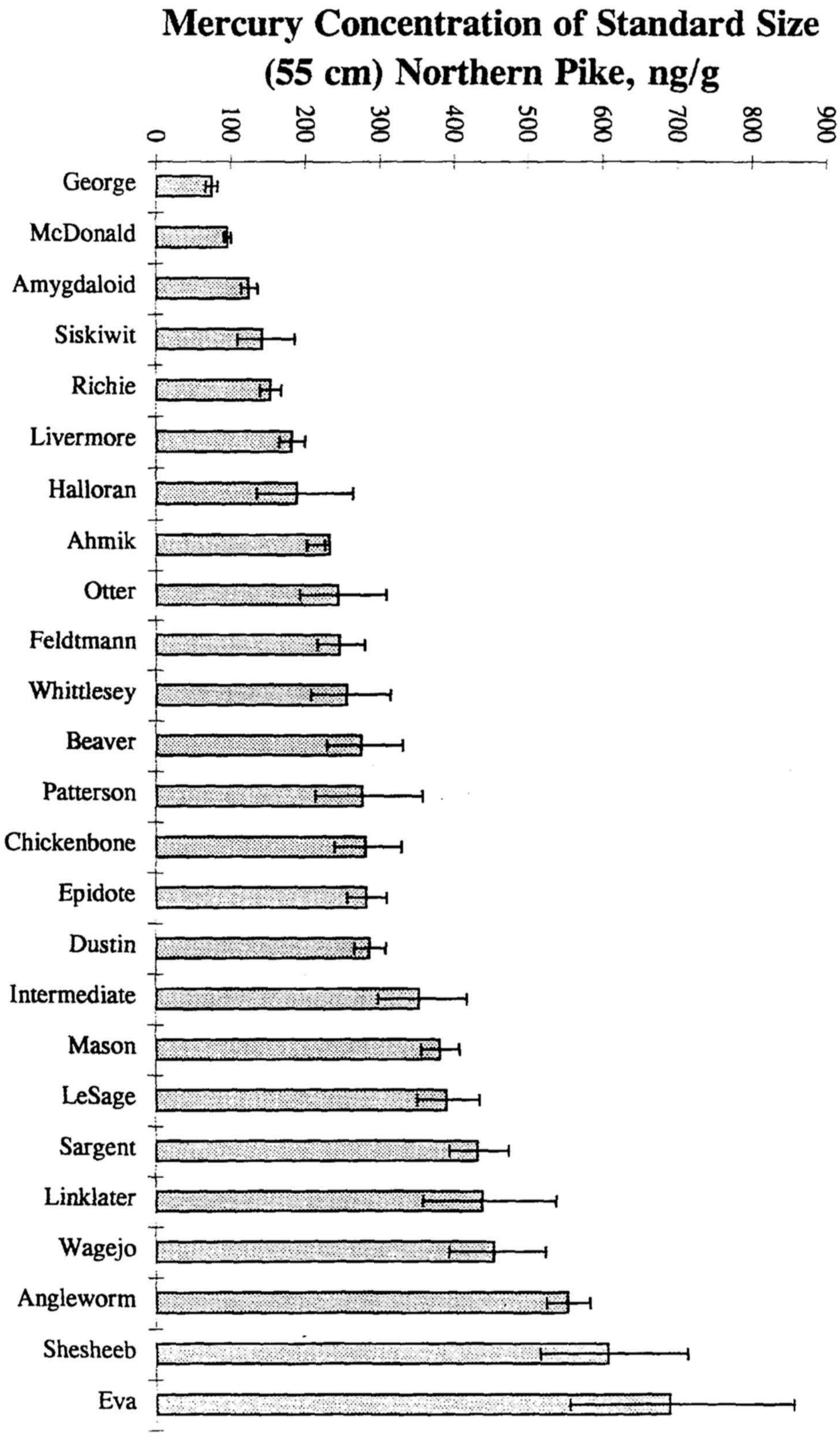

Figure 19. Mercury concentrations in standard size (550 mm) northern pike (*Esox lucius*) from 25 inland lakes in Isle Royale National Park, 1995–1996. Vertical bars equal SE of the mean.

475 ng/g in 1971. Comparable values from the present study were 190 ng/g from Whittlesey Lake and 219 ng/g from Chickenbone Lake.

Mercury concentrations in nine lake trout from Siskiwit Lake, which ranged in length from 264 to 702 mm, ranged from 152 to 617 ng/g (Table 15). Similar concentrations were present in 10 lake trout collected as part of this survey that were analyzed by the Michigan Department of Environmental Quality (Figure 21). Based on a regression of total lengths and Hg concentrations, the Hg concentration in a 440-mm trout from Siskiwit Lake would be 265 ng/g. For comparison, the median value was 260 ng/g (range 50–1,160 ng/g) for 440 mm lake trout from 91 Ontario lakes (McMurtry et al. 1989). Although Hg concentrations generally increased with length, Hg levels in two larger fish were no higher than in fish 200 to 300 mm shorter. The reason for this is unknown. It could, however, result from individual differences in diets, with more contaminated trout preying mostly on fish, whereas those with lower Hg levels consumed mostly zooplankton and invertebrates. The food habits analysis, however, doesn't support this hypothesis, as fish were the primary food of all sizes of lake trout.

Mercury concentrations in white suckers from Hatchet Lake, which ranged from 30 to 75 ng/g, were similar to values reported for white suckers from lakes in Michigan's upper peninsula (Grieb et al. 1990). It was expected that Hg concentrations in lake whitefish from Desor Lake might be abnormally high because of their piscivorous food habits. But, the concentrations, which ranged from 150 to 363 ng/g, were similar to those reported for lake whitefish populations in Manitoba (Bodaly et al. 1984) and Quebec (Verdon et al. 1991).

Management Implications

Fish Communities

The fish communities of Isle Royale's inland lakes are unique, despite having relatively low species diversity and consisting of common species that have large geographic ranges. As a result of their presence in aquatic islands on the largest island in the largest lake in the world, they have avoided the homogenization that has occurred in many mainland lakes as the result of human activities (Radomski and Goeman 1995). Introductions or invasions of nonindigenous species seemingly have either been unsuccessful or not occurred. One possible exception to this is the walleye, the origin of which is still being investigated. Unlike its mainland counterparts, the fish fauna seems virtually unmodified from its natural state. For this reason alone, every effort should be made to protect Isle Royale's entire indigenous fish fauna.

Increasingly, ecologists have recommended that efforts for conserving biodiversity be focused on fish faunas or assemblages, rather than individual species (Angermeier and Schlosser 1995; Mina and Golubtsov 1995). This concept is certainly consistent with NPS policy, which emphasizes the maintenance of all the components and processes of naturally evolving ecosystems, including the natural abundance, diversity, and ecological integrity of the flora and fauna (U.S. National Park Service 1988). Isle Royale's remote location and its status as both a National Park and an International Biosphere Reserve should facilitate the use of a management program based on this concept. Although not all human-induced effects (i.e., atmospheric deposition of contaminants, climate change) can be controlled, the continued prohibition of fish stocking and use of live bait will certainly make maintaining the ecological integrity of the native fish fauna less complicated. The long-term implications of this cannot be overemphasized because of the significant threat that introductions, be they legal or illegal, pose to native fish populations and communities (Moyle et al. 1986; Li and Moyle 1993).

Conserving the fauna in this way will also allow its constituent populations, including the unique phenotypes identified by Koelz (1931) and Hubbs and Lagler (1949), to continue along their evolutionary pathways (Sada et al. 1995). Protected from human disturbance, they may eventually evolve into taxonomically distinct units. Whereas extensive speciation has generally been thought to be unlikely because of the relatively young age of the Great Lakes and associated smaller lakes (Magnuson

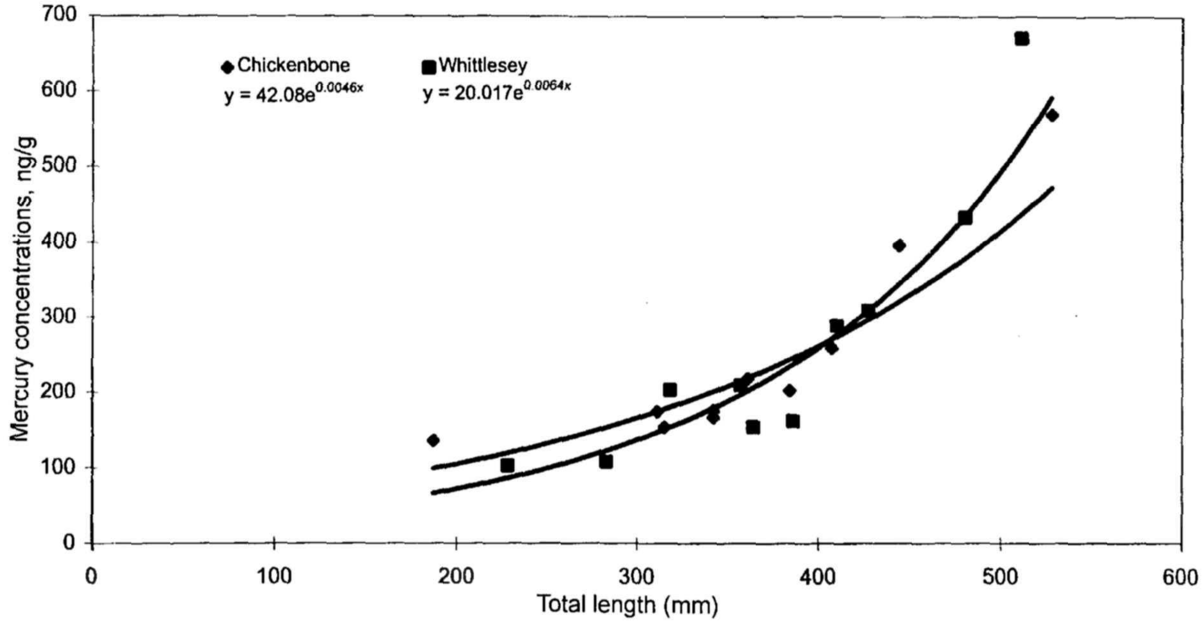

Figure 20. Exponential increases in mercury concentrations with size of walleye (*Stizostedion vitreum*) from Chickenbone and Whittlesey lakes, Isle Royale National Park, 1995.

1976), there is evidence that, under the right circumstances, phenotypic and genotypic divergence can occur on time scales of decades rather than centuries (Crowder 1984; Schluter 1994; Healey and Prince 1995). To detect such change will require detailed morphological and phylogenetic investigations of members of Isle Royale's fish fauna.

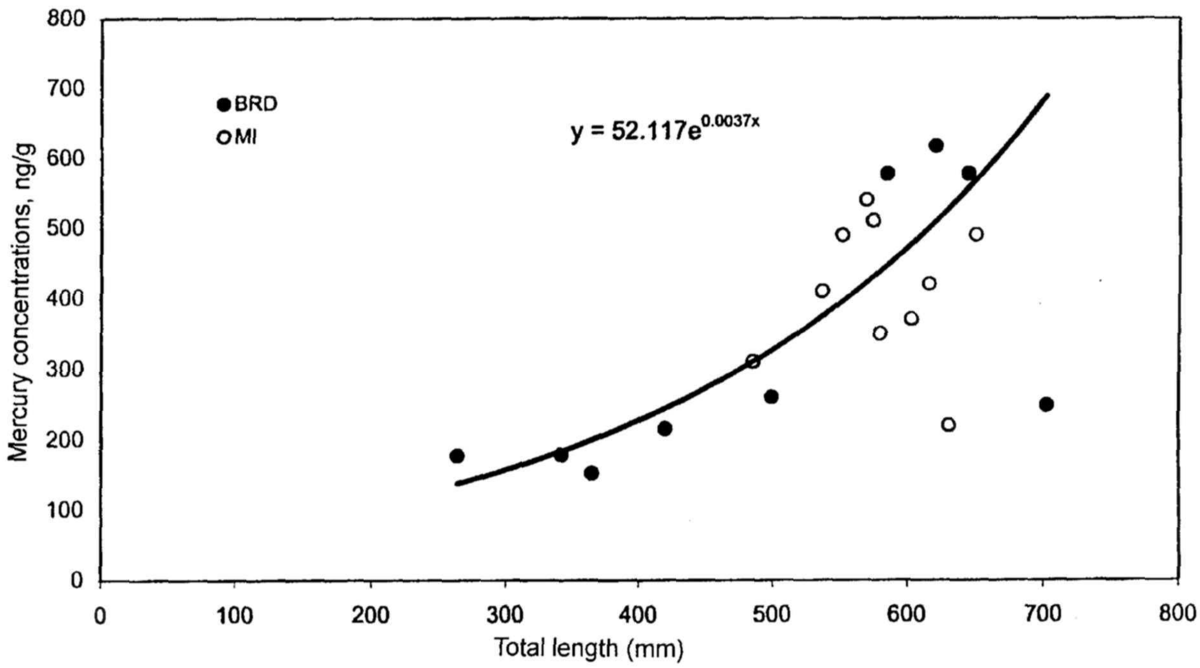

Figure 21. Exponential increases in mercury concentrations with size of lake trout (*Salvelinus namaycush*) from Siskiwit Lake, Isle Royale National Park, 1996. BRD Fillet were fish analyzed as part of this study and MI Fillet were fish analyzed by the Michigan Department of Environmental Quality. Regression excludes the two outlier values.

Changes in the fish communities can also be expected. Since 1929, the composition of the fish communities in several lakes has changed as a result of the immigration or extinction of species already residing in the inland lakes. Changes resulting from such natural processes, which are an integral part of the functioning of natural systems, will continue. Extinction is more likely to prevail in isolated lakes where the probability of invasion is low (Magnuson et al. 1998), whereas immigration will play a larger role in lakes with more open hydrological connections. In the latter lakes, the rate of species turnover also will be higher (Magnuson 1976).

Although it did not occur in the 68-year interval between this survey and Koelz's, colonization by species new to the Isle Royale archipelago is likely to occur at some time in the future. Under NPS policy, such an event would be acceptable if the colonizer is a species native to the Lake Superior watershed. However, given current fish distributions in Lake Superior, there is a strong probability that Isle Royale's waters, including the inland lakes, could be invaded by one of the many species that have been introduced into the watershed by humans. The ruffe, since it was first detected in Duluth harbor of Lake Superior in 1986, has spread both east and north, with specimens having been collected in the Thunder Bay, Ontario, harbor (Pratt et al. 1992). Invasion by this European percid or any of the other nonindigenous species now present in Lake Superior could have widespread effects on Isle Royale's aquatic communities (Vitousek 1990). Regular monitoring of the fish communities in Isle Royale's large embayments and more accessible inland lakes, while not preventing such invasions, could provide the information needed to allow timely management or control actions.

Recreational Fishing

In national parks, the primary goal of recreational fishing is to provide the angler with a quality fishing experience while preserving the natural aquatic ecosystem (U.S. National Park Service 1991). The focus of fisheries management, particularly in wilderness parks such as Isle Royale, is to provide fishing for native species in natural surroundings. The emphasis is on preserving or restoring natural aquatic habitats; the natural abundance, age, and size distribution of native fish; and associated terrestrial species and habitats (U.S. National Park Service 1988). It is recognized, however, that the harvesting of fish results in some alteration of the aquatic ecosystem.

This emphasis on native species and natural processes precludes the use of more intrusive fisheries management methods such as habitat manipulation, the stocking of nonnative species, and removal of nondesirable species. As a result, the primary tool left for management is regulations, which includes length limits, creel limits, closed seasons, gear restrictions, and refugia (Noble and Jones 1993). Isle Royale provides a dramatic example of season and refugia regulation because the entire park is closed from November through mid-April. At present, the main gear regulation is that only artificial baits can be used in the inland waters. Lead sinkers and jigs can still be used. Investigations have shown that these items pose a potential threat to common loons (*Gavia immer*; Ensor et al. 1992; Franson and Cliplef 1992). As a result, they have been banned in Yellowstone National Park and all Canadian national parks, and a statewide ban is to go into effect in the year 2000 in New Hampshire. Investigations should be initiated to determine if they pose a threat to Isle Royale's common loons, which commonly nest on the inland lakes.

Michigan Department of Natural Resources statewide length and creel limits for individual fish species apply to the inland lakes of Isle Royale. The rationale for the 610 mm (24 inches) minimum size limit for northern pike is that (1) it is more attractive to anglers than the former 508 mm (20 inches) minimum and (2) it will maintain the abundance of pike that are important in preventing the stunting of yellow perch in northern Michigan lakes (Michigan Department of Natural Resources 1992). Because angler values about walleye emphasize harvest levels, the size limit was set at the length (381 mm, 15 inches) that modeling results indicated would provide the maximum harvest (Michigan Department of Natural Resources 1992).

Creel limits are used so that the harvest can be distributed more equitably. Michigan daily creel limits are any combination of 5 fish for northern pike and walleye, 50 for yellow perch, 12 in any combination for lake whitefish and cisco, and 3 for lake trout (minimum length 254 mm). On Isle Royale, as well as in most other fisheries, creel limits are generally ineffective as a means of regulating exploitation because most anglers do not harvest their limit (Noble and Jones 1993). For example, 70% of Isle Royale anglers did not harvest any northern pike and 16.7% only harvested one pike.

The effectiveness of length limits, however, is dependent on exploitation rates, growth rates, and the structure of the fish community (Kempinger and Carline 1978). Whereas minimum length limits have been effective in situations with high harvest or low recruitment (Noble and Jones 1993), their use with northern pike and walleye has frequently not produced positive results. They have resulted in reduced angling yields, slower growth rates, poorer condition, stockpiling of fish below the size limit, and a disproportionate harvest of females (Snow and Beard 1972; Casselman 1975; Kempinger and Carline 1978; Serns 1978). Similar reductions in yield were evident in simulation modeling results (Latta 1972; Dunning et al. 1982; Snow 1982). Minimum length limits may actually have little effect or be of little value in waters such as those inland lakes where harvest may be low or even nonexistent (Nobel and Jones 1993).

In the majority of the inland lakes, the moderate to high densities of slow-growing northern pike are more likely caused by factors such as the inherent low productivity of these waters (Mosindy et al. 1987), lack of suitable-sized prey (Diana 1987), limited coolwater refuges for summer growth (Headrick and Carline 1993), and limited aquatic vegetation (Casselman and Lewis 1996). With the 610-mm length limit, the fishery is basically catch-and-release for all pike except a disproportionately large number of females. Assuming harvest levels remain low, the principal effect of this selective removal will be to perpetuate the dominance of smaller fish in these populations. However, even a minor increase in harvest levels could affect the long-term viability of the populations. An experimental fishery in a small Ontario lake removed 50% and 43% of the annual adult production of northern pike and walleye even though fishing pressure was only 1.24 angler-hours/ha (Mosindy et al. 1987). Similar levels of fishing pressure presently are occurring on Richie, Chickenbone, Intermediate, and Whittlesey Lakes (Table 14). Simulation modeling of an increase in the harvest of larger female pike (660 mm) and a subsequent decrease in egg production produced a significant decline in population size over a 50-year period (Dunning et al. 1982). The effect was greater than that predicted for a 508-mm limit (Dunning et al. 1982). More frequent and intensive monitoring of the fish populations will be needed to determine the possible effects of the fishery, including the effect of the 381-mm size limit for walleyes. Initial investigations should focus on the most intensively fished lakes.

Based solely on the biological characteristics of the northern pike and walleye populations, protected slot size limits may actually be a more appropriate management tool. In theory, by allowing the harvest of some fish below the slot size, a slot size limit takes advantage of a surplus of recruits and channels additional energy into midsize fish, which then survive and grow out of the protected slot into the harvestable size range (Nobel and Jones 1993). The slot size fish may provide a substantial catch-and-release fishery. The biological requirements of slot size limits are good natural reproduction and slow growth and high natural mortality, especially of small fish (Brousseau and Armstrong 1987). However, like the minimum size limits, they also require high angling effort—particularly of the smaller fish—to be effective. Slot limits were effective in the management of largemouth bass (*Micropterus salmoides*) when anglers harvested 67–95% of the fish that were less than slot size (Eder 1984; Neumann et al. 1994). Slot limits applied to northern pike in five Minnesota lakes, while reducing the exploitation of slot length fish, did not result in any consistent changes in population size structure after 4 years (Pierce and Tomcko 1997). After 8 years, however, it seems the number of larger pike is increasing in some of the populations (R. Pierce, Minnesota Department of Natural Resources, personal communication).

Because they are a relatively new concept, most slot limit regulations for coolwater species are considered experimental. As determined from present visitor use patterns and fish population characteristics, Richie and Chickenbone Lakes would seem to be the most likely sites for testing the effectiveness of slot length limits on Isle Royale.

Siskiwit Lake is the only inland lake that provides the cold, well-oxygenated waters lake trout need to flourish. Temperatures in the hypolimnion are less than 10° C and dissolved oxygen concentrations are higher than 6 mg/L, conditions considered optimum for lake trout (MacLean et al. 1990). Lake trout, because they are restricted to such cold, unproductive lakes and have slow growth, late maturity, and low reproductive potential, produce low, sustainable yields. As a result, they are extremely sensitive to exploitation. Fortunately, the park is closed in winter, when lake trout are particularly vulnerable to fishing.

The 20–30% estimate of total annual mortality obtained from the ML400 analysis suggests exploitation is not a problem for the Siskiwit Lake trout population at this time. However, because ML400 is an imprecise estimator of total mortality (Siesennop 1998), it is difficult to establish with certainty the status of the population, or whether it is being affected by the fishery. A more thorough understanding of these factors will be needed to ensure the long-term sustainablity of the lake trout population. Because angling effort is the primary determinant of harvest, a logical first step would be to determine the amount of fishing effort and harvest. This could be done either by using a traditional creel survey or a more economical alternative such as Ontario's midday activity count method (Lester et al. 1991). Use of the latter method would facilitate comparisons with numerous other lake trout fisheries. Additional biological information could also be collected through the angler survey and from the establishment of an assessment netting program. Data from these programs will be needed for population analyses and for assessing the possible ecological implications of manipulating harvest. A broader perspective such as this needs to be taken in developing fishing regulations, which traditionally have been developed on a population or single-stock level (Johnson and Martinez 1995).

Two other factors that need to be considered in evaluating the effectiveness of regulations for all species are hooking mortality and noncompliance with size limits. Hooking mortality has generally been found to be low (<10%) for northern pike, walleye, and lake trout (Beukema 1970; Falk et al. 1974; Falk and Gilman 1975; Payer et al. 1989; Schaefer 1989). Higher mortality was typically associated with the use of live bait, which is not allowed on Isle Royale. This suggests that regulations such as size limits that require the release of fish are a viable management tool.

Noncompliance has the potential to be a more serious problem, both biologically and socially. This is particularly true in areas such as Isle Royale where enforcement is limited because of remoteness and limited personnel. Based on lengths of fish measured by creel clerks and tag returns, mean noncompliance rates were 13% and 19% in Minnesota lakes where slot limits for northern pike were being evaluated (Pierce and Tomcko 1997). The portion of sublegal largemouth bass in an Oklahoma fishery varied seasonally from 8 to 67% (Glass 1984). Socially, legal anglers indicated that observing illegal harvests had a negative effect on the satisfaction level (Gigliotti and Taylor 1990). To overcome this problem will require a significant educational and promotional effort involving anglers, biologists, and law enforcement personnel. Even then, some anglers will likely ignore the regulation.

Inventory and Monitoring

Obviously, the 66-year interval between this survey and Koelz's does not fulfill the "regular intervals" for inventory and monitoring called for in the National Park Service management policies for natural resources (U.S. National Park Service 1988). Sampling at such a long interval only documents change—it does not provide the information required to understand the forces that are driving the change. More frequent monitoring is needed to obtain such information.

Lake-type or classification systems are commonly used by many state and provincial natural resource agencies to facilitate the management of the large number of lakes they are responsible for. The basic assumption behind this approach is that lakes with similar habitats will support similar fish communities, and thus can also be managed similarly (Leach and Herron 1992). This community approach certainly seems applicable to Isle Royale's inland lakes, particularly those with active recreational fisheries. In such lakes, intensive monitoring is needed to obtain the data on fish population characteristics required to ensure the long-term sustainability of the fish population and the maintenance of a quality fishing experience for the public. Fishery managers in Michigan and Minnesota attempt to survey actively managed lakes at least every 5–6 years. If a new management practice is implemented, surveys to evaluate the action are typically conducted annually for a number of years. Selection of representative lakes could conceivably overcome some of the costs, both biological and monetary, associated with such intensive, quantitative monitoring activities.

In lakes with limited recreational fishing, presence–absence data obtained by regular monitoring with multiple gear types will allow assessment of changes in community composition and species richness and biodiversity (Jackson and Harvey 1997). The sampling effort required will be dictated by the distribution and abundance of the rarest species because the rarer they are, the more difficult they are to collect (Green and Young 1993). This type of program would seem to have the most potential for detecting invading species, and thus should also be conducted on the lakes being more intensely managed for recreational fishing. Similar monitoring of large, protected embayments around Isle Royale could conceivably provide advance warning of possible invasions by exotic species into the inland lakes. Because of the threat posed by such an invasion, such surveys should be conducted at no less than 3- to 5-year intervals.

Further monitoring of limnological attributes and other biological components of the aquatic communities could be used to refine or develop a new classification system for Isle Royale's inland lakes. Depending on project or management objectives, it could also be used in selecting lakes for assessment of larger issues such as atmospheric contamination and climate change.

Conclusion

The fish communities of Isle Royale's inland lakes have remained intact, seemingly because of their relative inaccessibility and the remoteness of the island archipelago. The wild fish populations, although not necessarily having the characteristics prized by anglers, continue to be an integral component of the park ecosystem. They are a vital link in the ecological food web, serving as both predator and prey. They support a small but—to many visitors—gratifying recreational fishery. To ensure their long-term sustainability in the face of ever-increasing anthropogenic stresses will require constant vigilance and our gaining a deeper understanding of how and what they need to function.

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Appendix A

Scientific and common names of fish species found in 32 inland lakes in Isle Royale National Park, Michigan, along with species abbreviations used in the text.

Scientific name	Common name	Abbreviation
Coregonus artedi	cisco	TLC
Coregonus clupeaformis	lake whitefish	LKW
Salvelinus fontinalis	brook trout	BKT
Salvelinus namaycush	lake trout	LAT
Esox lucius	northern pike	NOP
Couesius plumbeus	lake chub	LKC
Margariscus margarita	pearl dace	PRD
Notemigonus crysoleucas	golden shiner	GOS
Notropis atherinoides	emerald shiner	EMS
Notropis heterodon	blackchin shiner	BCS
Notropis heterolepsis	blacknose shiner	BNS
Notropis hudsonius	spottail shiner	SPO
Notropis volucellus	mimic shiner	MMS
Phoxinus eos	northern redbelly dace	NRD
Phoxinus neogaeus	finescale dace	FND
Pimephales promelas	fathead minnow	FHM
Semotilus atromaculatus	creek chub	CRC
Catostomus commersoni	white sucker	WTS
Percopsis omiscomaycus	trout-perch	TRP
Lota lota	burbot	BUB
Culaea inconstans	brook stickleback	BST
Pungitius pungitius	ninespine stickleback	NST
Lepomis gibbosus	pumpkinseed	PMK
Etheostoma exile	Iowa darter	IOD
Perca flavescens	yellow perch	YEP
Percina caprodes	logperch	LGP
Stizostedion vitreum	walleye	WAE
Cottus bairdi	mottled sculpin	MTS
Cottus cognatus	slimy sculpin	SMS
Cottus ricei	spoonhead sculpin	SHS

Appendix B

Back-calculated total lengths (mm) of northern pike from Isle Royale National Park inland lakes, 1995–1996.

Lake			Age (years)										
Code	Sex	N	1	2	3	4	5	6	7	8	9	10	11
AHM	f	6	158	326	469	576	563	—	—	—	—	—	—
AHM	m	5	165	353	—	—	—	—	—	—	—	—	—
AMY	f	5	183	370	506	553	594	—	—	—	—	—	—
AMY	m	2	191	348	483	531	555	571	584	—	—	—	—
ANG	f	16	181	364	484	531	569	602	653	—	—	—	—
ANG	m	11	175	346	469	524	554	569	—	—	—	—	—
BEA	f	20	235	377	485	534	553	556	583	—	—	—	—
BEA	m	14	224	377	479	536	552	572	—	—	—	—	—
CHI	f	15	214	367	463	538	591	677	—	—	—	—	—
CHI	m	20	206	350	443	513	542	601	615	629	—	—	—
DUS	f	4	188	355	453	550	588	581	—	—	—	—	—
EPI	f	3	217	340	438	529	595	634	651	647	—	—	—
EPI	m	2	169	309	425	—	—	—	—	—	—	—	—
EVA	f	5	201	311	430	503	526	—	—	—	—	—	—
EVA	m	2	182	324	424	479	—	—	—	—	—	—	—
FEL	f	68	206	376	516	600	630	650	683	—	—	—	—
FEL	m	36	190	350	479	549	573	600	624	—	—	—	—
GEO	m	4	223	382	492	613	—	—	—	—	—	—	—
HAL	f	53	226	429	537	598	615	637	650	668	—	—	—
HAL	m	37	204	398	510	560	586	605	610	617	—	—	—
INT	f	24	199	359	464	522	548	553	—	—	—	—	—
INT	m	21	210	366	463	500	524	535	547	—	—	—	—
LES	f	27	182	307	410	482	521	569	591	—	—	—	—
LES	m	14	173	317	427	491	523	552	574	—	—	—	—
LIN	f	11	169	304	436	507	535	570	551	—	—	—	—
LIN	m	7	159	298	419	479	517	536	—	—	—	—	—
LIV	f	16	230	387	488	556	590	596	583	601	—	—	—
LIV	m	9	219	398	496	558	578	—	—	—	—	—	—
MAS	f	12	152	275	393	438	492	—	—	—	—	—	—
MAS	m	3	167	303	400	478	—	—	—	—	—	—	—
MCD	f	33	223	406	536	586	598	612	597	—	—	—	—
MCD	m	13	208	394	517	567	588	601	—	—	—	—	—
OTT	f	16	212	362	453	505	526	546	528	538	—	—	—
OTT	m	14	207	364	456	487	488	—	—	—	—	—	—
PAT	f	6	164	334	452	508	563	—	—	—	—	—	—
RIC	f	39	208	345	429	511	561	647	—	—	—	—	—
RIC	m	23	194	322	428	505	527	—	—	—	—	—	—
SAR	f	50	209	389	494	537	565	582	598	—	—	—	—
SAR	m	27	196	363	465	515	537	557	545	542	—	—	—
SHE	f	2	178	303	422	493	524	534	—	—	—	—	—
SHE	m	3	142	272	384	471	515	537	—	—	—	—	—
SIS	f	3	220	414	530	656	730	746	799	829	937	959	983
SIS	m	2	220	379	587	639	686	—	—	—	—	—	—
WAG	f	10	185	328	428	470	486	502	501	—	—	—	—
WAG	m	7	163	321	415	446	465	463	472	482	—	—	—
WHI	f	11	240	418	514	554	581	—	—	—	—	—	—
WHI	m	8	249	420	509	547	571	535	553	614	—	—	—

Appendix C

Back-calculated total lengths (mm) of yellow perch from inland lakes in Isle Royale National Park, Michigan, 1995–1996.

Lake			Age (years)											
Code	Sex	N	1	2	3	4	5	6	7	8	9	10	11	12
AHM	f	3	87	152	210	245	—	—	—	—	—	—	—	—
AMY	f	4	47	71	99	106	122	—	—	—	—	—	—	—
AMY	m	3	47	65	92	110	—	—	—	—	—	—	—	—
ANG	f	20	50	79	108	138	157	167	—	—	—	—	—	—
ANG	m	15	51	82	114	139	153	177	—	—	—	—	—	—
BEA	f	14	52	98	152	212	252	303	327	358	376	—	—	—
BEA	m	6	46	84	132	156	—	—	—	—	—	—	—	—
BEN	f	76	60	135	174	216	251	279	278	279	—	—	—	—
BEN	m	124	60	129	172	207	232	253	268	—	—	—	—	—
CHI	f	50	54	92	138	181	215	242	261	278	303	314	—	—
CHI	m	25	54	89	129	162	191	216	232	—	—	—	—	—
DUS	f	2	53	89	144	—	—	—	—	—	—	—	—	—
FEL	f	59	55	97	136	160	185	203	196	204	—	—	—	—
FEL	m	11	52	91	120	142	160	180	218	—	—	—	—	—
FOR	f	32	67	95	123	154	178	197	245	—	—	—	—	—
FOR	m	9	65	90	116	142	157	—	—	—	—	—	—	—
GEO	m	3	64	118	—	—	—	—	—	—	—	—	—	—
HAR	f	104	77	106	136	164	201	239	272	295	294	269	289	311
HAR	m	3	75	102	128	154	189	—	—	—	—	—	—	—
INT	f	22	51	74	104	129	155	181	—	—	—	—	—	—
LES	f	23	55	102	134	164	187	212	—	—	—	—	—	—
LIN	f	6	53	76	117	147	—	—	—	—	—	—	—	—
LIN	m	3	55	87	102	131	—	—	—	—	—	—	—	—
LIV	f	54	52	94	137	177	200	226	231	240	—	—	—	—
LIV	m	4	57	91	128	167	184	—	—	—	—	—	—	—
MAS	f	8	50	71	94	124	140	—	—	—	—	—	—	—
MAS	m	3	50	67	89	122	—	—	—	—	—	—	—	—
MCD	f	26	51	99	144	181	220	245	—	—	—	—	—	—
MCD	m	6	47	88	128	153	168	—	—	—	—	—	—	—
PAT	f	4	56	97	148	—	—	—	—	—	—	—	—	—
RIC	f	27	50	82	113	140	175	203	222	244	251	269	285	300
RIC	m	7	52	73	101	137	165	177	—	—	—	—	—	—
SIS	f	35	62	98	140	—	—	—	—	—	—	—	—	—
SIS	m	8	64	97	—	—	—	—	—	—	—	—	—	—
WAG	f	9	80	157	223	272	300	314	328	338	344	344	348	—
WHI	f	37	61	98	126	163	196	—	—	—	—	—	—	—
WHI	m	28	62	96	118	151	175	186	196	208	—	—	—	—

Appendix D

Total length (mm) at age of white suckers from inland lakes in Isle Royale National Park, 1995–1996.

Lake		Age (years)														
Code	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ANG	9	—	—	—	450	—	—	—	513	485	497	491	526	—	—	—
CHI	8	160	244	—	—	—	480	—	—	444	—	—	465	—	—	—
DES	203	127	181	207	234	266	298	321	308	319	305	335	384	412	262	461
DUS	4	—	—	—	324	432	480	—	—	—	—	—	—	—	—	—
FEL	23	—	—	—	—	—	472	377	558	512	507	511	514	497	556	534
HAR	119	—	175	239	278	310	314	336	330	—	—	—	—	—	—	—
HAT	103	—	—	173	183	200	236	267	274	308	320	371	317	357	—	401
INT	8	—	179	—	437	—	—	—	—	—	—	—	—	—	—	565
JOH	2	—	—	—	—	178	—	—	—	—	—	—	—	—	—	—
RIC	80	—	194	279	335	361	—	464	408	473	490	490	492	495	491	526
SAR	8	—	232	—	325	—	—	543	—	—	—	—	—	—	—	—
SIS	56	120	203	310	450	—	—	—	476	485	—	502	474	—	—	—

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13. ABSTRACT (Maximum 200 words)
Fish communities in 32 of Isle Royale National Park's inland lakes were surveyed in 1995–97 to determine if their composition had changed significantly since 1929 when the last complete survey was conducted. Gill nets, seines, and minnow traps were used for sampling the lakes, the surface areas of which were 1.2–1,635 ha and maximum depths of which were 1.5–46.3 m. The 1995–97 collections contained 28 of the 30 fish species reported in 1929. No new fish species were collected. Observed changes in the fish communities included no change (14 lakes), additional species (11 lakes), and undetected species (12 lakes). In five lakes, both species gains and losses were observed. Most gains seemed to be because of upstream dispersal from a downstream lake or a Lake Superior cove at the outlet of the watershed. Sculpins (*Cottus* sp.) and other small, demersal species accounted for most of the incidences where species were not detected. Species richness was 2–15 species per lake with 24 lakes having 5 or fewer species. Significant positive relations existed between the number of species and lake area and maximum depth. Isle Royale lakes contained moderate to high densities of northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), the two most widespread species. The average mercury concentration in standard-sized (550 mm) northern pike from 25 Isle Royale lakes was 304 ng/g (n = 135, range 74–693 ng/g). Compared to those of mainland lakes and adjacent Lake Superior, the fish communities in Isle Royale's inland lakes have changed relatively little since 1929. As a result, continued conservation of these native fish communities will provide further opportunities for understanding issues such as dispersal, isolation, and speciation.

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